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# SMELL AND TELL: BEHAVIOR ASSOCIATED WITH CHEMOSENSORY STIMULI IN GUATEMALAN BEADED LIZARDS (*HELODERMA CHARLESBOGERTI*)

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**Abstract.**—Intraspecific communication via chemosignals has been linked to important natural history aspects in lizards, including honest signaling tied to reproductive success and conspecific displays of sociality. Chemosignals can be used over significant spatial and temporal parameters, allowing for inconspicuous interaction by some species. This type of cryptic communication is not easily detected, but researchers can obtain baseline lizard signaling capabilities by quantifying tongue-flick (TF) rate toward conspecific scents. We tested chemosignaling behavior in endangered Guatemalan Beaded Lizards (*Heloderma charlesbogerti*) by evaluating TF response toward same-sex and opposite-sex conspecific stimuli and control treatments. Our suspected sources of pheromones for determining conspecific scent recognition were shed skin and used substrate. Age and reproductive cycle of trial subjects had no discernable effect on TF rate, but sex was a significant factor. Both males and females displayed differential TFs between treatments from opposite-sex and same-sex donor individuals. Male lizard TF response was significantly different between all treatments, including controls. Females had lower and less pronounced differential TFs towards treatments than males, as female TF response was only significantly different between opposite-sex stimuli towards control and same-sex stimuli treatments. We conclude that nonvolatile chemosignals are present in *H. charlesbogerti* biomaterials, with the degree of behavioral response varying depending on sex and presented stimuli. Our study not only adds to our understanding of intraspecific chemosignaling in helodermatid lizards, but also provides information that could lead to more comprehensive conservation programs for *H. charlesbogerti*.

**Key Words.**—cues; discrimination; ethology; pheromones; reptiles; signals; squamates; tongue-flick

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## INTRODUCTION

Chemical signals are important components of social interaction in many animals (Wyatt 2014), including reptiles (Mason and Parker 2010). Pheromones are a specialized type of chemosignal that elicit physiological and behavioral responses in conspecifics (Karlson and Lüscher 1959). Squamate pheromones originate from epidermal/femoral glands (Mason 1992; Martín and López 2014; reviewed in Mayerl et al. 2015), cloacal glands (Cooper and Trauth 1992; Cooper and Pérez-Mellado 2002), feces (Moreira et al. 2008; Bull et al. 2014), and skin (Mason and Gutzke 1990; Mason et al. 1990; Weldon et al. 2008). Pheromones are a principal chemosignaling constituent of squamate social behavior (Shine et al. 2002; Martín et al. 2007; Bull et al. 2014; Baeckens and Whiting 2021). They can be specific to distinct

phylogenetically divergent, but sometimes sympatric, animal lineages (Symonds and Elgar 2008); including morphologically cryptic lineages of lizards (Scott et al. 2015; Zozaya et al. 2019). As such, research exploring behaviors associated with conspecific chemical recognition regarding sociality is valuable to understanding the natural history of specific lizard clades.

Vomerolfaction is the process of chemical perception using the vomeronasal organs (Cooper and Burghardt 1990a), which anatomically lie at the base of the nasal cavity and are relatively developed in squamates compared to other tetrapod lineages (Halpern 1992; Schwenk 1995; Filoramo and Schwenk 2009). The tongue delivers molecules to the paired vomeronasal organs (Houck 2009), which detect important environmental stimuli (Graves and Halpern 1990). This enables perception of large and

nonvolatile molecules in squamates (Burghardt 1980; Filoramo and Schwenk 2009).

Researchers commonly use differential tongue-flick (TF) rates in reptiles to assess vomerolfaction discrimination capability and response to chemosensory stimuli (Cooper et al. 1996; López et al. 1998; Saviola et al. 2013). Differential TF rates in lizards have been associated with mate choice (Font et al. 2012; Baeckens et al. 2017a), sex discrimination (Cooper et al. 1996; Gonzalo et al. 2004), species-specific recognition (Barbosa et al. 2006; Labra 2011), and conspecific familiarity (Font and Desfilis 2002; Gabirot et al. 2012). Due to the secretive nature of some lizards, TF rate is a valuable tool to discern subtle chemosignal recognition between conspecifics.

Helodermatid lizards engage in social interactions that potentially involve pheromonal components, such as combat, pairing, courtship (Beck 2005; Mendelson and Hill 2020), trail following (Radovanovic 2014; Erica Nowak, unpubl. report), and cohabitation or frequent usage of shelters by multiple individuals (Beck and Lowe 1991; Beck and Jennings 2003; Ariano-Sánchez and Salazar 2015; Gienger et al. 2021). During the mating season, Gila Monsters (*Heloderma suspectum*) use the cloaca to engage in scent-marking behavior (Beck 1990; Strong 1996), which likely is associated with cloacal ventral and scent glands (Gabe and Saint-Girons 1965; Whiting 1969). The skin of Gila Monsters contains possible chemosignals, including identified sex steroids (Weldon and Bagnall 1987; Schuler et al. 2020) and

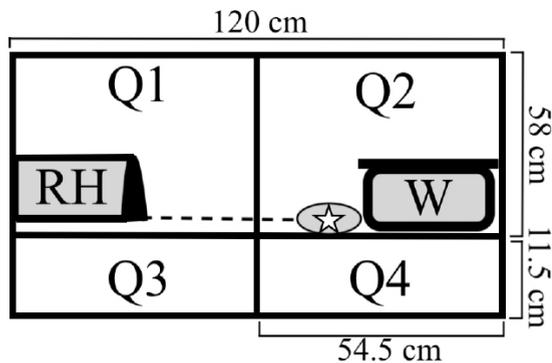
lipids associated with heat-shock response (Torri et al. 2020). Therefore, it should be expected that helodermatid lizards employ chemosignals in some fashion to aid in these social behaviors.

Helodermatid lizards rely heavily on olfactory and vomeronasal faculties to detect prey, using the relatively great surface of their tongues (Cooper 1995). Helodermatid lizards possess deeply forked tongues similar to those of proficient trail-following lizards (Schwenk 1994) and have a relatively higher baseline TF rate than many other lizard families (Bissinger and Simon 1979; Cooper and Arnett 2001; Baeckens et al. 2017b). Enhanced vomerolfaction usage observed in helodermatid lizards includes an elevated TF rate after biting a mouse than to controls (Cooper and Arnett 1995), extended poststrike TF searching behavior compared to many other lizards (Cooper et al. 1994), and the ability to follow prey chemical trails (Garrett et al. 1996). There has been no published research on helodermatid behavioral responses toward non-prey chemosensory stimuli or intraspecific pheromonal communication, however, which prompted our research.

The Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) is classified as Endangered under the Convention on International Trade in Endangered Species of Wild Fauna and Flora Appendix I (CITES Appendices. 2023. Available from <https://cites.org/eng/app/appendices.php> [Accessed 10 August 2023]). *Heloderma charlesbogerti* is endemic to Guatemala, inhabiting the Motagua Valley (Campbell and Vannini 1988) along with several disjunct populations

**TABLE 1.** Morphometrics and temperature recordings of the Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) at Zoo Atlanta, Georgia, USA. Unique ID at Zoo Atlanta is the individual, sex as male (M) or female (F), age, age class categorized as either subadult (SA) or adult (A), snout-vent length (SVL), weight, ventral body surface temperature (average  $\pm$  standard deviation), and dorsal body surface temperature.

Individual	Sex	Age (y)	Age Class	SVL (cm)	Weight (g)	Ventral (°C)	Dorsal (°C)
18R008	F	3	SA	33.7	1,000	27.11 $\pm$ 0.42	26.08 $\pm$ 0.26
16R006	M	5	SA	37.5	1,233	24.43 $\pm$ 0.76	24.92 $\pm$ 1.95
16R008	F	5	SA	36.2	1,335	24.80 $\pm$ 1.19	24.98 $\pm$ 1.21
16R012	F	5	SA	39.4	1,204	21.74 $\pm$ 1.23	22.71 $\pm$ 1.81
14R023	F	7	A	36.8	1,426	24.46 $\pm$ 1.58	24.16 $\pm$ 0.0
13R027	M	9	A	37.5	1,430	22.60 $\pm$ 0.95	23.19 $\pm$ 1.33
13R029	M	9	A	40.0	1,270	25.57 $\pm$ 1.75	25.22 $\pm$ 1.09
A06110	F	> 22	A	44.5	1,500	23.69 $\pm$ 0.87	24.28 $\pm$ 1.38
A06105	F	> 24	A	43.2	1,829	25.74 $\pm$ 1.49	25.64 $\pm$ 1.28
A06109	M	> 24	A	45.1	2,450	20.94 $\pm$ 1.21	21.17 $\pm$ 1.29
A06103	M	> 29	A	41.3	1,380	26.99 $\pm$ 0.82	25.76 $\pm$ 0.74



**FIGURE 1.** Front view of each 56 cm deep enclosure for testing Guatemalan Beaded Lizards (*Heloderma charlesbogerti*). Upper levels (Q1 and Q2) are connected, while lower levels (Q3 and Q4) are drawers and only accessible by conspicuous  $10 \times 7.5 \times 5$  cm entrances from Q1 and Q2, respectively. Rock hide (RH:  $30 \times 23 \times 11$  cm) is where study lizards began each trial, with stimuli (star) placed 50 cm (dotted line) from RH entrance and in front of the water container (Width:  $30 \times 20 \times 10$  cm). A 2.5 cm layer of coconut fiber substrate covered the floor in all quadrants and a heat bulb provided a basking spot above the RH.

historically occupying the Pacific versant (Anzueto and Campbell 2010, Dyson et al. 2022). Motagua Valley habitat is a seasonally dry Tropical Deciduous Forest, with increased *H. charlesbogerti* activity and larger home ranges coinciding with the wet season (Ariano-Sánchez and Salazar 2015; Ariano-Sánchez et al. 2020). To test our hypothesis that pheromonal cues are employed and function in helodermatids, we conducted experimental trials on captive *H. charlesbogerti* using TFs as a quantitative metric of vomerolfaction. We predicted that TF response would be significantly higher towards conspecific

scent stimuli than to controls, while differences in TF response would also be explained by sex of the conspecific scent donor lizard.

## MATERIALS AND METHODS

**Study animals and time period.**—We tested 11 *H. charlesbogerti* (six females, five males) from August 2021 to May 2022 at Zoo Atlanta in Atlanta, Georgia, USA. This time period encompassed three distinct reproductive life-history stages for animals at Zoo Atlanta. Carruth (2015) determined the active mating season was August-September, coinciding with peak testosterone levels in males, and the egg-laying season was October-December, coinciding with spiked estradiol levels in some ovulating females. A simulated dry season was initiated January-May, coinciding with reduced activity in wild *H. charlesbogerti* following egg-laying (Ariano-Sánchez and Salazar 2015), although Zoo Atlanta specimens continued to occasionally accept food during this time. The lizards collectively differed by sex, age, and body size (Table 1). To standardize hunger levels, we fed study animals up to 10% of their body weight in rats, mice, and/or chickens 4 d before each trial.

**Enclosure design.**—We housed lizards in separate individual enclosures that were divided into four quadrants (Q1-Q4; Figs. 1, 2). Each enclosure contained a 2.5 cm substrate layer of coconut fiber in Q1-Q4, a water bowl in Q2, and a shelter covered by rocks (RH: rock hide) in Q1. A heat lamp above

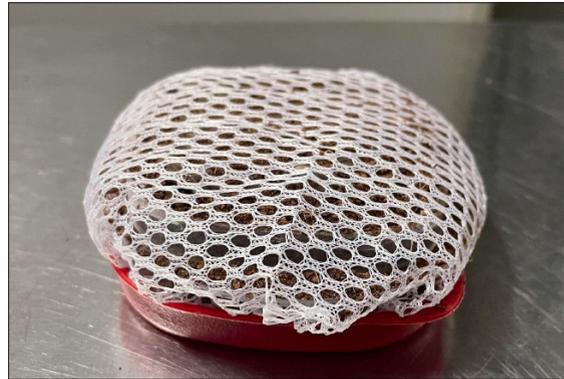


**FIGURE 2.** Still-frame from a trial of Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) individual 18R008 approaching the stimuli package from the rock hide. Perspective is from a mounted GoPro camera attached to the ceiling in quadrant 2 (Q2).

the RH provided a 12L:12D light cycle and basking area. We limited the humidity gradient to 40–60% by minimally misting in enclosures, therefore reducing the effects humidity can have on pheromonal expression (Martin et al. 2015). We monitored temperatures using EL-USB-1 Dataloggers ( $\pm 0.5^\circ\text{C}$ ; Lascar Electronics, Erie, Pennsylvania, USA) and monitored humidity via JEDEW mini hygrometers ( $\pm 5\%$  relative humidity; Shenzhen Weihou Technology Company, Ltd., Nanshan, China).

**Chemosensory stimuli.**—We grouped treatments by presented stimuli, consisting of: (1) substrate from enclosures of the trial specimens (NC: negative control); (2) substrate from enclosures of the trial specimens with cologne (PC: positive control); (3) same-sex conspecific shed skin and substrate (SS: same-sex); and (4) opposite-sex conspecific shed skin and substrate (OS: opposite-sex). We opportunistically collected shed skin 1–10 mo prior to testing and stored samples at  $-16.7^\circ\text{C}$  for preservation. We presented stimuli in a  $7.5 \times 7.5 \times 2.3$  cm plastic container covered by mesh containing nine holes/cm<sup>2</sup> and each hole  $2.5 \times 1$  mm (Fig. 3). For each stimulus, we obtained substrate from a vacated quadrant respective to treatment type and placed substrate under the mesh of the stimulus package. For the PC treatment, we administered one spray of cologne (Instyle Fragrances, Guilford, Connecticut, USA) on the mesh surface of the stimuli container. For the OS and SS conspecific treatments, we placed conspecific shed skin directly under the mesh surface of the stimulus package with the collected substrate.

**Experimental design.**—All trials took place within the home enclosure for each lizard (Fig. 2). We completed an initial substrate change with freshly hydrated coconut fiber in each enclosure, followed by a 28-d habituation period preceding experimentation. We conducted trials between 0800–1600 once every 14 d for each individual lizard. For a repeated measures experimental design, we tested all four treatments on each lizard twice ( $n = 8$ ), with the order being randomized. For each conspecific treatment, one stimulus package contained shed skin and used substrate from an adult and the other stimulus package from a subadult. A GoPro Hero 3 camera (GoPro, Inc., San Mateo, California, USA; settings = 120 fps, wide fov) was mounted to the ceiling of Q2 for recording trials (Fig. 2). Prior to each trial, we obtained ventral and dorsal body surface temperatures, as well as stimulus temperature  $< 2.5$  cm from the source using



**FIGURE 3.** Stimulus package for testing Guatemalan Beaded Lizards (*Heloderma charlesbogerti*) containing one of the four treatments used in trials.

an H1020 Helect infrared thermometer (JEWY Tech Company, Ltd., Shenzhen, China). Temperature differences  $> 5^\circ\text{C}$  can significantly affect TF rate in skins (Cooper and Vitt 1986) and wild *H. charlesbogerti* show greater activity intensity with increasing ambient temperatures (Ariano-Sánchez et al. 2022). Therefore, we eliminated trials during analysis in which the ventral or dorsal body surface temperature was  $> \pm 2.5^\circ\text{C}$  from the respective average of lizards.

To begin each trial, we placed the focal lizard under the RH in Q1 with a nontransparent barrier in front of the entrance to prevent exit. After a 10 min habituation period, a common protocol in animal behavior studies (Tatem et al. 2014), we placed the stimulus package in Q2, began video recording, and removed the RH barrier. Following Valdecantos et al. (2020), trials included a first latency (i.e., TF in any direction), second latency (i.e., TF toward the stimulus package), and 10 min of subsequent recording. We did not walk by or watch ongoing trials after the second latency to avoid distracting the trial subject. During later video review, we counted TFs that made direct contact with the stimulus package (DTF: direct tongue-flick) to include both volatile and nonvolatile chemosignals that lizards obtain via TFs to conspecific bodies or substrates (Cooper 1994; López et al. 2003; López and Martín 2011). We eliminated trials during analysis that had  $< 2$  DTFs.

**Data analysis.**—We used the statistical software R (R Core Team 2022, version 4.3.1) for all analyses, accepted significance at  $\alpha = 0.05$ , and created figures using ggplot2 (Wickham 2016). We used Generalized Linear Mixed Effects Models with Poisson regression to identify significant factors explaining DTFs using package glmmADMB (Skaug et al. 2016). Our

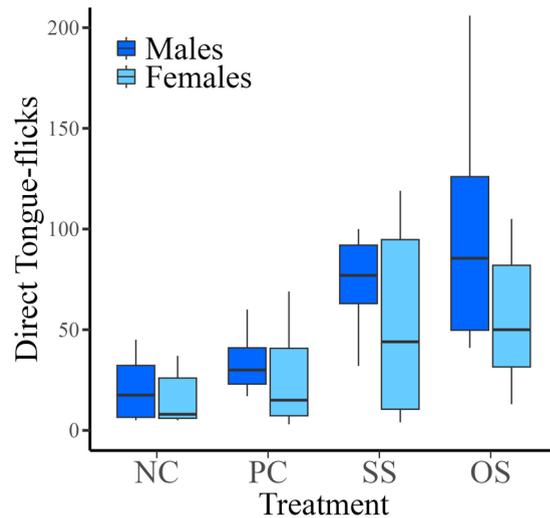
**TABLE 2.** List of hypothesized models as a function of explanatory variables for direct tongue-flick response in all focal Guatemalan Beaded Lizards (*Heloderma charlesbogerti*). Variables include Treatment (negative control, positive control, same-sex conspecific stimuli, and opposite-sex conspecific stimuli), Sex (male and female), RepSeason (three reproductive time periods trials took place within), and Age (subadult and adult). A random effect for individual lizards was included for each model. Evaluation of the best approximating model is in bold and based on Akaike’s Information Criterion ( $AIC_c$ ), difference between  $AIC_c$  and the top-ranking model ( $\Delta AIC_c$ ), and number of parameters in the model (K).

Model	Explanatory variables	$AIC_c$	$\Delta AIC_c$	K
1	Treatment+Sex	767.330	0	6
2	Treatment+Sex+Age	770.053	2.713	7
3	Treatment+(RepSeason+Age)*Sex	820.479	53.14	10
4	Treatment+Age	842.950	75.61	6
5	Treatment+RepSeason+Age+Sex	898.388	131.05	8
6	Treatment+RepSeason	967.599	200.26	6
7	null	1366.963	599.62	1

full model was  $DTFs \sim Treatment + Sex + Age + RepSeason + (1|Lizard)$ , with predictors being the four treatments, sex of focal lizards, age class of focal lizards, and the three reproductive time periods trials took place within (RepSeason) with individual lizards used as a random intercept. We assessed the significance of each predictor and their interactions by comparing Akaike’s Information Criterion ( $AIC_c$ ) values during model selection using package MuMIn

**TABLE 3.** Direct tongue-flicks (DTFs) of Guatemalan Beaded Lizards (*Heloderma charlesbogerti*) for each treatment and the post hoc pairwise estimated marginal means  $P$ -values for males and females regarding treatment. Treatments include negative control (NC), positive control (PC), same-sex conspecific (SS), and opposite-sex conspecific (OS). The abbreviations SD = standard deviation and SE = standard error.

Treatment	Average DTF $\pm$ SD	Post-hoc Comparison	Estimate ( $\pm$ 1 SE)	Z-value	$P$ -value
<b>Males</b>					
NC	21.2 $\pm$ 18.9	NC vs PC	0.583 (0.134)	4.363	< 0.001
PC	34.2 $\pm$ 17.0	NC vs SS	1.323 (0.119)	11.16	< 0.001
SS	74.1 $\pm$ 24.4	NC vs OS	1.653 (0.121)	13.627	< 0.001
OS	96.1 $\pm$ 56.9	PC vs SS	0.740 (0.164)	4.506	< 0.001
		PC vs OS	1.070 (0.170)	6.291	< 0.001
		SS vs OS	0.330 (0.143)	2.303	< 0.001
<b>Females</b>					
NC	16.4 $\pm$ 14.4	NC vs PC	-0.123 (0.160)	-0.767	0.841
PC	26.0 $\pm$ 25.3	NC vs SS	-0.219 (0.241)	-0.909	0.762
SS	53.7 $\pm$ 50.4	NC vs OS	1.136 (0.129)	8.801	< 0.001
OS	56.4 $\pm$ 34.4	PC vs SS	-0.097 (0.343)	-0.282	0.990
		PC vs OS	1.259 (0.202)	6.222	< 0.001
		SS vs OS	1.355 (0.249)	5.441	< 0.001



**FIGURE 4.** Direct tongue-flicks of Guatemalan Beaded Lizard (*Heloderma charlesbogerti*) for treatments in males and females. Treatments include negative control (NC), positive control (PC), same-sex conspecific (SS), and opposite-sex conspecific (OS). Plots show the median (horizontal line) and interquartile ranges (IQR; box). Vertical lines represent quartile 1–1.5  $\times$  IQR and quartile 3 + 1.5  $\times$  IQR.

(Bartoń 2023). Overdispersion of our best fit model was visually inspected using Pearson residuals of the plot. Post-hoc pairwise comparisons between treatments were conducted using Tukey’s method from the multcomp package (Hothorn et al. 2023).

## RESULTS

Average temperature for each enclosure was  $23.6^{\circ} \pm 1.98^{\circ} \text{C}$  (mean  $\pm$  standard deviation). The overall mean ventral and dorsal body surface temperatures for each lizard (Table 1) were  $24.7^{\circ} \pm 2.37^{\circ} \text{C}$  and  $25.0 \pm 2.41^{\circ} \text{C}$ , respectively, with only two trials removed due to ventral or dorsal temperature of the lizard exceeding  $\pm 2.5^{\circ} \text{C}$  from their average. Stimuli mesh surface temperature for all treatment types was  $24.1^{\circ} \pm 1.64^{\circ} \text{C}$ .

In total, a majority of trials contained  $> 2$  DTFs ( $n = 50$ ). The best-fit model (Table 2) confirmed by  $AIC_C$  comparison for total DTFs was  $\text{DTFs} \sim \text{Treatment} + \text{Sex} + (1|\text{Lizard})$ . Overall, there was a significant effect from treatments ( $Z = 14.57$ ,  $df = 3$ ,  $P < 0.01$ ) and between sexes ( $Z = -3.36$ ,  $df = 1$ ,  $P < 0.01$ ) on DTFs. Males displayed a higher DTF amount (mean  $64.3 \pm 46.23$ ) than females ( $38.7 \pm 36.01$ ). Because DTFs varied between sexes, we concentrated our analysis of DTF response toward treatments on males and females separately. For males, DTFs differed significantly between all treatments (Tukey HSD,  $P < 0.001$ ; Table 3, Fig. 4). For females, DTFs only significantly differed between OS stimuli towards the NC, PC, and SS stimuli treatments (Tukey HSD,  $P < 0.001$ ; Table 3, Fig. 4).

## DISCUSSION

We found our hypothesis predictions were met and vomerolfaction discriminatory behavior exists in helodermatid lizards, as both male and female *H. charlesbogerti* had higher conspecific scent DTFs than the NC and displayed significant differential DTF responses between OS and SS stimuli treatments. This indicates shed skin and used substrate from conspecifics contained pheromones used for signaling. Of the different signals animals use for communication, chemosignals have been the least studied (Symonds and Elgar 2008), in part, because they are difficult to record (Doody et al. 2021). In non-avian reptiles, cues also consist of visual color/pattern (Schwenk 1995; Leal and Fleishman 2004; Batabyal and Thaker 2017) and movement (Persons et al. 1999; Steinberg et al. 2014). Helodermatid lizards have relatively low metabolic rates (Beck 1990) and apparent inferior vision (Underwood 1970; Bogert and del Campo 1993), but they do interact with one another (Beck 1991; Beck and Lowe 1991) and therefore chemosignaling may be a predominant

method of communication based on our results.

In our experiment, males displayed a greater DTF response to conspecific treatments compared to females, which is consistent with other chemosensory studies (Cooper and Steele 1997; Baird et al. 2015; Scott et al. 2015); however, results should be interpreted cautiously as TF rate could be a defective metric for evaluating overall female vomerolfaction capability (Font et al. 2012). Females in our study exhibited high within-treatment variability, displaying no significant DTF differences between the NC and PC or between SS stimuli to either control, while differences between OS stimuli to both controls were significant. Similar to previous chemosensory studies that also contain pungency control inconsistencies pertaining to a NC (Cooper and Burghardt 1990b; Fernández-Rodríguez and Braña 2022), cologne may serve as a faulty PC to assess if discrimination capabilities potentially exist, due to their inherent noxious properties for some lizards (Dial and Schwenk 1996; Cooper 1998). Likewise, it is possible there were pheromones present in other areas of the body that were not reflected sufficiently in our stimuli, thereby yielding high variability in female DTFs.

Pheromones are a continually available and presumably metabolically inexpensive source to produce chemosignals (Duvall 1986) and may be condition-dependent, as they are best used during certain times of the year to reflect physiological traits of the sender (Martín and López 2015; Baeckens et al. 2017a). We tested *H. charlesbogerti* from August–May, which contains several reproductive life-history stages in males and females at Zoo Atlanta (Carruth 2015; Levine et al. 2022). We found no influence of reproductive cycle affecting DTFs, indicating that chemosensory capabilities toward conspecifics are not necessarily influenced by reproductive state. That is not to say there are not potentially concealed chemosignals that exist as a combination of compounds (Baeckens 2019), however, and are related to time-sensitive reproductive quality and fitness aspects, as information from pheromones have elicited behavior in other lizards regarding reproductive condition and status (Cooper and Pérez-Mellado 2002; Whiting et al. 2009; Scott et al. 2015; Goldberg et al. 2017).

Our study indicates there are potential long-lasting and resilient helodermatid chemosignals dispersed onto substrates (e.g., from fecal remnants, scent glands, or simply transferred across the epidermis)

and integrated within shed skin, while also retaining functionality even after freezing and for long amounts of time. Chemical signaling in lizards typically occurs via secretions originating from femoral glands (Houck 2009; Khannoon et al. 2010; García-Roa et al. 2017), which notably are absent in helodermatid lizards (Mayerl et al. 2015; Carvalho et al. 2021). Researchers conducting chemosensory capability testing will often employ fresh pheromonal stimuli immediately and directly from conspecific glandular regions (Cooper and Trauth 1992; Aragón et al. 2001; Cooper and Pérez-Mellado 2002; Martín and López 2008), allowing for conclusions to be drawn for lizards in close proximity to one another and from recently deposited cues. Conversely, our experimental design tested pheromones that were likely in a degraded state, as cutaneous samples were frozen 1–10 mo prior to testing, and substrate was collected from vacated quadrants, potentially mimicking spatially and temporally distant signals similar to natural conditions.

Overall conspecific treatment DTFs were significantly different from control treatments in all lizards. Both males and females displayed significant DTF differences between OS and SS conspecific stimuli, demonstrating pheromones containing information regarding sex of the donor lizard is present. Spatially distanced nonvolatile chemosignal communication encompasses significant drawbacks, including limited directionality of the sender and inability of the scent to travel quickly (Baeckens and Whiting 2021). For communication signals to be effectively used in seemingly solitary (Beck 1990) and seasonally active helodermatids (Ariano-Sánchez and Salazar 2015), their properties are expected to persist through potentially substantial temporal parameters to thus sustain detectability by a receiver (Alberts 1992). The ability of *H. charlesbogerti* in our study to display behavioral (i.e., TF) differences toward and between conspecific chemosignals in shed skin and substrate provides insight into pheromonal use by helodermatid lizards. Furthermore, knowledge of chemosignal usage in this endangered species can inform conservation initiatives in the context of understanding natural history aspects of the focal species.

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