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BEHAVIORAL RESPONSES OF ADULT AND NEONATE *SCELOPORUS CONSOBRINUS* LIZARDS TO PREDATORY ODORS

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Abstract.— Lizards of the genus *Sceloporus* are known for their ability to detect conspecific odors. This study will determine whether they can also use their chemosensory abilities to detect the odors of one of their predators: *Coluber flagellum* (Coachwhip). The experiment also looked for differences in behavioral reactions to predator odors between adult and neonate lizards. Behaviors of lizards to predatory snake odors on sheets of filter paper were recorded and compared to behaviors to a series of control odors (water, pungent odor, and non-predatory snake odor). We recorded the number of tongue flicks, substrate touches, glass jumps, tail wiggles, time spent cage dancing, time spent in retreat, and amount of time spent on filter paper by testing lizards for all four odor treatments. There were no significant differences in the number of times these behaviors were performed by lizards among the treatments. Thus, this study found no evidence that *Sceloporus* can distinguish the odors of the predatory snake *C. flagellum* from other odors. However, this study did show that neonate lizards exhibited fewer odor detection behaviors than adults, in particular adult males, and so are potentially less able to detect odors.

Key Words. *Sceloporus,* antipredator behavior, odor detection, age-class

INTRODUCTION

Lizards are common prey for carnivores that are agile enough to catch them. To reduce the risk of predation, lizards may alter their behaviors to avoid potential predators, or to reduce the chances of being detected by them (Bealor and Krekorian 2002; Aragón et al. 2008). Many lizard species use various cues such as visual, auditory, and chemical cues to detect predators (Bealor and Krekorian 2002; Downes 2002; Amo et al. 2004; Cantwell and Forrest 2013). Lizards commonly use visual cues to detect potential predators based on the speed and direction of an approaching threat (Amo et al. 2004). The use of auditory cues has been recorded in some lizard species such as *Anolis sagrei* (Cuban Brown Anole) in which the lizards were able to detect predatory birds based on bird calls (Ito and Mori 2010; Cantwell and Forrest 2013; Cox et al. 2016). Studies of members of the lizard families Lacertidae, Scincidae, and Xantusiidae have shown the potential for lizards to detect snake odors, and in some cases distinguish the odors of a predatory snake from those of a non-predatory snake (Van Damme and Quick 2001; Bauwens and Downes 2002; Downes 2002; Amo et al. 2004; Clark and Kabes 2016). The ability to detect predatory odors may be an adaptive behavior to avoid detection (Bealor and Krekorian 2002). Prey organisms that detect a predator's odor alter their behaviors in order to evade their attackers (Downes 2002). Some lizards use increased tongue flicks to pick up chemical signals that would alert them of predators, reduce movement to blend in with their environment, or begin tail undulations to entice the predator to focus on the lizard's (expendable) tail (Bauwens et al. 1986). For example, a study of *Plestiodon* (formerly *Eumeces*) *laticeps* (Broad-headed Skink) showed that when the skink was introduced to a predatory odor, it significantly increased tongue flicking compared to a blank control (Cooper 1990). Neonate lacertid lizards presented with predatory snake odors responded by increasing the rate of tongue flicks, foot shaking, tail undulation, and while moving slowly, releasing a sudden burst of speed in a

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random direction (Van Damme et al. 1995). Detection of predatory odors can allow a lizard to find shelter or alter its behavior and reduce the chance of it being consumed by a predatory snake.

Lizards of the North American genus *Sceloporus* (family Phrynosomatidae) are generally considered to have weaker olfactory and vomerolfactory abilities than those of the Lacertidae and Scincidae (Vitt and Caldwell 2013). Though *Sceloporus* lizards are territorial and rely heavily on visual cues for communication, several species of *Sceloporus* have been shown to also rely on odor cues to detect the presence of potential rivals and mates (Campos et al. 2017). This ability to detect conspecifics has been studied in several species of *Sceloporus* adults and juveniles, including Yarrow's Spiny Lizard (*Sceloporus jarrovi*) (Bissinger and Simon 1981), the Eastern Fence Lizard (*Sceloporus undulatus*) (Campos et al. 2017), and the Striped Plateau Lizard (*Sceloporus virgatus*) (Castellano et al. 2011). When conspecific chemical cues are placed in a territory, adults of at least some *Sceloporus* species are capable of detecting the odor and are able to determine the approximate size, age, and sex of the individual that left the cue (Bissinger and Simon 1981; Campos et al. 2017). The fact that some *Sceloporus* species have the ability to detect and obtain information from chemical cues from conspecifics suggests they may have the potential for detecting predatory odors. Although studies have shown many lizard species have the ability to detect predatory odors (Curtis et al. 1989; Bauwens and Downes 2002; Downes 2002), to our knowledge, only one has been conducted on a member of the *Sceloporus.* Simon et al. (1981) studied the reactions of Yarrow's Spiny Lizards, *Sceloporus jarrovi*, in an observation chamber divided in half with one half provided with a paper towel floor impregnated with odors of a predatory snake and the other half provided with a clean paper towel. They found no differences in tongue-flick rate or time spent in each half of the chamber and concluded this lizard species could not detect predator odors. However, this study did not include non-predatory snake odor or novel odor controls and involved only a single species of *Sceloporus* (a genus with over 100 species; Rodda 2020) and so should not be considered the final word on the ability of species of this genus to use odors to detect predators.

One under-studied aspect of detection of predator odors by lizards is the possibility that lizards of different ages may differ in their ability to detect predator odors or differ in their reactions to these odors. For example, adult lizards may rely more on detection and recognition of environmental odors, and so may show different reactions than young, immature, and inexperienced lizards. On the other hand, neonates are much smaller and more vulnerable to predation and so may be expected to have a well-developed chemical sense that enables them to detect predator odors better than adults, or to show more pronounced anti-predator behavior when a predator odor is detected compared to adult conspecifics. This intriguing possibility has rarely been studied in any lizard species, (though see Van Damme et al. 1995; Stapley 2003) and only once in a species of *Sceloporus* (Simon et al. 1981).

The two purposes of this study are (1) to determine if the Prairie Lizard, *Sceloporus consobrinus* can detect and react to predatory snake odors and distinguish them from odors of harmless sources; and (2) to determine if there are any differences in odor detection or related behaviors between adult versus neonate when they are near a predatory odor.

MATERIALS AND METHODS

Study Animals and Captive Maintenance— The Prairie Lizard, *Sceloporus consobrinus* (formerly *S. undulatus hyacinthinus*) is a semi-arboreal lizard that is common in open forests of eastern Oklahoma and is prey for a variety of snakes and other predators. They spend much of their time in brush piles and fallen logs near trees where their gray color with brown streaks provide camouflage when they are on trees or logs (Conant and Collins 1998).

Research began near the end of April 2018 when Prairie Lizards became active and ended in mid-September 2018. Adult lizards were captured throughout the time of study, but the neonates were captured from mid-July through September after hatching. Twenty adults, nine females and eleven males, and ten neonate Prairie Lizards were captured by lasso or by hand from an oak-hickory forest at Sparrowhawk Primitive Area, Cherokee County, Oklahoma, (35.959181, -94.901086). To obtain odors from a predatory snake, a known predator of lizards, a Coachwhip (*Coluber flagellum*, Beane 2013), was captured by hand from Disney, Oklahoma, (36.475344, -95.010717). To obtain odors from a snake that is not a predator of lizards, a Ring-necked snake (*Diadophis punctatus*) was captured by hand from Camp Buster in Cherokee county, Oklahoma, (35.959444, -95.182912); Ring-necked snake diets usually consist of fossorial organisms such as earthworms (Fitch 1982). All animals were returned to the Bioscience Research Facility (BRF) on the campus of Northeastern State University in Tahlequah, Oklahoma. Snout-vent length measurements (SVL) were recorded to the nearest mm for each specimen. Mass of each organism was also recorded to the nearest 0.1 g using a triple beam balance. Captive maintenance for Prairie Lizards was like that described in Myers and Paulissen (2017). Each lizard was housed in individual 30.5 x 14.0 x 7.6 cm plastic containers. These containers were lined with paper towels on the floor and contained a cardboard retreat (one-half arc of a 10 cm cardboard tube). Each container had a small dish of water and lizards were fed daily; adult lizards were fed crickets and the neonate lizards were fed small crickets, mealworms or termites. Each container had a heat lamp connected to a timer set at 12 hr:12 hr light:dark photoperiod. The Coachwhip was housed in a 10-gallon glass aquarium (50.2 x 26.4 x 30.5 cm) and the Ring-necked Snake was housed in a plastic container (30.5 x 14.0 x 7.6 cm). Both snake containers contained a water dish, a light source with a timer set to 12 hr:12 hr light:dark photoperiods and floors lined with 15 cm Whatman filter papers to collect odors (see Experimental Design below). The Coachwhip was fed 1-2 Prairie Lizards from a site separate from the capture site once a week. The Ring-necked Snake was fed earthworms once a week obtained from areas around the BRF.

*Experimental Design***—** The Coachwhip cage had 9-12 Whatman filter papers as its flooring and the Ring-necked Snake cage had 1-2 circular Whatman filter papers as its flooring. As the snakes moved around in their cages to explore their environment, they rubbed their odors on the filter papers (Clark and Kabes 2016). Filter papers were placed in the Coachwhip tank for a week and then collected and stored in a zip lock bag. Filter papers were placed in the Ring-necked snake tank and collected every 2-3 days and were stored in a zip lock bag (since the

Ring-necked Snake's cage was smaller, the snake was positioned on the papers at all times due to the tank size). The odor-absorbed filter papers were kept at room temperature to prevent condensation from degrading the filter paper odors. After enough odor-absorbed filter papers had been collected, the snakes were released to their original habitats. We used a store-bought body spray, *Bod for Men™*, that was diluted with distilled water as a pungent odor control to see how lizards react to strong, novel chemical odors and used water as a control on the filter paper. The pungent control spray was a 10% dilution, and this was to prevent any chemical lingering of the body spray during the trial. We applied the pungent odor dilution by spraying it directly onto a filter paper. Distilled water was sprayed directly onto a filter paper as a blank control for the experiment.

A trial began by placing a single lizard into a 10-gallon glass observation tank (dimensions: 50.2 x 26.4 x 30.5 cm) and allowing it to become accustomed to the tank for approximately 24 hours. The observation tank was lined with paper towels as flooring, a cardboard retreat (half-arc of toilet paper roll) and had two 60-Watt lights suspended from the top; these lights were set to the same photoperiod as the home containers. The lizard had access to a small dish of water and food during this acclimation period. After the 24-hour acclimation period, but just before the trial began, the food and water dishes were removed to remove any odors they might have produced.

The first odor paper from one of the four odor treatments (water control, predatory snake, non-predatory snake, or pungent odor control) was cut in half to form two semicircular halves; each was placed on one of two equally sized semicircular pieces of plastic in the observation tank. Placing the odor paper halves on the semicircle pieces of plastic reduced the chances of any odors transferring onto the floor of the observation tank. The pieces of semicircle plastic were placed in the middle of the glass on opposite sides (front and back) of the observation. The lizard remained in the observation tank during the <30 second process of placing the semicircle odors and plastics. To reduce any chance of human odors being transferred, nitrile gloves were worn any time dealing with filter papers or with lizards during the trials. Two cameras were arranged to view the long-side profile and a top, diagonal view into the observation tank. The camera with a long-side view of the tank recorded all lizard behaviors near the odor treatments. The top diagonal camera looked into the observation tank in case the lizard moved into any blind spots of the other camera. While the cameras were recording, no one was allowed into the room so that the lizards' behaviors were not influenced by human presence.

A trial lasted one hour. Each lizard was presented with one of four odors: water control, predatory snake odor, non-predatory snake odor, or pungent control odor in random sequence. There were 15-minute periods between each odor trial to reduce possible stress and to allow time for the lizard to rest from the previous trial. During the beginning of the resting period, the odor paper was pulled out along with the plastic semicircles while the lizard remained wherever it was during the previous trial. At the end of the resting period, a new set of semicircles was placed in the observation tank and a different odor from the last which begins a new trial. After the trials, lizards were released at their site of capture.

As a form of positive control, we repeated the experimental protocol with two specimens of another lizard, the Little Brown Skink (*Scincella lateralis*), that were collected from the same location as the *Sceloporus* lizards used in this study. The Little Brown Skink is a member of the family *Scincidae* which is known to have well developed chemical senses and to use them to detect and react to odors of predators (Cooper 1990). This was done to ensure that the odors deposited on the Whatman filter paper by the predatory snake were of sufficient strength to be detectable by a species of lizard that is known to detect predatory odors. The skinks' behaviors observed for the water control and predatory snake odors were the number of total detect behaviors (see below) and amount of time spent in retreat.

Data Analysis— The recordings were reviewed and behaviors and movements for each lizard during each of the four odor trials were recorded. The number of times a lizard flicked its tongue into the air (tongue flicks) and touched its tongue to a surface (substrate touches) was counted. These two variables were added together to create a new variable called "total detect" that counted the number of times a lizard exhibited odor detection behaviors. The number of times the lizard exhibited escape behaviors such as a jump towards the glass (glass jump) and the amount of time the lizard spent pacing its cage rapidly back and forth with its forelegs on the glass ("cage dancing") were also recorded. The number of times the lizard wiggled its tail (tail wiggles) was also recorded to note how often the lizard tried to focus any potential predators towards its tail. The amount of time in seconds the lizard spent in the retreat was recorded along with the amount of time in seconds the lizard spent on a filter paper.

We compared the mean number of Total Detect behaviors, Glass Jumps, and Tail Wiggles and the mean amount of time lizards spent Cage Dancing, Sitting on the Filter Paper, and Lying in the Retreat across the four odor treatments using Friedman tests as the assumptions for parametric tests were strongly violated by the data. To look for differences in the Total Detect variable among the three age and sex classes of lizards (males, females, and neonates), we performed a mixed ANOVA on the ranks of the raw data to look for significant within-subject effects, between-subject effects, and interactions. Once a significant between-subjects effect was identified, we performed Tukey's HSD post-hoc tests to determine which age/sex classes of lizards differed from one another. All statistics were run using either MYSTAT or IBM SPSS Statistics version 25.

RESULTS

Little Brown Skink Odor Detection Trials- During these odor detection trials, the two lizards exhibited almost the same number of Total Detect behaviors in the water control treatment (mean= 28.5) as in the predatory snake odor treatment (mean = 27.5). One skink performed twice as many Total Detect behaviors during the predatory trial as during the water control trial; the other skink was just the reverse. However, both spent a greater amount of time in the retreat during the predatory snake odor trial (mean = 1238 seconds) versus the water control trial (mean = 614 seconds). This result suggest that the skinks were able to detect the predatory snake odor and responded by taking shelter in the retreat.

Prairie Lizard Comparison Among Odor Treatments— No significant differences were detected among any of the four odor trials (control, predatory snake, non-predatory snake, pungency control) for Prairie Lizards for any of the variables measured (Table 1). For example,

Table 1. Comparison of behavioral measures of responses of Prairie Lizards (*Sceloporus consobrinus*) to four odor trials; N = 31 (20 adults, 11 neonates). Values are means ± SE number of times a behavior was performed during a 60 min trial for the first three variables and the mean ± SE number of seconds a behavior was performed during a 60 min trial for the last three variables. "*P* Value" refers to *P* value for Friedman tests; there was insufficient data to conduct this test for the variable "Tail wiggles."

VARIABLE	Water Control (C)	Predatory Snake Odor (P)	Non-Predatory Snake Odor (NP)	Pungency Control (Pun)	*P* value
Total Detect	2.2 ± 0.69	4.5 ± 1.3	1.8 ± 0.57	1.8 ± 0.55	0.221
Glass Jumps	1.8 ± 0.81	1.3 ± 0.7	1.4 ± 0.9	0.6 ± 0.4	0.322
Tail Wiggles	0 ± 0	0.065 ± 0.065	0.065 ± 0.065	0.032 ± 0.032	-----
Time Cage Dancing (sec)	0 ± 0	7.1 ± 4.7	25.4 ± 17.6	0.2 ± 0.2	0.089
Time on Filter Paper (sec)	138 ± 46.9	252 ± 91	226 ± 99.7	397 ± 135.2	0.650
Time in Retreat (sec)	0 ± 0	0.1 ± 0.1	0 ± 0	0.3 ± 0.3	0.572

although the mean number of Total Detect behaviors was higher for the predatory snake odor than for any of the other odor treatments (Table 1), there were no significant differences in the mean number of Total Detect behaviors among the four odor treatments (Friedman test $P = 0.221$; Table 1). Similar results were obtained for both males and females when they were analyzed separately (Friedman tests; all $P > 0.05$).

Similarly, there were no significant differences among the escape behaviors (Table 1). The mean number of Glass Jumps, mean number of Tail Wiggles, mean time spent Cage Dancing, and mean time Spent in the Retreat did not differ among the four odor treatments. Although lizards spent more time Sitting on the Filter Paper during the pungency trials than during the other odor trials (Table 1), the differences among the four odor treatments were not statistically significant (Freidman test: $P = 0.572$).

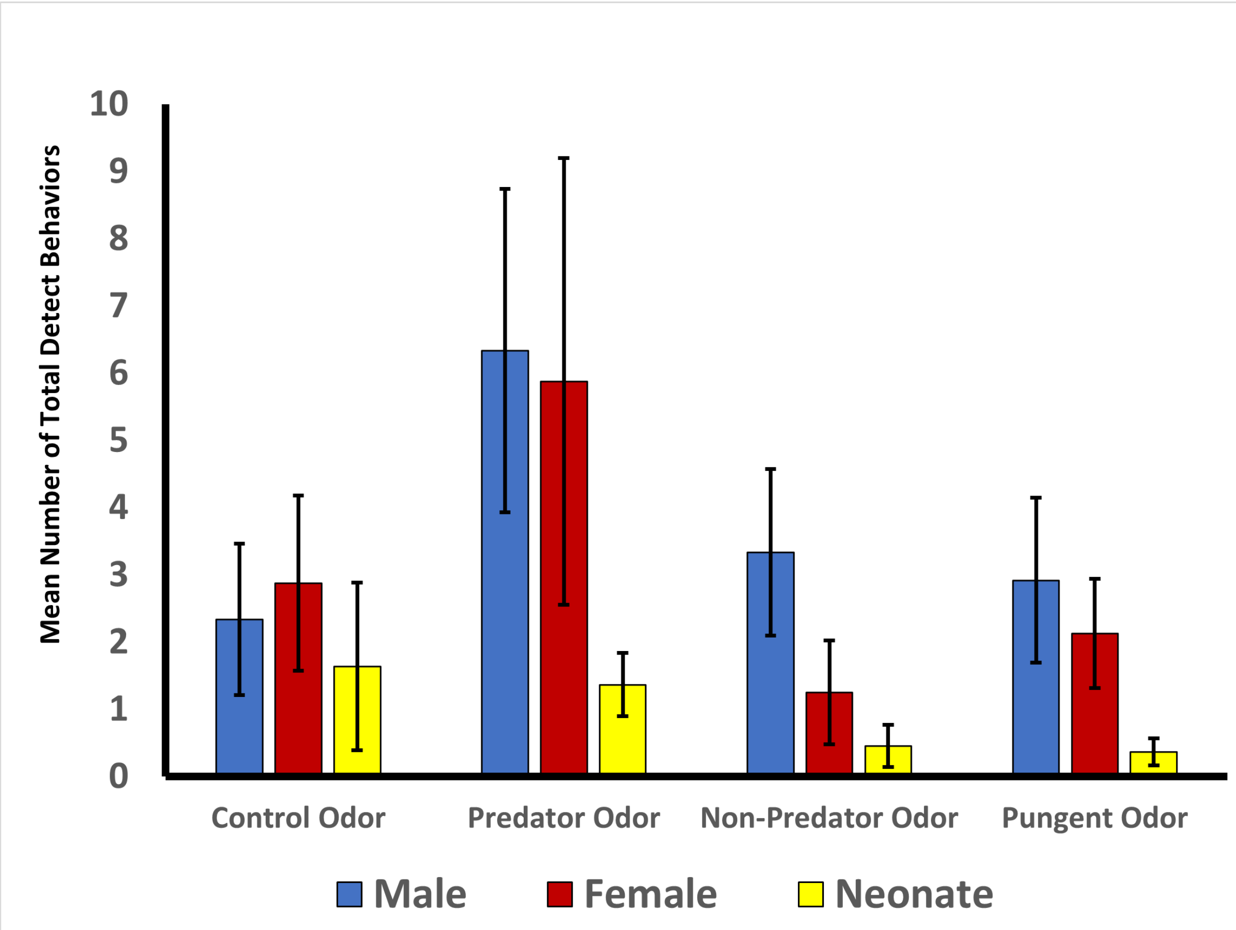
Comparison of Males, Females, and Neonates— The mixed ANOVA using ranks of the Total Detect variable showed no significant within-subject effect (F = 0.020; df = 3, $P = 0.996$) and no significant interaction with age/sex class effect (F = 0.429; df = 6; $P = 0.858$) which indicate no differences among the four odor treatments for this variable. However, there was a significant between-subject effect (intercept: F = 327.95; df = 1; $P < 0.001$: age/sex class: F = 4.05; df = 2; $P = 0.028$) indicating there was a significant difference in Total Detect Behavior among males, females, and neonates. The mean number of Total Detect behaviors was lower for neonates than for either males or females (Figure 1). Tukey's post-hoc test showed there was a significant difference between males and neonates ($P = 0.023$), but not between females and neonates ($P = 0.219$), nor between males and females ($P = 0.688$), possibly due to the high degree of variability in number of Total Detect behaviors among females (Figure 1).

DISCUSSION

During the predatory snake odor trials, both Little Brown Skinks spent more time in the retreat compared to the water control trials. This provides support for the idea that this species could detect the predatory snake odors on the filter paper and exhibited the appropriate response of attempting to hide from the potential predator in its environment. Because this research protocol was adequate to demonstrate that Little Brown Skinks could detect and react to predatory snake odors, it should also be adequate to demonstrate that other species of lizards can do the same if they have sufficient predator odor detection capacities.

Our results, however, indicated no such predator detection capacities in this population of the Prairie Lizard. There were no significant differences between control and predatory snake odor, non-predatory snake odor, or pungent control odor for any of the variables that were measured. The lizards did show a tendency to exhibit more detection behaviors in the predatory snake odor trials than in the other trials, although the difference in the mean number of Total Detect behaviors performed in the predatory snake odor trials and control trials narrowly failed to reach statistical significance (Table 1). However, one male lizard showed a high number of detection behaviors, specifically tongue flicking, during the predatory snake odor trial and this may have skewed the results. This also suggests that there is a great deal of variation in the ability or willingness to detect a predator's odor; for example, this male lizard may have had prior experience with a Coachwhip at some point. Unexpectedly, the lizards frequently sat on the filter papers that had odors on them, or walked across them without giving any obvious indication that they even noticed that the filter paper was there. However, there were nine trials where lizards paused on the filter paper and begin to touch the filter paper with their tongues 1-3 times. (During the Little Brown Skink trials, the skinks did something similar, pausing at the filter papers and touching their tongues to the substrate or flick their tongues.) An intriguing result, although it was not statistically significant, was that lizards spent more time on the filter paper during the pungent odor trials than the control trials (Table 1). It is possible that the

Figure 1. Mean number of times odor detection behaviors were exhibited by adult male, adult female, and neonate Prairie Lizards (*Sceloporus consobrinus*) exposed to water control, predatory snake odor, non-predatory snake odor, and pungent odor on filter paper during 60-minute trials. Total Detect = number of {tongue flicks, substrate touches, and substrate touches to filter paper}. Bars are means and error bars are +/- 1 SE. Mixed ANOVA on ranks demonstrated a significant between-subjects effect; Tukey's post-hoc tests showed a significant difference between males and neonates, but not between females and any other age/sex class (see Results). Sample sizes are: males = 12; females = 8; neonates = 11



lizards detected the strong odor and may have been attempting to determine what the odor was by remaining on the filter paper with the pungent odor. It may also be that *Sceloporus* has a chemical sense system that is specifically tuned to detect odors of conspecifics for communication purposes but is not sufficiently strong in its capabilities to detect predator odors. Skinks, such as the Little Brown Skink, which rely much more on chemical detection for foraging, may not be so limited.

Time spent in the retreat did not differ significantly among the four odor treatments. This is not surprising since the Prairie Lizard is semi-arboreal and so frequently seeks to escape by running up trees rather than hiding under objects (Conant and Collins 1998). When the lizards were kept in their home containers, they normally sat on pieces of wood rather than hiding under their cardboard retreat. Even after human interactions, such as feeding, lizards did not retreat to the shelter, but instead began cage dancing or readjusting themselves on the underside of the wood trying to make themselves unseen. The Little Brown Skink lizards spent time in their retreats during the trials, perhaps a more appropriate shelter for them given their litter cryptozooid habit (Rodda 2020).

One unexpected result of this study was the significant differences in Total Detect behaviors displayed by adult versus neonate lizards: neonates exhibited fewer total detect behaviors across treatments than adults with the difference reaching statistical significance between adult males and neonates (Figure 1). The differences between adults and neonates may be due to the developmental stage of the sensory organs such as the vomeronasal system which continues to develop after birth/hatching in snakes (Holtzman 1998). On the other hand, a study conducted on the development of vomeronasal abilities of a Common Gartersnake (*Thamnophis spp.*) indicated that the vomeronasal organ requires very little time before it is considered a fully developed organ (Holtzman and Halpern 1990). However, vomeronasal organ development may be different in lizards, especially in a species that is considered to have a weaker vomeronasal ability. Alternatively, neonate *Sceloporus* lizards may depend on cryptic behaviors more than adults and therefore may be reluctant to move or engage in chemical detection behaviors (such as tongue-touching) that might betray their presence to a predator. A study of flight initiation distances (FIDs) of the Florida Scrub lizard, *Sceloporus woodi* showed neonates had significantly shorter FIDs than adults, suggesting they employ crypsis rather than flight to escape predators (Stiller and McBrayer 2013). Studies of the abilities and responses of neonate, juvenile, and adult lizards need to be conducted to better understand how antipredator behaviors change during ontogenetic development, especially considering our finding of an ontogenetic difference in odor detection behaviors.

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