

# The Use of Chemical Cues by Granite Night Lizards (*Xantusia henshawi*) to Evaluate Potential Predation Risk

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**Squamate reptiles have highly developed chemosensory systems used to detect both predators and prey. Although the general ability of squamates to assess predation risk using chemical cues is well known, the detail to which squamates can make discriminations concerning risk is largely unexamined. Granite Night Lizards (*Xantusia henshawi*) are habitat specialists that live in exfoliations of granite boulders in dense populations. We measured the responses of Granite Night Lizards to the scent of a sympatric predator, the Lyre Snake (*Trimorphodon lyrophanes*), maintained on two different diets (lizard-fed and mouse-fed), as well as a non-predatory snake (the Shovelnose Snake, *Chionactis occipitalis*) and a blank control. We also evaluated the potential use of conspecific chemical cues to assess predation risk by quantifying the response of lizards to the scent of both calm and stressed conspecifics. We collected scents for both experiments on paper pads, which we then placed at the entrance of a shelter within a testing arena containing a focal lizard. We then used video cameras to record the behavior of focal lizards over a 60-minute period. We found that, compared to the blank control, Night Lizards in the presence of chemical cues from snakes took longer to enter the shelter, spent longer investigating chemical cues, and traveled further before entering the shelter. Lizards also spent longer investigating chemical cues from Lyre Snakes than Shovelnose Snakes. However, there were no significant differences between responses to lizard-fed and mouse-fed Lyre Snake chemical cues. We also found no evidence that lizards use conspecific chemical cues to evaluate predation risk. This study demonstrates that Granite Night Lizards can use chemical cues from their predators to assess predation risk, but further research is needed to assess whether these responses differ based on the diet of the predator.**

**I**N order to survive, individuals must be able to make accurate and timely decisions about their environment, including assessing predation risk. Although risk assessment can rely on visual or auditory cues emanating directly from nearby predators, strategies that allow animals to detect and respond to their predators before they themselves are detected are particularly advantageous (Downes and Shine, 1998; Apfelbach et al., 2005). Chemosensory cues allow individuals to investigate their habitat and indirectly assess conspecifics and predators that are no longer physically present (e.g., Duvall et al., 1980; Bofill and Lewis, 1999; Gonzalo et al., 2006; Clark, 2007). The use of chemical cues in predator detection has been studied across many taxa (Kats and Dill, 1998), including reptiles (Bealor and Krekorian, 2002; Amo et al., 2004), birds (Amo et al., 2008), amphibians (Sullivan et al., 2002; Gonzalo et al., 2006), and fishes (Ferrari et al., 2006). In addition to general predator detection, several species are also capable of identifying and determining relative predation risk based on cues derived from the diet of the predator (e.g., Pillay et al., 2003; Vilhunen and Hirvonen, 2003; Sullivan et al., 2004; Dixson et al., 2012).

By using diet-based chemical cues to assess relative predation risk, individuals can more effectively balance the trade-off between anti-predator behavior and other activities (e.g., foraging for food and mates). Responses to predator chemical cues have been mostly studied in aquatic and marine systems (fishes: Gelowitz et al., 1993; Vilhunen and Hirvonen, 2003; Ferrari et al., 2006; Dixson et al., 2012; larval amphibians: Laurila et al., 1997; Gallie et al., 2001; microcrustaceans: Laforsch and Beccara, 2006). Aquatic studies are ideal for analyzing the response to chemical cues through the fluidity of water and the ability to control cues at a desired concentration. In comparison, terrestrial studies are potentially more difficult due to the volatile nature of many airborne chemical cues. Nevertheless, several studies in

terrestrial systems have also demonstrated that prey display anti-predator behaviors in response to predator chemical cues (e.g., Thoen et al., 1986; Van Damme and Quick, 2001; Bealor and Krekorian, 2002; Stapley, 2003; Amo et al., 2004). Many squamate lizards have been shown to differentiate predator cues. For example, Mountain Log Skinks (*Pseudemoia entrecasteauxii*) alter their choice of predator-scented shelters based on the potential risk posed by each predator (Stapley, 2003). Amo et al. (2004) found that, when presented with the scent of saurophagous snakes, Wall Lizard (*Podarcis muralis*) tongue flick rate correlated with the degree to which the snake was a lizard specialist. These previous studies on lizards did not control predator diet, and so do not differentiate between species-derived and diet-derived chemical cues.

Although it is clear that predator odors may induce anti-predator behavior in lizards (Sullivan et al., 2002; Stapley, 2003; Amo et al., 2004), other sources of chemical cues that could also be used in risk assessment have not been well investigated. For example, chemical cues from conspecifics are known to be an important source of information about the environment. Conspecifics can directly and indirectly communicate where they are aggregated (Briones-Fourzan et al., 2008), body condition (Shine et al., 2003), or the location of potential mates (Merte et al., 2010). Recent studies have also found that some taxa use conspecifics chemical cues to assess potential predation risk (Pastro and Banks, 2006). Because the physiological state (e.g., stressed or calm) of an individual can influence their chemical signature (e.g., Cocke and Thiessen, 1986), chemical cues indicative of predator detection represent a source of public information potentially useful in risk assessment. Both conspecifics and heterospecifics that share predators may use such cues. This chemosensory-based risk assessment from sympatric species has, again, been most well studied in aquatic systems (Brown and Godin, 1997; Chivers et al., 2002; Laforsch and Beccara,

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2006; Briones-Fourzán et al., 2008). Some terrestrial studies have been conducted on amphibians (Marvin and Hutchison, 1995; Lampe et al., 2011) and rodents (Cocke and Thiessen, 1986; Pastro and Banks, 2006) but not squamate reptiles.

Predator- and conspecific-derived cues indicating species, stress state, diet, are not the only factors that can influence an individual's risk assessment. In many species, males and females assess risk differently (Matity et al., 1994; Lailvaux et al., 2003; Swaisgood et al., 2003; Vanhooydonck et al., 2007; Frommen et al., 2009; Noble et al., 2012). These differences are likely due to the variation in reproductive cost between the sexes and are often modulated by reproductive state (Bauwens and Thoen, 1981; Downes and Bauwens, 2002; Frommen et al., 2009). Females across many taxa will exhibit less risky behaviors and will often rely more on crypsis than fleeing to avoid detection (Kissner et al., 1997; Lailvaux et al., 2003; Frommen et al., 2009).

As a group, squamate reptiles are well known to use chemosensory cues to assess both predators and conspecifics (Duvall et al., 1980; Glinski and Krekorian, 1985; Keverne, 1999; Whiting, 1999). Although some studies have shown that lizards can react to predators according to how likely those predators are to prey on lizards (Van Damme and Quick, 2001; Stapley, 2003), no previous research has examined the importance of predator diet in these responses. Additionally, although squamates often utilize conspecific cues in kin recognition (Main and Bull, 1996; Bull et al., 2001) and finding mates (Duvall et al., 1980; Bofill and Lewis, 1999), we know of no studies that have examined the potential for squamate reptiles to use conspecific cues to assess predation risk.

In this study, we used chemosensory cues derived from both predators and conspecifics to examine risk assessment in Granite Night Lizards (*Xantusia henshawi*). Granite Night Lizards are geographically restricted to granitic habitats found in southern California and Baja California Norte, where they use crevices and exfoliations as shelter sites (Lee, 1975). Although these lizards are locally common and occur in high densities in these isolated areas, they are quite secretive and spend the bulk of their time sheltering. All members of this clade exhibit a low dispersal rate and occupy stable shelter sites in high densities (Lee, 1975; Fellers and Drost, 1991; Davis et al., 2011). Granite Night Lizards have a variety of predators, including the Lyre Snake (*Trimorphodon lyrophanes*), a saurophagus (lizard-eating) snake that also frequently occupies rock crevices (Cowles and Bogert, 1935; Lee, 1975). Granite Night Lizard's major defense against predation is their use of crypsis and avoidance, and they most likely rely on a well-developed olfactory and vomer-olfactory system, much like those found in other squamate reptiles (Schwenk, 1985).

Because they are syntopic with a saurophagus snake and occur at high population densities, we hypothesized that this species could use chemical cues derived from both predators and conspecifics to evaluate predation risk. Specifically, we asked the following questions: 1) Do Granite Night Lizards alter their behavior in the presence of predator chemical cues, and if so, are their responses dependent on the diet of that predator? 2) Do Granite Night Lizards alter their behavior in the presence of chemical cues from stressed conspecifics in a manner consistent with predation risk assessment?

## MATERIALS AND METHODS

Due to logistical constraints on animal housing, we conducted experiments in two rounds, using different wild-caught individuals for each round. We established an initial captive colony of 23 Granite Night Lizards (10 males, 13 females) used in the conspecific experiment. Twenty of these individuals (8 males, 12 females) were also used in the predator experiment. All individuals were collected from populations in eastern San Diego County (5 September 2011–21 October 2011). An additional 25 individuals (14 males, 11 females) were collected for a second round of both conspecific and predator trials (11 February 2013–5 April 2013). In total, we sampled 45 individual lizards for the predator experiments (22 males, 23 females) and 48 individual lizards for the conspecific experiments (24 males, 24 females). Upon initial capture, we measured snout–vent length to the nearest 0.5 mm, mass to the nearest 0.25 g, and sexed the lizards. They were housed in plastic bins in a large rack system with paper substrate, a water bowl, and a small plastic shelter. Each lizard was fed ten small mealworms (*Tenebrio molitor*) dusted with vitamin supplements each week. The housing room and trial room were kept at 24°C, with a 12:12 light-dark cycle.

The test arena consisted of twelve 36 cm x 40 cm plastic cubicles. We provided each lizard with a 15 cm x 15 cm granite tile shelter, made up of two tiles and spacers (0.5 cm thick) creating a crevice for the lizards. After individuals completed trials and before the next acclimation period, we cleaned arenas by washing them with a solution of Quatricide® PV Disinfectant (Mesquite, Nevada), rinsing them with water, and air drying them to remove any residual chemical cues left by lizards and filter pads. Trials were recorded with video cameras, either a Sony digital video camera recorder (model number DCR-SR85; Minato-ku, Tokyo, Japan) or a Bell & Howell HD Camcorder (model number DNV900HD; New York, NY), mounted above the arena.

**Experimental design.**—We conducted informal pilot trials using a simultaneous choice design with a predator-scented shelter on one side of the arena and an unscented shelter on the other side. Observations during these trials qualitatively indicated that lizards exhibited anti-predator responses throughout the test arena, meaning that they were probably able to detect and respond to the predator scent from a greater distance than the length of the testing apparatus. These observations led us to believe that if we offered lizards a simultaneous presentation of chemical cues it would be difficult to ascribe changes in the behavior of the lizard to one or the other of the two cues. Therefore, we designed a series of sequential choice tests with only one of four treatments present at a time, so that we could compare responses to each chemical cue in isolation. Observations made during pilot trials were anecdotal and used to guide our experimental design and develop an ethogram (Table 1) for data analysis in the experimental trials.

**Experimental methods.**—We placed test lizards in the clean arenas with granite tile shelters and allowed them to acclimate for 48±2 hours before the start of the trial. The acclimation period allowed lizards to familiarize themselves with the test arena and granite shelter and reduce exploratory behavior. After this acclimation period, we moved lizards to a corner of the arena away from the granite shelter and placed them under a plastic hide box. We then placed a

**Table 1.** Ethogram of observed behaviors of *Xantusia henshawi*.

Behavior	Description
DISTANCE	Distance in cm moved during a one-minute subsample of every five minutes of the trial period
RETREAT	Lizard moves towards the entrance of the shelter, then turns and moves away
ESCAPE	Lizards attempt to leave the arena by climbing, scratching, and jumping at the walls
LATENCY TO SHELTER	Time from when the hide box covering the lizard was removed until the lizard enters the shelter or 60 minutes have passed
PAD CONTACT	Amount of time the lizard is near (within 2 cm) or in contact with the filter pad, recorded in seconds
MOVEMENT RATE	The average distance (in cm) covered in a 2-second interval (averaged over all 2-second movement data)

Whatman 15 cm filter pad scented with either snake chemical cues (see predator experiment) or a conspecific chemical cues (see conspecific experiment) in the front of the granite shelter opening. The plastic hide boxes were then removed, we left the room, and lizards were left to investigate the arena and filter pad for 60 minutes. Behavioral data were extracted by reviewing video recordings at a later date. Video reviewers were blind to the treatment type in order to minimize potential viewer bias. From the videos, we quantified the behaviors listed in Table 1 for the first 60 minutes, or until the lizard entered the granite tile shelter. All lizards were tested against all scent treatments in a random order. Lizards were rested in their home cage for at least 72 hours between each trial.

We used tracking software (Tracker version 4.82) to evaluate rates and distances of lizard movement. Although tracking software greatly facilitates estimates of distances moved and movement rate, due to lighting contrasts in the arena, the software was not always able to accurately follow lizards and frequently needed to be manually corrected. In order to reduce the amount of manual effort, we chose to subsample lizard movements, rather than calculate movements for the entire trial. We sampled the first minute of movement for each lizard within each five-minute segment and tracked them at two-second intervals to estimate the distance covered during exploratory behaviors. Individuals observing video tracking software were also blind to the treatment and individual identity of the lizards in the arena at the time of analysis.

**Predator experiment.**—Individual lizards were exposed in a random order to chemical cues from: (1) a Shovelnose Snake ( $n = 4$ ) maintained on a diet of mealworms; (2) a Lyre Snake ( $n = 3$ ) maintained on a diet of lizards (*Anolis* sp. and *Hemidactylus* sp.); (3) a Lyre Snake ( $n = 3$ ) maintained on a diet of small mammals (*Mus musculus*); or (4) a blank control. The Shovelnose Snake is a small, non-predatory fossorial snake used as a biologically relevant control scent. The Lyre Snake is an ecologically relevant predator scent because it is a common saurophagus snake syntopic with Granite Night Lizards. Although there is not a published dietary analysis for Lyre Snakes, unpublished reports have found Granite Night Lizards in the stomachs of Lyre Snakes (Harry W. Greene, pers. comm.). While collecting Granite Night Lizard specimens, we also collected four Lyre Snakes occupying the same general microhabitat as Granite Night Lizards.

We presented chemical cues on Whatman 15 cm filter pads imbued with the scent of test snakes. Test snakes were all fasted the week prior to testing to avoid excessive defecation on the filter pad and were left on the pads for 48 hours. Direct use of feces was avoided in order to observe the lizards'

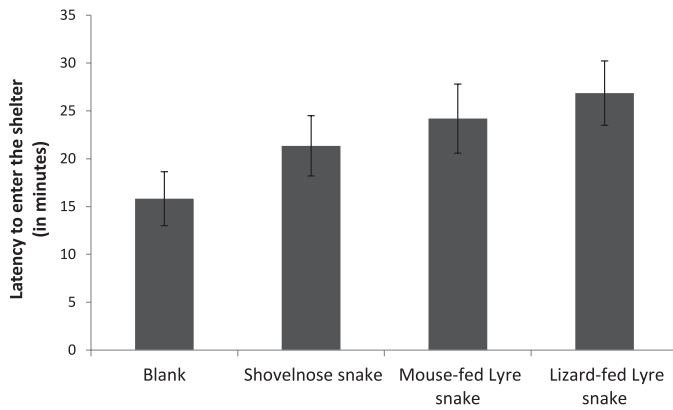
reactions to the general scent of the snakes and to determine if predator diet cues were detectible through the snake scent alone. If a snake did defecate on the pad we gently removed all feces before the pad was introduced to the testing arena, though this only occurred six times out of 135 trials.

**Conspecific experiment.**—The general experimental design for conspecific experiments was identical to the predator scent trials, except lizards were tested with filter pads from: (1) a stressed conspecific, (2) a calm conspecific, and (3) a blank control. All conspecific scent donor lizards were placed inside a 90 mm petri dish with a dampened Whatman 15 cm filter pad. We sealed the dish with parafilm to exclude any ambient chemosensory cues. In order to remove potential responses based on mating or courtship, we paired donors and test lizard by sex, so each lizard was tested against an individual of its same gender. We also paired lizards by size to reduce variability in responses that may be size-mediated (such as territoriality). Dishes containing calm lizards were covered and left undisturbed for 20 minutes. Although we initially tried to use natural predators (Lyre Snakes) to elicit stress responses in scent donors, we found that both snakes and lizards did not react strongly to each other. This may have been due to the lack of chemical cues, as our design required us to chemically isolate conspecifics from predators. Thus, in order to achieve a consistent stress response, a human was used as a surrogate predator. One of us (LEK) repeatedly tapped at the petri dish over a 20-minute period in order to harass the lizard and produce a consistent visual stress response, as noted by an arched body posture, fleeing, freezing, and deep breathing from the lizards.

**Statistical analysis.**—In order to assess the behavioral reactions of test lizards, we analyzed six behaviors indicative of responses to chemical cues (Table 1): (1) latency to enter the shelter, (2) the total time lizards spent in contact with the scented pad, (3) the distance traveled during the subset of time the lizards were tracked, (4) the number of escape attempts, (5) the number of retreats from the shelter before entering, and (6) the movement rate of the lizards during the subset of time the lizards were tracked. Both the escapes and retreats were adjusted to a 1–5 Likert scale to assist with the wide range of variation in counts. Due to limited video resolution, it was not possible to accurately assess tongue-flick rate, so this behavior was not quantified. Values are given as mean  $\pm$  se.

Because we used a repeated-measures design, we analyzed lizard responses to scent treatments using linear mixed models (LMM for continuous response variables) and generalized linear mixed models (GLMM with a Poisson distribution for count responses variables). We used the lme4





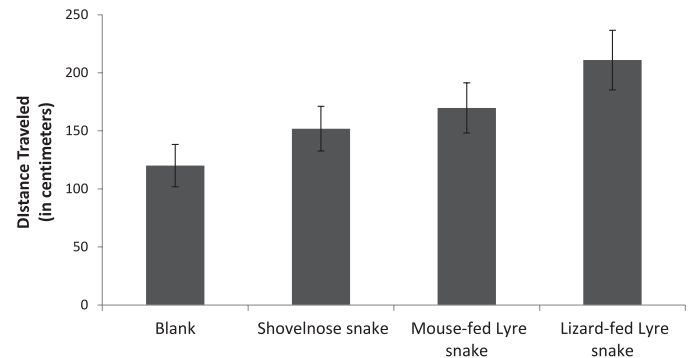
**Fig. 1.** Mean amount of time individuals of *X. henshawi* spent investigating arena before entering granite shelter when exposed to different predator scents. Planned comparisons showed a significant difference between the aggregate of the snake treatments and the blank control ( $F_{1,134} = 9.06$ ,  $P = 0.003$ ), but no difference between the Shovelnose Snake treatment and the aggregate of Lyre Snake treatments ( $F_{1,88} = 0.93$ ,  $P = 0.34$ ), or between Lyre Snake treatments ( $F_{1,43} = 2.33$ ,  $P = 0.13$ ). Bars represent average  $\pm$  SE.

package in R version 3.0.2 to build mixed effect models with maximum likelihood estimation of variance components. We incorporated both individual identity of the lizards and time of year (first or second round trials) into the model as random factors. We specified lizard sex and treatment and their interaction as fixed factors. We determined significance of fixed factors using the afex package, implementing the Kenward-Roger correction for LMMs and likelihood ratio tests for GLMMs. When necessary, we transformed data for LMMs to meet the assumptions of normality and heterogeneity of variance.

When the treatment effect was significant we implemented an orthogonal planned comparison, as this is a more powerful and appropriate approach than conducting all possible pairwise comparisons (Ruxton and Beauchamp, 2008). We implemented planned comparisons by rerunning LMMs or GLMMs with treatment categories altered to reflect each comparison in turn. In the predator experiment, we wanted to know if lizards responded to snake scents more strongly than blank controls, and if so, whether the species or diet of the snake was important. Thus, we undertook the following planned comparisons: (1) control versus the aggregate of all snake treatments, (2) Shovelnose Snake versus the aggregate of Lyre Snake treatments, and (3) mouse fed Lyre Snake treatment versus lizard fed Lyre Snake treatment. In the conspecific experiment, we wanted to know if lizards respond more strongly to conspecific scent than to blank controls, and if so, whether the state of the conspecific was important. Thus, we implemented the following planned comparisons: (1) control versus aggregate of conspecific treatments, and (2) stressed versus unstressed conspecific treatments.

## RESULTS

**Predator experiment.**—The latency to enter shelter data were transformed to the  $1/6^{\text{th}}$  power to meet assumptions of normality and heterogeneity of variance. Neither sex nor the interaction between sex and treatment significantly affected the latency for lizards to enter shelter (interaction  $F_{3,129} = 1.51$ ,  $P = 0.21$ ; sex  $F_{1,48} = 1.34$ ,  $P = 0.25$ ). However, the overall

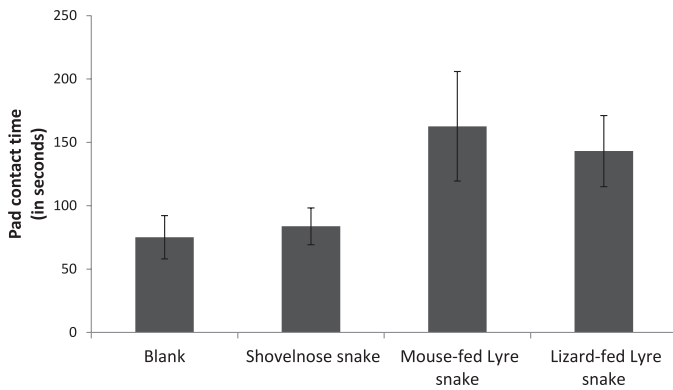


**Fig. 2.** Mean total distance moved by *X. henshawi* before entering granite shelters. Planned comparisons showed a significant difference between the aggregate of the snake treatments and the blank control ( $F_{1,134} = 7.03$ ,  $P = 0.009$ ), but no difference between the Shovelnose Snake treatment and the aggregate of Lyre Snake treatments ( $F_{1,88} = 1.82$ ,  $P = 0.18$ ), or between Lyre Snake treatments ( $F_{1,43} = 2.53$ ,  $P = 0.12$ ). Bars represent average  $\pm$  SE.

effect of treatment was significant ( $F_{3,132} = 3.82$ ,  $P = 0.011$ ), and planned comparisons revealed that individuals exposed to snake scents took significantly longer to enter their shelter than lizards exposed to the blank control (control =  $15.8 \pm 2.8$  min, snake scents =  $24.1 \pm 1.9$  min,  $F_{1,134} = 9.06$ ,  $P = 0.003$ ). However, latency to enter shelter was similar when lizards were exposed to Shovelnose Snakes and Lyre Snakes (Shovelnose Snakes =  $21.3 \pm 3.1$  min, Lyre Snakes =  $25.5 \pm 2.4$  min,  $F_{1,88} = 0.93$ ,  $P = 0.34$ ), and mouse-fed and lizard-fed Lyre Snakes (mouse-fed Lyre =  $24.2 \pm 3.4$  min, lizard-fed Lyre =  $26.9 \pm 3.6$  min,  $F_{1,43} = 2.33$ ,  $P = 0.13$ ; Fig. 1).

Distance data were log transformed to meet assumptions of normality and heterogeneity of variance. As with latency, neither sex nor the interaction between sex and treatment significantly affected the overall distance lizards moved (interaction  $F_{3,129} = 0.49$ ,  $P = 0.69$ ; sex  $F_{1,48} = 0.01$ ,  $P = 0.97$ ), but the overall effect of treatment was significant ( $F_{3,132} = 3.77$ ,  $P = 0.012$ ). Planned comparisons revealed that individuals exposed to snake scents moved further than lizards exposed to the blank control (control =  $120 \pm 18$  cm, snake scents =  $177 \pm 13$  cm,  $F_{1,134} = 7.03$ ,  $P = 0.009$ ). However, movement was similar when lizards were exposed to Shovelnose Snakes and Lyre Snakes (Shovelnose Snakes =  $152 \pm 19$  cm, Lyre Snakes =  $190 \pm 17$  cm,  $F_{1,88} = 1.82$ ,  $P = 0.18$ ), and mouse-fed and lizard-fed Lyre Snakes (mouse-fed Lyre =  $170 \pm 22$  cm, lizard-fed Lyre =  $211 \pm 26$  cm,  $F_{1,43} = 2.53$ ,  $P = 0.12$ ; Fig. 2).

The pad contact data were square root transformed to meet assumptions of normality and heterogeneity of variance. Neither sex nor the interaction between sex and treatment were significant factors affecting how long lizards were in contact with filter pads (interaction  $F_{3,129} = 0.49$ ,  $P = 0.69$ ; sex  $F_{1,48} = 0.01$ ,  $P = 0.97$ ), but the effect of treatment was significant ( $F_{3,132} = 3.81$ ,  $P = 0.012$ ). Planned comparisons revealed that individuals exposed to snake scents investigated filter pads longer than lizards exposed to the blank control (control =  $75 \pm 17$  s, snake scents =  $113 \pm 12$  s,  $F_{1,134} = 7.05$ ,  $P = 0.009$ ). Similarly, lizards investigated the scents of Lyre Snakes longer than those of Shovelnose Snakes (Shovelnose Snakes =  $84 \pm 14$  s, Lyre Snakes =  $153 \pm 26$  s,  $F_{1,88} = 4.90$ ,  $P = 0.03$ ). However, lizards responded similarly to filter pads from mouse-fed and lizard-fed Lyre Snakes (mouse-fed Lyre =



**Fig. 3.** Mean amount of time *X. henshawi* spent investigating filter pads containing chemical cues from different predators. Planned comparisons showed a significant difference between the aggregate of the snake treatments and the blank control ( $F_{1,134} = 7.05$ ,  $P = 0.009$ ), and a significant difference between the Shovelnose Snake treatment and the aggregate of Lyre Snake treatments ( $F_{1,88} = 4.90$ ,  $P = 0.03$ ), but no difference between Lyre Snake treatments ( $F_{1,43} = 0.32$ ,  $P = 0.58$ ). Bars represent average  $\pm$  SE.

163 $\pm$ 43 s, lizard-fed Lyre = 143 $\pm$ 28 s,  $F_{1,43} = 0.32$ ,  $P = 0.58$ ; Fig. 3).

Movement rate data were transformed to the 1/6<sup>th</sup> power to meet assumptions of normality and heterogeneity of variance. During the subset of time movement was monitored, lizards moved, on average, 0.19 $\pm$ 0.01 cm/s. Neither treatment, sex, nor their interaction were significant factors affecting movement rate (treatment  $F_{3,129} = 0.44$ ,  $P = 0.72$ ; sex  $F_{1,48} = 1.81$ ,  $P = 0.18$ ; interaction  $F_{3,129} = 0.88$ ,  $P = 0.45$ ). Lizards exhibited an average retreat score of 2.1 $\pm$ 0.1, and retreats from the pad were not significantly different by treatment, sex, nor their interaction (treatment  $\chi^2 = 2.60$ ,  $df = 3$ ,  $P = 0.46$ ; sex  $\chi^2 = 0.25$ ,  $df = 1$ ,  $P = 0.62$ ; interaction  $\chi^2 = 0.13$ ,  $df = 3$ ,  $P = 0.99$ ). Additionally, lizards exhibited an average escape score of 1.8 $\pm$ 0.1, and escape behavior was not significantly different by treatment, sex, nor their interaction (treatment  $\chi^2 = 6.39$ ,  $df = 3$ ,  $P = 0.09$ ; sex  $\chi^2 = 1.05$ ,  $df = 1$ ,  $P = 0.30$ ; interaction  $\chi^2 = 3.28$ ,  $df = 3$ ,  $P = 0.35$ ).

**Conspecific experiment.**—Data transformations for continuous variables were as described in predator experiment above. In the experiment with conspecific chemical cues, neither treatment, sex, nor their interaction were significant factors affecting latency to enter shelter (treatment  $F_{2,92} = 0.98$ ,  $P = 0.38$ ; sex  $F_{1,48} = 1.88$ ,  $P = 0.18$ ; interaction  $F_{2,92} = 1.91$ ,  $P = 0.15$ ; average latency to enter shelter = 17.5 $\pm$ 1.5 min), distance moved (treatment  $F_{2,92} = 1.14$ ,  $P = 0.33$ ; sex  $F_{1,48} = 1.26$ ,  $P = 0.27$ ; interaction  $F_{2,92} = 0.41$ ,  $P = 0.66$ ; average distance moved = 118 $\pm$ 8 cm), time spent investigating the pad (treatment  $F_{2,92} = 0.67$ ,  $P = 0.51$ ; sex  $F_{1,48} = 0.08$ ,  $P = 0.77$ ; interaction  $F_{2,92} = 0.34$ ,  $P = 0.72$ ; average time investigating pad = 75 $\pm$ 8 s), movement rate (treatment  $F_{2,92} = 0.07$ ,  $P = 0.93$ ; sex  $F_{1,48} = 0.01$ ,  $P = 0.97$ ; interaction  $F_{2,92} = 2.64$ ,  $P = 0.08$ ; average movement rate = 0.18 $\pm$ 0.01 cm/s), or retreats from the pad (treatment  $\chi^2 = 0.42$ ,  $df = 2$ ,  $P = 0.81$ ; sex  $\chi^2 = 0.01$ ,  $df = 1$ ,  $P = 0.99$ ; interaction  $\chi^2 = 0.52$ ,  $df = 2$ ,  $P = 0.77$ ; average retreat score = 1.6 $\pm$ 0.08). For escape behavior, neither treatment nor the interaction between treatment and sex was significant (treatment  $\chi^2 = 0.14$ ,  $df = 2$ ,  $P = 0.93$ ; interaction  $\chi^2 = 0.24$ ,  $df = 2$ ,  $P = 0.89$ ), but females exhibited higher levels of escape behavior than males (average escape

score of females = 1.7 $\pm$ 0.2, males = 1.2 $\pm$ 0.09,  $\chi^2 = 5.15$ ,  $df = 1$ ,  $P = 0.02$ ).

## DISCUSSION

**Predator experiment.**—We found that, compared to blank control trials, Granite Night Lizards exposed to the scent of snakes took longer to enter the shelter, explored the arena more, and spent longer assessing scented filter pads. Thus, it is clear that Granite Night Lizards can use chemosensory cues to detect snakes. We also found some support for the ability of Granite Night Lizards to discriminate among predatory and non-predatory snakes, given that they spent more time investigating filter pads imbued with the scent of Lyre Snakes compared to Shovelnose Snakes. However, our results do not support the hypothesis that the diet of the predator plays a strong role in this assessment, as we found no significant difference among the Lyre Snake treatments (Lyre Snakes fed lizards versus Lyre Snakes fed mice).

Granite Night Lizards may not use diet-derived cues to discriminate among predators and instead may exhibit a generalized anti-predator response to chemical cues from snakes. Previous research has shown that other lizards respond in this fashion towards snake scents regardless of diet (Bealor and Krekorian, 2002). This generalized response may be more appropriate for species eaten by generalist predators, in that a generalist snake that could eat a small mammal might also readily consume lizards if given the opportunity. As Lyre Snakes are known to eat lizards as well as occasionally mice, a generalized response to chemical cues from Lyre Snakes (regardless of diet) may be adaptive (Webb et al., 2009, 2010a). It is also possible that Granite Night Lizards did not exhibit stronger anti-predator responses to Lyre Snake chemical cues in our study because they had visual information available that indicated no snake was actually present; for example, Pike et al. (2010) found Velvet Geckos use visual cues to avoid predatory centipedes that can be present in their preferred rock crevice microhabitat.

Another possibility is that Granite Night Lizards do use diet-based cues to assess predation risk, but the assessment is more specific than our diet treatment could reveal. We fed Lyre Snakes non-xantusiid lizards (commercially available anoles and geckos) due to logistical constraints on collecting large enough numbers of Granite Night Lizards for snake food. However, experiments in other taxa have shown that diet-based predator discrimination can be specific to the species of prey being ingested (Pillay et al., 2003; Sullivan et al., 2004). If Lyre Snakes had been maintained on a diet of xantusiid lizards, Granite Night Lizards may have reacted more strongly during experimental trials.

Our findings of increased responsiveness to snake chemosensory cues are generally similar to past studies on other lizard species, but direct comparisons are difficult given the wide variation in methodology and species tested. We have reviewed the available literature on the ability of lizards to discriminate among snake predators based on chemical cues in Table 2, classifying each study with respect to the lizard species tested, snake species tested, snake diets (if known), methodology, and results. Note that this table incorporates only studies with multiple species of snakes (predators versus non-predators) and does not include studies with single snake species or non-snake predators that are also conceptually relevant (e.g., Labra and Niemeyer, 2004; Lloyd et al., 2009).

**Table 2.** Summary of findings from studies assessing the responses of lizard species to chemical cues from predatory snakes.

Lizard species	Snake species (degree of risk)	Methodology	Snake diet	Snake sample size	Discrimination	Lizard response	Citation
<i>Pseudemoia entrecasteauxii</i>	<i>Drysdalia coronoides</i> (High) <i>Pseudechis porphyriacus</i> (Low) <i>Rhinoplocephalus nigrescens</i> (Low)	Scented shelter	Unknown	1 of each species	Yes	Stronger avoidance of riskiest snake	Stapley, 2003
<i>Plestiodon laticeps</i>	<i>Lampropeltis getulus getulus</i> (High) <i>Lampropeltis triangulus elapsoides</i> (High) <i>Heterodon platyrhinos</i> (Low)	Cotton applicator	Unknown	1 of each species	Yes	Significantly more tongue flicking towards high risk snake scents compared to control and low risk snake	Cooper, 1990
<i>Plestiodon okadae</i>	<i>Elaphe quadringata</i> (High) <i>Rhabdophis subminiatus</i> (Low)	Cotton applicator	Unknown	Unknown	Yes	Lizards sympatric with snake predators exhibit more tail displays and less tongue flicks to predatory snakes	Mori and Hasegawa, 1999
<i>Coleonyx brevis</i>	<i>Hypsigena torquata</i> (High) <i>Sonora semiannulata</i> (Low) <i>Gyalopion canum</i> (Low) <i>Phyllorhynchus decurtatus</i> (High)	Cotton applicator	Unknown	2–4 of each species	Yes	More tail displays and buccal pumping to sympatric predator <i>H. torquata</i> ; no tail displays to allopatric predator <i>P. decurtatus</i>	Dial and Schwenk, 1996
<i>Coleonyx variegatus</i>	<i>Phyllorhynchus decurtatus</i> (High) <i>Chionactis occipitalis</i> (Low)	Cotton applicator	Unknown	>1 per species	Yes	Defensive attacks, tail displays and tail displays with flight only occurred towards scent of high risk snake	Dial et al., 1989
<i>Hemidactylus frenatus</i>	<i>Acanthophis antarcticus</i> (High) <i>Antaresia maculosa</i> (High) <i>Boiga irregularis</i> (High) <i>Pseudechis colletti</i> (Low)	Scented shelter	Unknown	2 of each species	No	Avoided all snake species	Cisterne et al., 2014
<i>Gehyra dubia</i>	<i>Acanthophis antarcticus</i> (High)	Scented shelter	Unknown	2 of each species	No	No avoidance of any snake species	Cisterne et al., 2014

Table 2. Continued.

Lizard species	Snake species (degree of risk)	Methodology	Snake diet	Snake sample size	Discrimination	Lizard response	Citation
<i>Oedura lesueurii</i>	<i>Antaresia maculosa</i> (High) <i>Boiga irregularis</i> (High) <i>Pseudechis colletti</i> (Low) <i>Hoplocephalus bungaroides</i> (High) <i>Acanthophis antarcticus</i> (High) <i>Cryptophs nigrescens</i> (Moderate) <i>Demansia psammophis</i> (Moderate) <i>Vermicella annulata</i> (Low) <i>Cacophis squamulosus</i> (Medium) <i>Hemiaspis signata</i> (Low)	Scented pad	Not fed while in captivity	8 <i>H. bungaroides</i> 4 <i>A. antarcticus</i> 8 <i>C. nigrescens</i> 4 <i>D. psammophis</i> 8 <i>V. annulata</i> 4 <i>C. squamulosus</i> 3 <i>H. signata</i>	No	Geckos displayed anti-predator behaviors to all snakes	Webb et al., 2009
<i>Oedura lesueurii</i>	<i>Hoplocephalus bungaroides</i> (High) <i>Rhinoplocephalus nigrescens</i> (Low)	Scented pad	Not fed while in captivity	2 of each species	Yes (and no)	Geckos displayed anti-predator behaviors to all snakes	Webb et al., 2010a
<i>Oedura lesueurii</i>	<i>Hoplocephalus bungaroides</i> (High) <i>Rhinoplocephalus nigrescens</i> (Low)	Scented shelter	Live skinks	13 <i>H. bungaroides</i> 10 <i>R. nigrescens</i>	No	Geckos avoided shelters scented by both snake species	Downes and Shine, 1998
<i>Oedura lesueurii</i>	<i>Hoplocephalus bungaroides</i> (High) <i>Rhinoplocephalus nigrescens</i> (Low)	Scented shelter	Live skinks	4 of each species of high risk snakes, 1 <i>Leptotyphlops</i>	Yes	Significantly higher rate of locomotion when exposed to high risk scent, significant increase in tongue flick rate towards high risk snakes, latency of tongue flick was significantly reduced towards high risk scent	Webb et al., 2010b
<i>Aspidoscelis dixonii</i>	<i>Masticophis flagellum</i> (High)	Scented shelter	<i>Mus musculus</i> or <i>Anolis sagrei</i>				Punzo, 2007

Table 2. Continued.

Lizard species	Snake species (degree of risk)	Methodology	Snake diet	Snake sample size	Discrimination	Lizard response	Citation
<i>Lacerta vivipara</i>	<i>Masticophis taeniatus</i> (High)	Behaviors observed in predator/control cages	Unknown	1 of each species	Yes	Extensive use of slow walk, tail vibrations, and food shaking in cages containing high risk scent	Thoen et al., 1986
	<i>Arizona elegans</i> (High)						
	<i>Leptotyphlops humilis</i> (Low)						
	<i>Vipera berus</i> (High)						
	<i>Coronella austriaca</i> (High)						
<i>Natrix natrix</i> (Low)							
<i>Lacerta bedriagae</i>	<i>Coluber viridiflavus</i> (High)	Behaviors observed in predator/control cages	<i>C. viridiflavus</i> fed young mice <i>N. maura</i> fed fish	1 of each species	No	Tongue flick rate was the same for both snakes, but significantly more than controls	Van Damme and Quick, 2001
	<i>Natrix maura</i> (Low)						
<i>Podarcis tiliguerta</i>	<i>Coluber viridiflavus</i> (High)	Behaviors observed in predator/control cages	<i>C. viridiflavus</i> fed young mice	1 of each species	Yes	Tongue flick rate was higher for high risk snakes than the low risk snake	Van Damme and Quick, 2001
	<i>Natrix maura</i> (Low)		<i>N. maura</i> fed fish				
<i>Podarcis sicula</i>	<i>Coluber viridiflavus</i> (High)	Behaviors observed in predator/control cages	<i>C. viridiflavus</i> fed young mice	1 of each species	Yes	Tongue flick rate was higher for high risk snakes than the low risk snake	Van Damme and Quick, 2001
	<i>Natrix maura</i> (Low)		<i>N. maura</i> fed fish				
<i>Podarcis muralis</i>	<i>Coronella austriaca</i> (High)	Cotton applicator	Unknown	1 of each species, except 2 of <i>C. austriaca</i>	Yes	Significantly more tongue flicking towards high and "medium" risk snake scents, compared to controls and low risk snake	Amo et al., 2004
	<i>Malpolon monspessulanus</i> (High)						
	<i>Elaphe scalaris</i> (Medium)						
	<i>Natrix maura</i> (Low)						
<i>Dipsosaurus dorsalis</i>	<i>Lampropeltis californica</i> (High)	Behaviors observed in predator/control cages	<i>L. californica</i> fed neonatal mice <i>C. occipitalis</i> fed crickets and mealworms	3 <i>L. californica</i> , 6 <i>C. occipitalis</i>	Yes	TF not significantly different between snakes (but between controls), significant change in posture and behavior was noted in cages with scent of <i>L. californica</i> compared to other samples	Bealor and Krekorian, 2002
	<i>Chionactis occipitalis</i> (Low)						



The degree to which lizards discriminate among snake species based on chemical cues is variable (Table 2). For some lizards the species of snake has been found to be an important predictor of lizard response; other species seem to show generalized responses to all snakes. At least 12 species of lizard that have been shown to use chemical cues to discriminate among snake species (see Table 2 for citations). In contrast, four species were not found to exhibit stronger responses to the more saurophagous snake species (Van Damme and Quick, 2001; Webb et al., 2009; Cisterne et al., 2014). This variation may be due in part to how specialized the snake is as a predator, but it also may reflect differences in the threat sensitivity of different lizard populations or species (i.e., through adaptation to different levels of predation pressure). It is also possible that differences in methodology between these studies play a strong role. For example, studies by Webb et al. (2009, 2010a) found that Velvet Geckos exhibited similar anti-predator responses to a range of snakes that varied in the degree to which they were saurophagous. In a shelter choice experiment of the same species by Downes and Shine (1998), populations sympatric with both saurophagous (*Hoplocephalus bungaroides*) and non-saurophagous (*Rhinoplocephalus nigrescens*) snakes avoided shelters scented by saurophagous snakes, but not those scented by non-saurophagous snakes. Webb et al. (2009) suggested this discrepancy may be in part due to differences in the number of experimental snakes used to provide chemical cues, as earlier studies had relied on only two snakes. In support of this notion, Webb et al. (2010b) found Velvet Geckos equally avoided shelters scented by both *H. bungaroides* and *R. nigrescens* when multiple snakes (>10) were used to provide predator scent.

Other researchers have speculated that different lizard populations will vary in how they assess threat. House geckos native to northwestern Australia did not avoid shelters scented by sympatric snake species, whereas invasive Asian house geckos did (Cisterne et al., 2014). Cisterne et al. (2014) interpreted this pattern as evidence that the native species is more accurate in assessing threat from native predators and requires information beyond residual chemical cues to avoid shelter.

Given the diversity of studies examining lizard responses to predator chemical cues, we found it striking that the role of predator diet remains largely unexamined, as most past studies using snakes as scent donors do not indicate the maintenance diet of snake subjects (Table 2). We suggest that diet of snakes donating chemical cues be an important design consideration in future experiments of this type. This area of research would also benefit from more taxonomic diversity, as most studies have been conducted on lacertids and gekkonids (Table 2).

**Conspecific experiment.**—Lizards did not exhibit any overt behaviors in response to chemical cues from stressed conspecifics, indicating that they may not typically use chemical cues from conspecifics as a source of information about predation risk. However, it is also possible that the way in which we obtained conspecific chemical cues was not conducive to evaluation in this context. Studies of other taxa often use more robust conspecific chemical cues, such as chemicals derived from direct physical attacks or macerated prey tissue (Marvin and Hutchison, 1995; Lampe et al., 2011). Future experiments with lizards could simulate a physical attack by pinning and pinching donor lizards on

the filter pad, as in Lampe et al. (2011). Although macerated skin samples are often used as a source of conspecific alarm cues (Marvin and Hutchison, 1995; Brown and Godin, 1997), because snakes ingest their prey whole we felt the use of macerated tissues would not be ecologically relevant for our study system. We also note that many other studies have isolated chemical cues from conspecifics using methodology similar to ours. Such studies have found that territorial lizards can use chemical cues to avoid occupied territories or shelters or identify unfamiliar conspecifics (Alberts and Werner, 1993; Steele and Cooper, 1997; Aragón et al., 2001; Lopez and Martin, 2001). Chemical cues in these studies are related to body size, coloration, and fluctuating asymmetry, indicating that conspecifics may be able to obtain reliable information on a variety of morphological and physiological attributes from chemical cues alone (Aragón et al., 2001; Lopez et al., 2006). Hence, we believe it is feasible that some lizard species may use conspecific cues as a source of information about predators, even though we found no evidence for this in Granite Night Lizards.

In our analysis of the conspecific chemosensory trials only one behavioral factor was shown to be significant, which was the number of escapes. Escape behavior was higher in females than males and did not depend on experimental treatment. This finding indicates that females, in general, might be slightly more stressed in novel environments, such as testing arenas, than males. This corresponds with the findings of previous studies that show that males of many species may exhibit less risk avoidance than females (Kissner et al., 1997; Lailvaux et al., 2003; Frommen et al., 2009).

**Video tracking software.**—We used video tracking software in our analysis of lizard anti-predator behavior. Until recently, behavioral studies of this type have relied extensively on observations recorded during trials or post-trial video evaluation. These evaluations generally focus on count data and have not incorporated factors such as total distance traveled and movement rate. We found video tracking software to be a useful tool in quantifying these behaviors. In the herpetological literature, the use of video tracking software is rare, although it is gaining traction with other taxa. Kane et al. (2004) used video tracking software to quantify behavioral changes in fish exposed to sub-lethal levels of toxins (MS222). Salierno et al. (2008) also used video tracking software in order to do a quantitative movement analysis of the social Mummichog. Our use of video tracking software allowed us to show that the total amount of distance moved by lizards varies across experimental treatments.

**Sex differences.**—In studies of the chemical cues used by squamates to assess predation risk, most studies have not examined the effect of sex on prey species response (Van Damme and Quick, 2001; Bealor and Kerkorian, 2002; Amo et al., 2004) or have only examined the responses of one sex (females: Downes and Bauwens, 2002; males: Stapley, 2003). Studies examining chemical cue detection differences by sex in squamates have been conducted almost exclusively in the context of conspecific detection and assessment, and not predation risk. Studies that have included gender as a factor in the analysis have often found sex differences. Bofill and Lewis (1999) found that in the teiid lizard (*Ameiva exsul*) males were significantly more likely to respond to chemical

cues left by females than by other males. They did not find any notable difference in the females' reactions to males or females. Duvall et al. (1980) observed the same pattern of significant reaction by males to female scent, but no other combination. Had the Granite Night Lizards been exposed to the scent of opposite sex conspecifics, we might have expected a similar response, simply due to investigation of potential mates. Because we wanted to elicit responses to stress, we chose to remove gender as a potentially confounding factor. Although females were significantly more likely to try to escape regardless of the treatment in the conspecific experiment, neither gender responded strongly to conspecific chemical cues.

Although we did not find gender differences in responses to predator chemical cues, such differences have been found in other taxa, including other reptiles (Lailvaux et al., 2003; Vanhooydonck et al., 2007; Noble et al., 2012), fishes (Matity et al., 1994; Frommen et al., 2009), and small mammals (Swaigood et al., 2003). Generally, females will exhibit less risky behaviors, and when presented with an active predator will often depend more on crypsis versus fleeing to avoid detection (Kissner et al., 1997; Lailvaux et al., 2003; Frommen et al., 2009).

**Conclusions.**—Currently, very little is known about the potential for squamate reptiles to use predator diet as a source of information when assessing predator-derived chemical cues. Our experiments showed that Granite Night Lizards are able to assess chemical cues from predatory snakes and use them to modify their space use and behavior, but we found no evidence that the diet of the predator may be an important factor in these decisions. Future research should use predators that feed on conspecifics, rather than on broadly similar taxa (i.e., snake predators that have eaten Granite Night Lizards, rather than geckos and anoles). We also examined the potential use of chemical cues from conspecifics to assess predation risk using the same methodology and behavioral measures as in our examination of predator chemical cues. We found no significant differences in the behavior of lizards exposed to chemical cues of conspecifics that had been exposed to a simulated predator attack. Thus, direct assessment of predation risk through predator chemical cues appears to be more important than indirect assessment of predation risk through conspecific chemical cues. Future studies could employ more active simulation of predation to continue to evaluate if conspecific alarm cues could be an important source of information regarding risk assessment.

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