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Evidence of airborne chemoreception in the scorpion *Paruroctonus marksi* (Scorpiones: Vaejovidae)

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Abstract. Chemically induced predator avoidance behaviors exist in many arthropods. In this paper, we examined the behavioral responses of the desert scorpion, *Paruroctonus marksi* (Haradon, 1984), to airborne chemical cues from a natural predator, the larger scorpion *Hadrurus arizonensis* (Ewing, 1928). We used a Y-shaped, dual-choice olfactometer to test for avoidance behavior in the presence of a known predator, *H. arizonensis*. Prior to this study there has been little research done on chemically induced predator avoidance behaviors in scorpions. The results of this study suggest that *P. marksi* is capable of detecting a predator's airborne cues, though the nature and identity of these cues remain unknown, and it appears that the constellation array of the fixed finger does function in detecting these cues. We also discuss the importance of adaptive predator avoidance behaviors.

Keywords: Arachnid, arthropod, kairomone, pheromone, Y-tube olfactometer

Prey organisms demonstrate a variety of adaptations to defend themselves from predators. These adaptations can include morphological (e.g., spines and armor), biochemical (e.g., repellents, toxins, and resistance to these), behavioral (e.g., fleeing), or life history-based (e.g., delayed hatching) traits. Due to the unforgiving nature of predation, prey organisms are under strong selection to detect and avoid predators (Lima & Dill 1990; Lima 1998a,b). Early detection and recognition of predation risk represent important adaptations of predator avoidance. Thus, an organism will benefit from the use of multiple sensory inputs, including visual, tactile, and chemical cues.

Chemically mediated behaviors that reduce predation risk have received considerable attention among diverse taxonomic groups (for detailed reviews see Kats & Dill 1998; Dicke & Grostal 2001). The majority of studies have documented chemically mediated antipredator behaviors in aquatic organisms, with fewer focusing on terrestrial vertebrates (Hay 2009; Ferrari et al. 2010). Avoidance is often seen when prey are given a choice between an area that contains a predator, or cues of its presence, versus an empty area.

Arthropod prey species can perceive the chemical cues of a potential predator from either direct or indirect sources (Dicke & Grostal 2001). Direct chemical cues produced by the predator (kairomones) can be recognized by the prey. These cues derive from eggs, excreta, pheromones, and other byproducts that a prey animal can detect (Nolte et al. 1994; Hoffmeister & Roitberg 1997; Grostal & Dicke 2000; Dicke & Grostal 2001). In scorpions, Miller and Formanowicz (2010) demonstrated that male *Paruroctonus boreus* (Girard, 1854) significantly avoided areas exposed to direct cues from conspecific males. Indirect cues do not come from the predator itself, as they originate from injured or dead conspecifics (Chivers & Smith 1998; Huryn & Chivers 1999; Hoefler et al. 2012). To date, no study has demonstrated that scorpions can use indirect cues.

Scorpions can perceive their environment using multiple sensory systems. In addition to vision, which is well-developed and allows for image formation and identifying subtle changes in light magnitude (Schliwa & Fleissner 1980; Fleissner & Fleissner 2001), scorpions possess an assortment of mechano- and chemoreceptors that provide them with relevant information. For example, trichobothria react to horizontal air streams and possess directional sensitivity (Hoffman 1967). These or other structures might also facilitate detection of substrate vibrations (Brownell & Farley 1979a,b,c; Brownell & van Hemmen 2001). Pectines appear to be involved in chemically-mediated orientation behaviors such as mate recognition and possibly localization of water (Gaffin & Brownell 1992; Gaffin et al. 1992). Fingers of the pedipalps possess a constellation-shaped microscopic array of sensilla that are thought to be involved with chemoreception (Fet et al. 2006a,b).

Chemoreception is well developed in scorpions, but much remains to be learned about the structures, contexts, and behaviors involved. Several studies suggest that male scorpions can use substrate-borne pheromones to locate females (Gaffin & Brownell 1992; Melville et al. 2003; Taylor et al. 2012), but in the only study that examined airborne chemical transmission, males of *Centruroides vittatus* (Say, 1863) showed no tendency to move toward the female, though they responded when they contacted substrate-borne female deposits (Steinmetz et al. 2004). To demonstrate the role of pedipalps in chemoreception, Abushama (1964) offered fivekeeled gold scorpions (*Leiurus quinquestriatus* Hemprich & Ehrenberg, 1829) a choice between a compartment treated with various chemicals (chemical in petri dish) and an untreated compartment (empty petri dish). The scorpions moved away from most treated areas, and selected compartments that were either scent free or had the odor of cockroach (*Periplaneta americana*) prey. However, when the pedipalps (pincers) were painted over, the scorpions demonstrated reduced sensitivity to chemical odors. Abushama (1964) hypothesized that small hairs distributed over the pedipalps might be responsible for detecting airborne chemicals, but no further studies were conducted to support this claim. Fet et al. (2006a,b) subsequently described a constellation-shaped microscopic array of sensilla on the distal external portion of the fixed finger of the pedipalp in several scorpion species

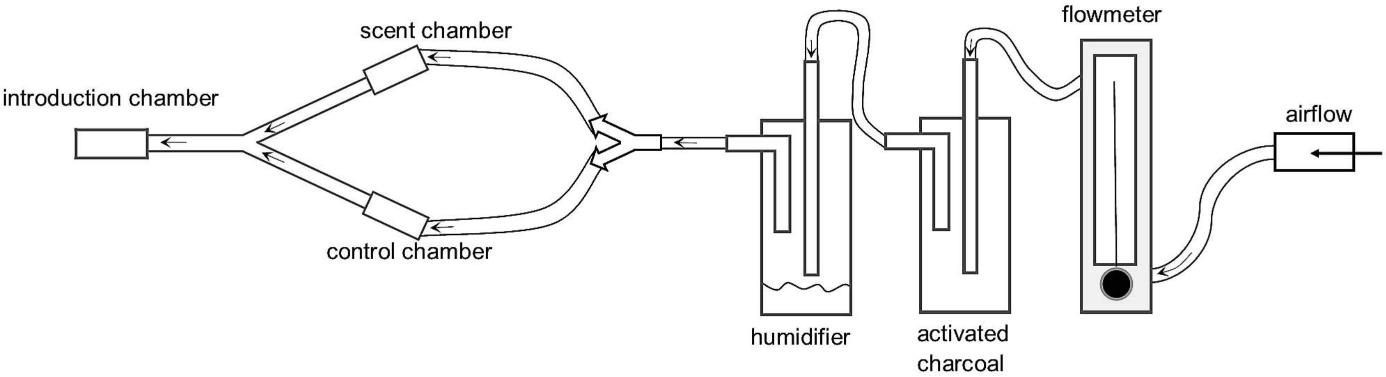

Figure 1.—Schematic of the glass Y-tube olfactometer used to test the response of adult *Paruroctonus marksi* scorpions to volatiles of *Hadrurus arizonensis* (predator). Test subjects were placed into the Introduction chamber from which they locomoted to the Y-intersection and then selected a Y-arm to enter. Arrows indicate the direction of airflow. See Methods for dimensions and further explanation.

(including *Paruroctonus*), and suggested that these structures serve a chemosensory role.

The purpose of the present study was to test two hypotheses. First, we hypothesized that the scorpion *Paruroctonus marksi* (Haradon, 1984) can detect the presence of a known scorpion predator (*H. arizonensis* (Ewing, 1928)) using airborne predator-derived chemical cues. We used a Y-tube olfactometer that provided simultaneous discrimination between two chemical environments, and quantified ambulatory behaviors that might be associated with the sampling of the airborne chemicals. Second, we hypothesized that constellation array sensilla on the pedipalp fingers are used to detect chemicals.

METHODS

Research animals.—We collected all specimens of *P. marksi* (mean prosoma and mesosoma combined 1.35 ± 1.19 cm) and *H. arizonensis* (3.5 cm) scorpions (all adult females) during mid-July and August at a single location in Lancaster, California (34°38′36” N, 118°11′38” W), using UV light. We used a single *H. arizonensis* (predator) for all trials. We housed *P. marksi* scorpions individually in clear plastic containers measuring 13 x 12 x 10 cm (L x W x H), and *H. arizonensis* in a 31 x 19 x 12 cm clear plastic container, with all containers having a sand substrate and a wet sponge. Scorpions were kept at 21–23°C and 55–60% relative humidity under a 12:12 h light:dark cycle. Scorpions were fed an appropriate-sized cricket once a week.

Olfactometer.—We examined the olfactory responses of *P. marksi* toward predator (*H. arizonensis*) odors using a Y-shaped glass tube olfactometer (3 cm inner diameter) with a long (11 cm) introduction arm and two short (7 cm) “choice” arms (Fig. 1). The angle between the two short arms was 65°. An introduction glass chamber (5 cm long with diameter of 2 cm) and two scent source glass chambers (11 cm long with diameter of 2 cm) were attached to the proximal end of the introduction tube and the distal ends of the choice arms, respectively; a fine mesh was located at 8 cm where the scent (marble, predator, or crickets) was placed behind it. The chambers could be disassembled for cleaning between trials. Airflow (250 ml/min) generated by the laboratory’s pressurized air system was purified via passage through activated charcoal (6–14 mesh) and then humidified to carry airborne chemicals more efficiently by passage through a bottle containing deionized water before entering the scent source chambers at the distal ends of the two choice arms. Before conducting the experiment, we visualized the airflow using dry ice in water to ensure that there was negligible air mixing at the Y-junction of the long arm of the olfactometer.

Behavioral assays.—For each trial, we first set up the two scent source chambers and turned on the airflow. Next, we placed a single specimen of *P. marksi* into the introduction chamber and connected the chamber to the proximal end of the long arm. The scorpion was then given 5 minutes to ambulate toward the Y junction and choose which arm to enter. If the scorpion remained in the long arm, it was recorded as No Response. Upon entering either of the short arms, the scorpion was given 1 additional minute before the choice was recorded. The test scorpions were small enough that they could turn around in the tubes, so if the scorpion entered an arm and then exited within the 1 minute time frame, the behavior was recorded. Two scorpions that showed No Response (did not leave the introduction chamber or stayed motionless in the long arm) were retested 10 days later. In addition to recording the choice of arms entered, we also noted the behavior exhibited by the scorpions.

Trials were conducted between the hours of 1900 and 2100 in a dimly lit room. To minimize the effect of any directional bias, we alternated the odor conditions of the right and left arms every three trials. In a supplemental trial, we confirmed the absence of a directional bias in 13 scorpions tested with both chambers empty (binomial test: $P = 1.00$). The scent chambers and Y-tube were cleaned with isopropyl alcohol and deionized water between trials.

Experiment 1.—We conducted two sets of trials to test whether *P. marksi* avoided the odors of a scorpion predator. For the predator scent trials, we placed a scorpion predator (*H. arizonensis*) in one scent source chamber and left the other chamber empty as a control. The *H. arizonensis* in the scent chamber was immobile and could not be seen through the fine mesh, thereby eliminating visual cues. We then tested the behavioral choices of 25 *P. marksi* scorpions. Because the scorpions might respond to non-chemical cues of the predator, such as altered airflow, we repeated the experiment with another 21 *P. marksi* scorpions, but substituted a presumably

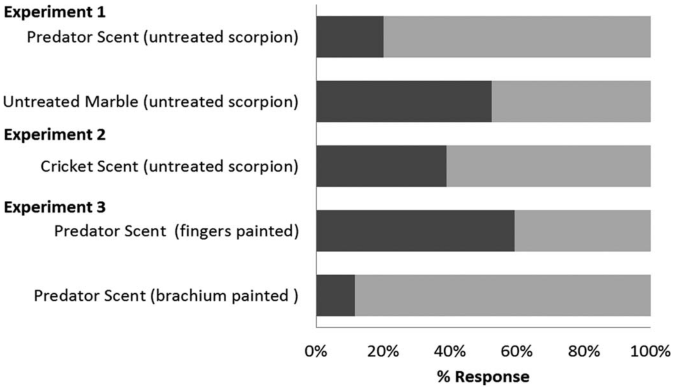

Figure 2.—Response of *Paruroctonus marksi* scorpions to various treatment groups in the Y-tube olfactometer. The light and dark areas of each bar represent, respectively, the percentage of scorpions that selected the arm containing a control odor (empty chamber) or an odor source (live *Hadrurus arizonensis* scorpion as a predator or a marble as a control). In Experiment 1 the scorpions avoided the predator scent odor but not the marble (control) while in Experiment 2 there was no significant response to Cricket odor, suggesting use of chemoreception for predator avoidance. In Experiment 3 the scorpions with sensilla-free brachium of the pedipalps painted over (as a control) avoided the predator scent, whereas those with the sensilla-bearing fingers of the pedipalps painted over showed no avoidance, suggesting a role a chemoreception for the sensilla of the pedipalp fingers.

chemically inert object, a glass marble (about 14 mm), in place of the predator odor. The presence of the *H. arizonensis* and marble did not disrupt airflow into the olfactometer.

Experiment 2.—We conducted 18 trials to test whether *P. marksi* responded to the non-predator odors (crickets). Each trial was conducted as described above with 5 crickets placed in the scent chamber. The presence of the crickets did not disrupt airflow into the olfactometer.

Experiment 3.—We conducted two more sets of trials to determine whether the constellation array of *P. marksi* plays a role in detecting predator odors. In the first trial, we tested 26 *P. marksi* with the aforementioned predator versus control conditions (Experiment 1) after painting the fingers of their pedipalps (Treated group) with non-toxic nail polish. We assumed this treatment impeded chemical detection of the predator scent. We then repeated the trial with another 26 scorpions having only the brachium (first segment before the chela) painted (Control group). No mortality was seen in the nail polish painted scorpions.

Data analysis.—For each experiment, we conducted a 2 × 2 (trial × choice) chi-square test (Zar 1996) to determine whether *P. marksi* choices were non-random. But for experiment 2, we conducted a 2 × 3 chi-square test. We computed phi (φ) as a measure of effect size, with values of $\sim$0.1, $\sim$0.3, and $\geq$0.5 deemed as small, medium, and large effects, respectively (Cohen 1988). We then tested simple main effects with a binomial test (Zar 1996). We used SPSS 13.0 for Windows (SPSS Inc, Chicago, IL, USA) with alpha set at 0.05.

RESULTS

Experiment 1.—The two trials testing predator scent and an airflow control yielded contrasting results ($\chi^2 = 5.28$, df = 1, asymptotic $P = 0.022$, $\varphi = 0.34$). Thus, the scorpions responded differently to the cues of a predator and an inanimate object. Scorpions given the choice between the scent of a predator versus no odor avoided the predator scent by selecting the arm of the control chamber (80.0%, $n = 25$, binomial asymptotic $P = 0.004$; see Fig. 2), whereas those given the choice between the marble versus no odor selected the arm of the control chamber at random (52.0%, $n = 21$; binomial asymptotic $P = 1.00$; Fig. 2).

Experiment 2.—There was no difference when it came to choosing between crickets (39%) versus no odor (61%) source ($n = 18$; binomial asymptotic $P = 0.48$; Fig. 2). Although experiment 2 was run separately from experiment 1, it was done in an identical manner, so we combined the trial to those of experiment 1 to run a 2 × 3 chi-square test, which showed contrasting results ($\chi2 = 8.58$, df =2, $P = 0.014$, $\varphi = 0.37$). Therefore, the scorpions responded differently to the cues of a predator, a non-predator (cricket), and an inanimate object.

Experiment 3.—The two trials testing sensory deprivation and its control likewise yielded contrasting results ($\chi^2 = 13.12$, df = 1, asymptotic $P < 0.001$, $\varphi = 0.50$). Thus, the scorpions responded differently depending on which portion of the chelae was painted. Scorpions that had their pedipalp fingers painted exhibited no predator avoidance (40.7%, $n = 27$; binomial asymptotic $P = 1.00$; Fig. 2), whereas control scorpions that had their brachium painted exhibited predator avoidance by preferentially selecting the arm of the control chamber (88.5%, $n = 26$; binomial asymptotic $P < 0.001$; Fig. 2).

Behavioral observations.—In all trials after a short pause in the introduction chamber, the scorpions slowly walked through the long arm of the Y-tube. Walking was interrupted with intermittent pauses before reaching the Y-junction. While traveling in the long arms, the scorpions repeatedly waved their pedipalps up and down. When the scorpions paused, the pedipalps were either kept in the up or down position until locomotion resumed. These behaviors were observed in all the trials regardless of scorpions being treated (painted or not) and type of odor source used. The scorpions that selected the side containing the predator generally exhibited a typical defensive posture with the metasoma arched above the body. In the trials in which scorpions selected the marble, empty, or cricket chambers, none of the scorpions exhibited a defensive posture and assumed a resting posture with the body resting low and legs withdrawn.

DISCUSSION

The results of this study suggest that *P. marksi* is capable of detecting a predator's airborne cues, though the nature and identity of these cues remain unknown. However, it is logical to conclude that airborne chemical cues may play a role in predator avoidance in this scorpion. Furthermore, the data suggest that the constellation array of *P. marksi* may play a role in allowing these scorpions to detect predator's airborne cues. We acknowledge that more studies, especially neuroethological studies, might shed more light on scorpion's use of airborne cues in avoiding redators.

Due to high densities, scorpions comprise an important food source for diverse predators. Polis et al. (1981) documented that the predators of scorpions were mainly other scorpions, followed by vertebrates and other invertebrates. Among scorpions, *H. arizonensis* is a frequent intraguild predator, with 30% of its diet composed of scorpions (Polis & McCormick 1987). Additional studies have also demonstrated that scorpion-scorpion predation is very common (Polis 1979; Polis & McCormick 1987). Therefore, being able to detect scorpion and other potential predators should feature prominently in the above-ground foraging behavior of scorpions.

Many studies have shown that the nature of chemical cues from predators can depend on the identity of the prey that is consumed (Chivers & Mirza 2001; Hoefler et al. 2012). We doubt the possibility that prior meals of *H. arizonensis* would serve as an indirect cue because both scorpion species used in this study were fed crickets for two months prior to the behavioral assay. Thus, the source of the airborne cues detected by *P. marksi* likely came directly from *H. arizonensis* itself.

Recent studies suggest that scorpions can use chemical cues in conspecific avoidance (Miller & Formanowicz 2010) and mate tracking (Gaffin & Brownell 1992; Melville et al. 2003; Steinmetz et al. 2004; Taylor et al. 2012). Miller & Formanowicz (2010) demonstrated that males of *Paruroctonus boreus* in an open Y-maze avoided areas exposed to other males of the same population. Furthermore, male *P. boreus* spent significantly more time in areas that previously contained females from the same population than in areas exposed to females from different populations. Taylor et al. (2012) used cuticular extracts from female *P. utahensis* (Williams, 1968) applied to the sand of the arena floor to induce pre-courtship behavior in males, thus demonstrating the existence of female pheromones. These studies highlight the importance of substrate-borne chemical cues in mate localization by male scorpions; however, the presence of airborne chemical cues was not eliminated, though its role in mate tracking was discounted (Steinmetz et al. 2004).

When studying the response of *L. quinquestriatus* to airborne chemical cues (naphthalene, cockroaches or conspecific scorpions), Abushama (1964) reported that scorpions placed in the preference chamber performed a stereotypical movement with raised pedipalps. When the appendages were painted over, this behavioral sensitivity to chemical cues was reduced. Abushama hypothesized that the pedipalps might be used as sense organs to detect airborne cues. We observed similar behavior in the present study. When *P. marksi* scorpions traveled in the long arm of the Y-tube, they ambulated while raising their pedipalps up and down repeatedly. Furthermore, the up-and-down movement of the pedipalps was exhibited most prominently at the junction of the Y-tube, suggesting a chemosensory function.

Fet et al. (2006a,b) described a constellation-shaped microscopic array of sensilla on the distal external portion of the fixed finger of the pedipalp in several scorpion species (including *Paruroctonus*). They hypothesized that the constellation array is a chemosensory structure possibly analogous to the palpal organ and Haller's organ on tarsi I in ticks. In our study, painting of the pedipalps blocked *P. marksi* discrimination between predator and control odors, whereas painting of the brachia did not alter avoidance of the predator. Thus, our results suggest that *P. marksi* uses this constellation array of pedipalp sensilla (or a yet unidentified structure) to detect the odors of predators.

To the best of our knowledge, this study is the first demonstration of scorpions using kairomones in predator avoidance. We do not know whether *P. marksi* detected *H. arizonensis* pheromones or other yet to be identified chemicals, and thus we recognize the need for further study to identify the source and nature of these airborne chemical cues.

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