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Rachel Hermanson

Western Oregon University, hermansr@wou.edu

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**Characterization of the Female Attractiveness Pheromone in the
Red-spotted Garter Snake,
*Thamnophis sirtalis concinnus***

By

Rachel A. Hermanson

An Honors Thesis Submitted in Partial Fulfillment
of the Requirements for Graduation from the
Western Oregon University Honors Program

Dr. Michael LeMaster
Thesis Advisor

Dr. Gavin Keulks
Honors Program Director

Western Oregon University

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ABSTRACT

Pheromones are chemical cues used to communicate between individuals within a single species. Previous work with reproductive pheromones in lower vertebrates has focused on the red-sided garter snake, *Thamnophis sirtalis parietalis*. Studies have shown that this species has a female attractiveness pheromone that elicits courtship behavior in males. Chemical analysis of this pheromone suggests that the composition of the female attractiveness pheromone varies among garter snake species. This study conducted trailing experiments to investigate whether methyl ketones contained in the skin lipids of red-spotted garter snakes, *Thamnophis sirtalis concinnus*, are responsible for eliciting male trailing behavior; hypothesizing that these cues, as observed with the red-sided garter snake, serve as the sexual attractiveness pheromone for this species. Males snake were tested on a y-maze with four different treatments: 1) a blank maze, 2) trails laid down by male red-spotted garter snakes, 3) trails laid down by female red-spotted garter snakes, and 4) trails composed of methyl ketone extracts from female red-spotted garter snakes. Males were found to actively trail both female trails and methyl ketone extract trials, supporting the role of methyl ketones as the sexual attractiveness pheromone for this species.

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INTRODUCTION

Communication is crucial to the survival and reproduction of animals. Animal communication is defined as the transmission of, reception of, and response to signals; a signal is a behavior that causes a change in another animal's behavior (Campbell & Reece, 2005). Animals communicate through a variety of methods, including the use of visual, auditory, chemical, tactile, and electrical signals. The type of signal used depends on the environment and lifestyle of the animal, as well as the cost to benefit ratio of the signal used.

Signal differences based on lifestyle are observed in many different groups of animals. For example, most mammals are nocturnal and therefore use olfactory and auditory signals because these forms of communication are not affected by a lack of light. An example of this is seen in kangaroo rats, who utilize foot-drumming as a main mechanism for communication (Randall, 2001). Alternatively, diurnal animals, such as the frog *Hylodes asper*, rely mainly on visual signals such as foot slapping (Haddad & Giaretta, 1999).

The ratio of cost vs. benefit, in terms of animal fitness, also plays a key role in the type of signals that evolve. If the cost of a behavior to the animal is greater than the benefit the animal receives from the behavior, the behavior will be selected against. This ratio can be seen in the vocal sac pulsing of the European tree frog (*Hyla arborea*). Brightly colored, conspicuously pulsing vocal sacs are preferred by females but detrimental to males; the more conspicuous the pulsing, the more energy used (Gomez

et al., 2009). However, because it dramatically increases a male's probability of successfully reproducing, this mode of communication has continued despite the cost.

The most ancient form of communication is believed to be chemically based (Bradbury & Verhencamp, 1998). Chemicals that are utilized for animal communication are termed semiochemicals (Wyatt, 2003). There are three classifications of semiochemicals: kairomones, allomones, and pheromones. Kairomones and allomones are chemicals released by one species that are detected by a different species. Specifically, kairomones are chemicals produced by one species, but benefit another species when received. For example, predatory beetles use the chemical cues of bark beetles—their prey—to hunt them (Raffa & Klepzig, 1989). Alternatively, allomones function opposite this; they harm the receiving species, while increasing the fitness of the emitter. This can be seen in bolas spiders which produce a chemical cue to lure moths as prey (Stowe et al., 1987).

Unlike kairomones and allomones, pheromones are chemical cues used for communication within a single species (Karlson & Lucher, 1959). Pheromones are divided into six groups based on their primary function: aggregation and host marking, territoriality and scent-marking, social organization recruitment, alarm, and sexual (Wyatt, 2003).

Aggregation and host-marking pheromones attract animals of either gender to a location near the source of the pheromone emitter. This leads to a grouping of conspecifics. An example of this class of pheromone can be seen in California spiny lobsters which form groups of up to 30 individuals in order to provide protection from predatory fishes (Zimmer-Faust et al., 1985). The gathering is elicited by chemicals

released by lobsters of either gender. The mass of spiny lobsters then deter predators with their antennae by waving them through den openings.

Territoriality and scent-marking pheromones are expressed as glandular secretions, feces, and urine, which mark the boundaries of an animal's territory. The Eurasian beaver (*Castor fiber*) marks its territory with castoreum and anal-gland secretions (Rosell et al., 1998). Anal secretions are emitted by expressing the anal glands via muscular control; castor sacs release castoreum which is flushed out the cloaca with urine. The composite mixture is deposited onto small piles of mud and debris around the beavers' territory. These marks communicate to other beavers that the territory is occupied.

Social organization pheromones are complex chemical mixtures, which are used to identify individuals within a species. This can be seen in the saddle-back tamarin which releases a pheromone that allows for others to identify not only their species and subspecies, but also the individual, gender, and current reproductive status of the individual (Epple et al., 1987). Other examples can be found in ants belonging to the family Formicidae. Such ants are eusocial and live in colonies dependent on classes (Jackson & Morgan, 1993). The species, colony, caste, age and gender of each ant are communicated to one-another via social organization pheromones contained in the individual's cuticle lipids (Dahbi et al., 1996).

Recruitment pheromones enable mass gathering of individuals to sites of new food sources, territory defense, or to perform a specific task. The ant *Camponotus socius* uses group recruitment to lead nest-mates to a new food site (Holldobler & Wilson, 1990). They do this by leaving chemical markers around the food site and a

trail of hindgut contents on their return to the nest. They then perform a waggle dance to alert nest-mates of the new site; the nest-mates subsequently follow the scout ant along the trail.

Alarm signals are utilized to warn conspecifics of danger or possible hazards in the environment. They are commonly used when an animal is dying, has detected a predator, or to alert a predator that it has been seen (Wyatt, 2003). The black-tailed deer uses a combination of pheromone and visual signals to alert nearby conspecifics of danger. When danger is detected the individual will expose its metatarsal glands on its hind legs, as well as lift its tail. This results in those nearby becoming more alert and often times leaving the area quickly (Quay & Muller Schwarze, 1970).

The most widely studied area of pheromone research involves sex pheromones. These pheromones are used for mate selection, whether through mate choice or same gender competitions. Pheromones are often used to communicate a prospective mate's social status, health, reproductive state, and genetic health (Wyatt, 2003). Dominance status is an important component in mate-choosing and can be communicated to a female via pheromones, such as those produced in the temporal glands of the bank vole (Kruczek, 1997). They can also be used to alert females of a male's location. For example, the male papaya fruit fly releases a pheromone signal when it has reached a fruit that is appropriate for female oviposition (Landolt et al., 1992).

The majority of sex pheromone research had been performed in insects. This is because insects have relatively simple systems that allow for the easy isolation of pheromone components. They can be said to be "hard-wired" to respond with stereotypical behaviors to pheromonal cues. An example of this is seen with the

African cockroach, *Nauphoeta cinerrea*. This species of cockroach has strong male-male competition, where the female chooses to mate with the dominant male. A three-component pheromone communicates the dominance of the male to conspecifics. The first component, when isolated, causes the male to appear to others, and behave, as a subordinate. The experimental addition of either other component results in the male being accepted by others as dominant, regardless of their actual social status in the colony (Moore et al., 1997).

Vertebrates have proven to be a more difficult clade of animals on which to conduct pheromonal research. Unlike insects, they depend on multiple cues to regulate behavior. The limited amount of pheromone research done in vertebrates has focused on lower vertebrates, such as reptiles, because their response systems are less complex. Previous studies examining vertebrate pheromones in reptiles include: femoral gland secretions in *Iguana iguana* (Alberts, 1993), female sex pheromone in *Eumeces laticeps* (Cooper et al., 1986), pheromone recognition in the skink *Egernia stokesii* (Bull et al., 2000), pheromone trailing behavior in the snake *Boiga irregularis* (Greene et al., 2001) and pheromonal gender discrimination in the lizard *Gerrhosaurus Nigrolineatus* (Cooper & Trauth, 1992).

Of all the reptilian species, probably the most extensively studied with regard to their sex pheromone system is the red-sided garter snake, *Thamnophis sirtalis parietalis*. Indeed, the first reptilian pheromone isolated and identified was the sexual attractiveness pheromone of the red-sided garter snake (Mason et al., 1989). This pheromone is composed of a series of saturated and monounsaturated long-chain methyl ketones. Sequestered in the skin lipids along the dorsum of the female, this pheromone

is responsible for eliciting courtship behavior when detected by a male. In addition, studies have also demonstrated that these same methyl ketones are responsible for mediating male trailing behavior during the reproductive season (LeMaster & Mason, 2001).

While much is known about the sexual attractiveness pheromone system of the red-sided garter snake, it is not known to what extent other garter snake species utilize similar chemical cues. Recent work has demonstrated that a closely related garter snake species, the red-spotted garter snake (*Thamnophis sirtalis concinnus*) contains similar methyl ketones in its skin lipids (E. Uhrig, personal communication). However, the behavioral significance of this new finding has yet to be investigated. Utilizing trailing experiments, the purpose of my research is to investigate whether methyl ketones contained in the skin lipids of red-spotted garter snakes are responsible for eliciting male trailing behavior for this species; hypothesizing that these cues, as observed with the red-sided garter snake, serve as the sexual attractiveness pheromone for this species.

MATERIALS AND METHODS

Animal Collection

Red-spotted garter snakes (*Thamnophis sirtalis concinnus*) were gathered from the E.E. Wilson Wildlife Area located approximately ten miles south of Monmouth, Oregon. The snakes were collected during the spring breeding season (February - May) of 2010. A total of 19 males and 10 females were gathered for the experiments with snakes housed at the laboratory of Dr. Robert T. Mason on the Oregon State University

campus. After the experiments were completed the male snakes were released, and the females retained in the Mason laboratory to be used in future research studies.

Behavioral Trials

The experimental maze was constructed from three boards in a y-shaped pattern with peg holes drilled in (Figure 1); the pegs were placed in the maze in order to provide the snakes with a vertical support structure to assist in movement. The maze was covered with brown parchment paper which was replaced after every trial to avoid possible contamination. Pegs were covered with cut straws; the straws were also replaced after each trial. An opaque container with a central opening was placed at the beginning of the maze to house the test snake at the start of each trial.

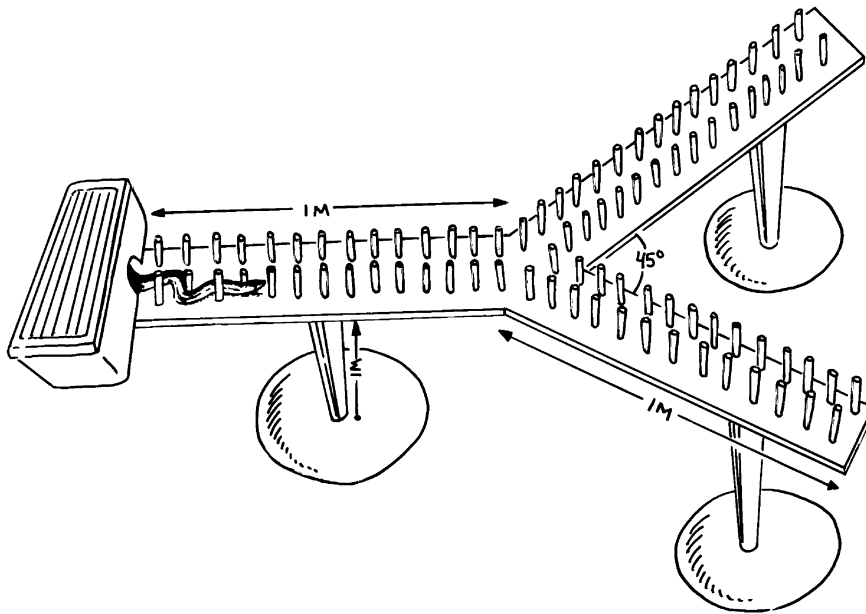


Figure 1: Diagram of experimental Y-maze used for trailing experiments (modified from LeMaster and Mason, 2001)

A total of four experiments were performed testing the response of male red-spotted garter snakes to 1) a blank maze, 2) trails laid down by male red-spotted garter snakes, 3) trails laid down by female red-spotted garter snakes, and 4) trails composed of methyl ketones extracted from female red-spotted garter snakes. Ten trials were run for each experiment. For the two experiments involving trails laid down by male and female red-spotted garter snakes, the trail producing snake was held by a researcher and rubbed dorsal-side down along the appropriate portions of the maze. For the experiment involving the methyl ketone extract, the extract was laid down via a glass pipette along the appropriate portions of the maze.

For each trial performed, the experimental male snake was brought from the housing facility to the experimental room in a pillowcase. It was then clipped with a number to assist in weighing and measuring it at a later time. A coin was subsequently flipped to decide which treatment was to be tested (e.g., male following female trail) and which arm the treatment would be applied to. Once the maze was properly prepared, the experimental male was placed in the opaque holding container. The exit door to the container was then removed and the snake was allowed to exit on its own accord. Male snakes that did not exit the enclosure in 5 minutes or who took longer than 10 minutes to complete the maze were disqualified and retested at a later date (n = 18 trials across the four experiments performed).

Each trial was videotaped using a Panasonic SDR-H18 recorder. The resulting videos were analyzed by myself who was blind to the experimental treatment at the time of analysis. Data collected from the video for each trial included: 1) time to exit the start box, 2) time spent investigating Y-juncture, 3) number of tongue-flicks exhibited at

Y-junction, and 4) arm chosen to follow. The data was subsequently analyzed using the SigmaStat 9.0 software package.

RESULTS

The average snout-vent length and mass of male red-spotted garter snakes used in the experiments was 47.8 (\pm 4.6) cm and 35.2 (\pm 10.2) g, respectively, while the average SVL and mass of female snakes was 54.7 (\pm 2.6) cm and 74.9 (\pm 11.9) g, respectively.

When presented with the control maze (both arms blank), male red-spotted garter snakes showed no preference for one blank arm over the other ($P = 0.656$; Table 1). When presented with a trail from a donor male snake versus a blank arm, males followed trails laid down by males in 4 out of 10 trials ($P = 0.656$; Table 1). When presented with a trail from a donor female snake, males chose the arm with the female trail over the blank arm in 9 out of 10 trials ($P = 0.001$; Table 1). Lastly, when presented with a trail composed of extracted methyl ketones from female skin lipids versus a blank arm, males chose the arm with the methyl ketone extract in 8 out of the 10 trials ($P = 0.023$; Table 1).

Condition	N	Arm Treatment	Number of times selected	P-value
Control	10	Blank	5	0.656
		Blank	5	
Males tested on male trails	10	Male skin rubbing	4	0.656
		Blank	6	
Males tested on female trails	10	Female skin rubbing	9	0.001
		Blank	1	
Males tested on methyl ketone trails	10	Methyl ketone trail	8	0.023
		Blank	2	

Table 1: Responses of male red-spotted garter snakes, *Thamnophis sirtalis concinnus*, to male, female, and methyl ketone extract trails when tested on a Y-maze. (NS=Not significant)

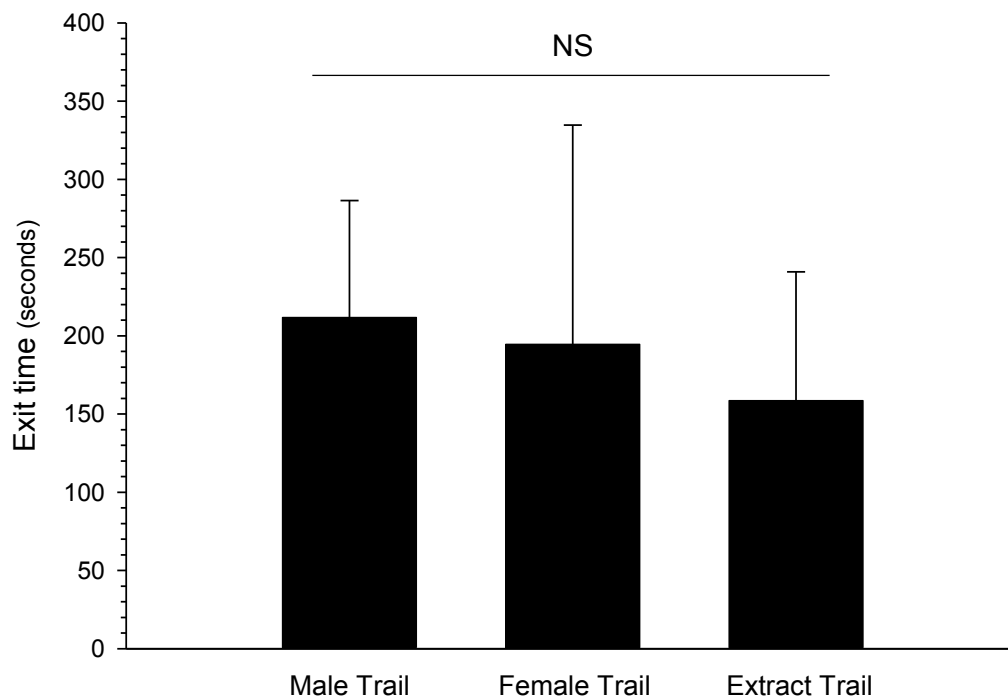


Figure 2: Graph showing exit time of each experimental treatment in seconds. Statistical analysis of exit time with these treatments was not significant.



Figure 3: Graph showing the time the male snake spent at the Y-junction of the maze in experimental treatment in seconds. Statistical analysis was not significant.

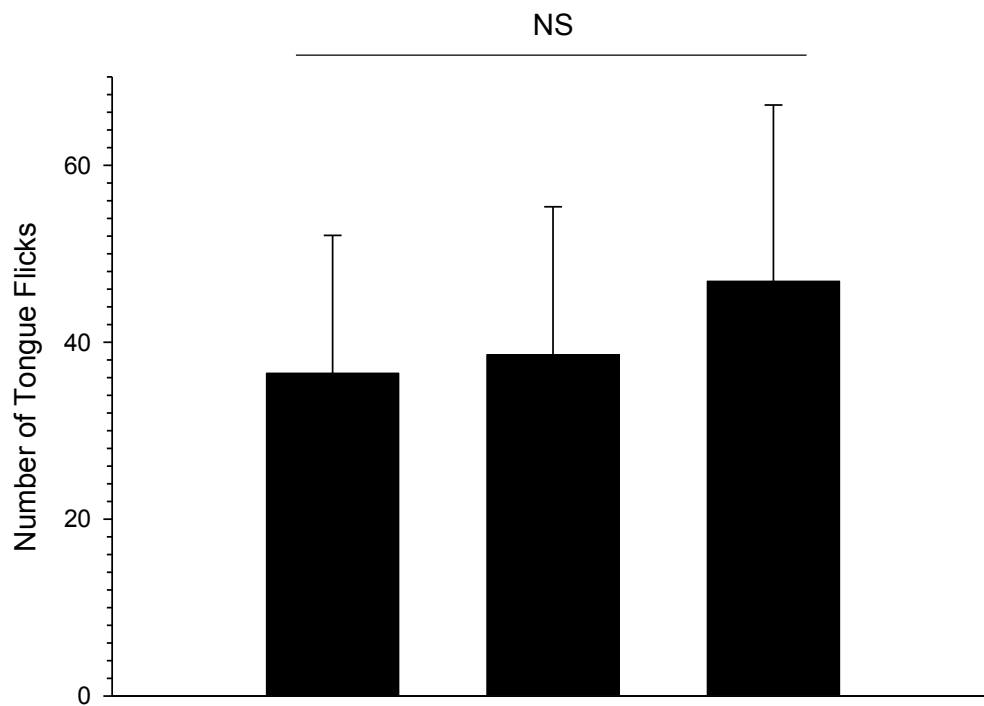


Figure 4: Graph showing number of tongue flicks exhibited by the male snake in each experimental treatment. Statistical analysis was not significant.

No significant difference was found between the experimental treatments in regards to exit time from start box (males on male trails = 211.7 (\pm 74.8) seconds, males on female trails = 194.6 (\pm 140.0) seconds, males on extract trails = 158.6 (\pm 82.3) seconds: ANOVA; $F = 0.689$; $P = 0.511$; Figure 2), time spent at the Y-juncture (males on male trails = 33.9 (\pm 14.8) seconds, males on female trails = 37.1 (\pm 18.0) seconds, males on extract trails = 60.9 (\pm 52.8) seconds: ANOVA on ranks; $H = 2.751$; $P = 0.253$; Figure 3), or the number of tongue flicks observed at the Y-juncture (males on male trails = 36.5 (\pm 15.6) tongue-flicks, males on female trails = 38.6 (\pm 16.7) tongue-flicks, males on extract trails = 46.9 (\pm 19.9) tongue-flicks: ANOVA; $F = 0.988$; $P = 0.385$; Figure 4).

DISCUSSION

The results of this study support the hypothesis that the methyl ketones found in the skin lipids of the red-spotted garter snake, *Thamnophis sirtalis concinnus*, represent the female attractiveness pheromone for this species. Male red-sided garter snakes demonstrated reproductive trailing behavior when presented with female trails, but not male trails, and continued to show such behavior when presented with isolated methyl ketone fractions from female skin lipids. These results align with previous work utilizing the red-sided garter snake (*Thamnophis sirtalis parietalis*), which demonstrated that male trailing behavior is mediated by the female attractiveness pheromone (LeMaster & Mason, 2001).

The fact that males were found to trail females in this study is not surprising; the ability of males to follow female trails has been observed in multiple garter snake species (reviewed in LeMaster et al., 2001). Garter snakes are a relatively solitary species and must locate potential mates during the breeding season. Due to their diminutive size, the ability to detect and follow skin lipid trails laid down on the substrate would greatly enhance their chances of locating a potential mate and siring offspring.

The inability of males to follow male trails was also an expected result. The ability of male snakes to follow trails left by other males is associated with species where there is male combat behavior observed (e.g., Gillingham et al., 1983). In such situations, it is important for males to locate other males within their territory before the intruder males have a chance to mate with local females. Male garter snakes are not known for demonstrating male combat behavior; this suggests that there is no evolutionary pressure to detect and follow male trails.

Previous work with the red-sided garter snake supports the hypothesis that the female reproductive pheromone is of the same composition as the trailing pheromone (LeMaster & Mason, 2001). In this study, I found that males trailed extracts of the methyl ketones which are known to function as the female sexual attractiveness pheromone for the red-sided garter snake (Mason et al., 1989). This strongly suggests that the methyl ketones found in the skin lipids of the red-spotted garter snake also serve as the female reproductive pheromone for this species. Interestingly, I found that males did not trail the extract trails as frequently as the actual female trails. This could be due to the residual hexane present in the extract, which is known to disrupt male

behavior (MPL, personal communication). Another possible explanation is that the extract did not contain an additional chemical component found in the skin lipids necessary for the male snakes to demonstrate full trailing behavior.

I did not find a significant difference in any of the additional behavioral measurements (exit time, time spent at Y-juncture, tongue flicks) taken in each trial when compared across experimental treatments. However, both time spent at the Y-juncture as well as tongue flick number increased in trials using methyl ketone extract compared to the trials on actual skin lipid trails. This could be because the female attractiveness pheromone was present in lower concentrations in the fractionated extract; thus, males needed to gather further chemical information before making a behavioral decision. If the number of experimental animals had been larger, I might have expected to see a significant result with respect to one or both of these behaviors.

Even though both species of garter snake appear to use methyl ketones as their female sexual attractiveness pheromone, previous work has demonstrated that the methyl ketone profiles of *Thamnophis sirtalis concinnus* and *Thamnophis sirtalis parietalis* are significantly different (E. Uhrig, personal communication). Thus, the female attractiveness pheromone could represent a possible reproduction isolation mechanism within garter snakes. Previous studies with the red-sided garter snake have found that males prefer females from their den when compared to females from other hibernacula (LeMaster & Mason, 2002). This preference was attributed to differences in the female sexual attractiveness pheromone. The pheromone may play a similar role within the red-spotted garter snake, especially in relation to the closely related northwestern garter snake, *Thamnophis ordinoides*. While both occupy the same

habitat, it would not reproductively benefit a male of one species to detect and follow females from a different species.

Future work on this project will focus on examining the methyl ketone profiles for multiple red-spotted garter snake females. Once these are collected, the pheromone can be compared to the chemical profiles of the red-sided garter snake and the Northwestern garter snake. This comparison will allow for further insight into the role of the female attractiveness pheromone in reproductive isolation. Comparisons may also be made with red-spotted garter snakes from different collection sites, observing whether there are behavioral and chemical differences between individuals from different sites. These experiments would aid in the continued understanding of the varied purposes of vertebrate pheromones and their role in evolution.

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