Conspecific trailing behaviour of red-sided garter snakes, *Thamnophis sirtalis parietalis*, in the natural environment

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The ability of animals to orient based on pheromonal cues in the environment can have significant consequences to their reproductive success and survival. For example, it is hypothesized that snakes use pheromone trails to locate potential mates during the breeding season and to locate winter hibernacula. Numerous studies have demonstrated that snakes are capable of detecting and following pheromone trails in the laboratory, but it has yet to be shown experimentally whether snakes use such behaviour in their natural environment. In this study, we conducted trailing experiments to test the response of adult red-sided garter snakes to pheromone trails on the natural substrate under naturally occurring conditions during two periods, the spring breeding season and the autumn migration back to the hibernacula. Male snakes detected and followed female trails in the spring, while neither sex displayed trailing behaviour during the period of autumn migration. Our results suggest that adult garter snakes use pheromone trails for locating potential mates during the breeding season and most likely rely on other mechanisms (e.g. visual cues) for navigation to overwintering hibernacula.

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An animal's survival and reproductive success is strongly dependent on its ability to locate necessary resources. Many vertebrates use chemical signals to orient towards potential resources, which may include mates (e.g. frogs, Wabnitz et al. 1999), food (e.g. rattlesnakes, Chiszar et al. 1990), breeding sites (e.g. salmon, Hasler 1960) and refuge (e.g. pigeons, Papi 1982). One type of chemical signal often used by vertebrates for orientation is pheromones. Pheromones are semiochemicals released by individuals that affect the physiology and behaviour of members of the same species (Karlson & Luscher 1959). Once deposited in the environment, a pheromone trail can guide a receiver directly to the location of the conspecific producer.

Conspecific trailing behaviour is widespread in snakes, with numerous species within at least five families demonstrating the behaviour (Ford 1986). In snakes, conspecific trailing behaviour is mediated by pheromones sequestered on the skin, which are laid down along with skin lipids as a snake passes across the substrate (Noble 1937). Subsequent snakes encountering the trail are able to transport the pheromonal cues via tongue flicking to the vomeronasal organ in the roof of the mouth where the cues are detected (Kubie & Halpern 1979; Halpern &

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Kubie 1983). Snakes are believed to use pheromone trails for aggregating, locating potential mates during the breeding season and locating winter hibernacula (reviewed in Ford 1986; Mason 1992; Mason et al. 1998).

Most reports document the occurrence of conspecific trailing behaviour during the breeding season and describe male snakes seeking out sexually attractive females (e.g. Noble 1937; Ford 1981, 1982; Lillywhite 1985; Andrén 1982, 1986). Less is known about the role of pheromone trails in locating winter hibernacula. Communal denning is a strategy often used by northern temperate snakes to escape the harsh winter conditions experienced at higher latitudes (Gregory 1984), and conspecific trailing behaviour has long been suspected to aid snakes during travels to the hibernacula (Noble & Clausen 1936; Hirth 1966). Previous laboratory work has demonstrated that both juvenile snakes (Heller & Halpern 1981; Brown & MacLean 1983; Graves et al. 1986) and adult snakes (Ford 1981; Constanzo 1989) are able to detect and respond to pheromone trails during periods when snakes are actively migrating.

Here, we report two experiments designed to investigate conspecific trailing behaviour in the natural environment for the red-sided garter snake. To our knowledge, this is the first study to field-validate laboratory and anecdotal observations of conspecific trailing behaviour in snakes. The need to field-validate laboratory observations in behavioural ecology has received recent attention (e.g. fish alarm pheromone: Magurran et al.

1996; Smith 1997), raising questions concerning the role of experimentation in behavioural ecology studies (Ylönen & Wolff 1999). With this study, we are attempting to ascertain whether conspecific trailing behaviour is biologically significant to red-sided garter snakes in their natural environment.

Our two major aims in this study are to (1) determine whether red-sided garter snakes respond to pheromone trails in the natural environment and (2) evaluate the role of conspecific trailing behaviour for this species in locating potential mates during the breeding season and locating overwintering hibernacula. Annual aggregations of red-sided garter snakes at underground hibernacula in Manitoba, Canada are unique natural phenomena representing the highest concentrations of snakes in the world (Gregory 1984). For these populations, mating occurs at the hibernacula immediately following spring emergence (Gregory 1977). After mating, snakes disperse to the summer ranges, which can be quite distant from the hibernaculum (>15 km Gregory & Stewart 1975), before returning in early autumn along well-defined travel lanes to the same hibernaculum used over previous winters (Gregory 1974; Macmillan 1995). If pheromone trails are used in the natural environment for locating mates and winter hibernacula, then red-sided garter snakes should detect and follow pheromone trails presented on the natural substrate under naturally occurring conditions during the spring breeding season and the period of autumn migration back to overwintering hibernacula.

METHODS

Study Population and Site

We conducted our research at the Narcisse Wildlife Management Area, in the Interlake region of Manitoba, Canada (50°44′N, 97°34′W). The Narcisse Wildlife Management Area contains three hibernacula in close proximity to one another, with each hibernaculum possessing in excess of 20 000 red-sided garter snakes during the winter months (R. T. Mason, unpublished data).

All trailing experiments were performed on the natural substrate (tall grass prairie, Shay 1984) adjacent to the hibernacula in May (breeding season) and September (period of migration) of 1997. Testing days and times of day (1000–1600 hours) were chosen so that all trials were conducted under similar ambient conditions (mostly sunny skies with light winds and temperatures of 15–20°C), which correspond with conditions when red-sided garter snakes are most active. We collected adult snakes (snout–vent length (SVL)>40.0 cm for males; SVL>50.0 cm for females) on the morning that behavioural tests were to be performed and returned them to the point of capture following testing. Spring individuals (N=72) were collected at the hibernacula as the snakes emerged from winter dormancy and autumn individuals (N=92) were collected approximately 800 m from the hibernacula as the snakes actively migrated back to the hibernacula.
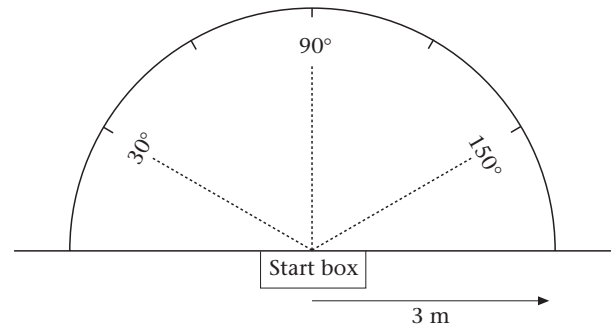

Figure 1. Diagram of experimental plot used for trailing experiments. Plots were established in a natural field with snake trails laid down randomly in one of three directions (30, 90, or 150°).

Behavioural Trials

In both spring and autumn, we tested the response of (1) males to female trails, (2) males to male trails, (3) females to female trails and (4) females to male trails. Snakes were tested on plots mapped out on the natural substrate using small flags. Each plot consisted of a semicircle with a radius of 3 m (Fig. 1). A small, opaque box with a single opening onto the semicircle was placed at the radial centre of the semicircle. All plots were laid out facing in a northeasterly direction with each trial performed on an independent plot. Plots were faced in the same direction for the sake of uniformity after initial examinations showed no difference in the behaviour of the snakes across multiple compass headings.

For each trial, we randomly laid down a snake trail at one of three angles: 30, 90 or 150°. We chose multiple angles to control for external factors (e.g. solar cues, landmarks) that might bias the direction of the test snake. Trails were laid down by randomly selecting a stimulus snake (male or female depending on the treatment) and sweeping it through the grass once, beginning at the exit to the opaque box and ending at the edge of the semicircle at the appropriate angle. Care was taken to cover the cloacal opening of the snake so that contamination from cloacal gland secretions did not occur. A second 'trail' was also laid down in each plot by sweeping our index finger through the grass in the same manner that the real stimulus was applied, but at a different angle than the stimulus trail. This was done to control for mechanical disturbance to the substrate and human skin lipid contamination.

Once the trail was established, we placed a randomly chosen test snake into the opaque box and allowed it to acclimate for 5 min. The opening onto the semicircle was then uncovered and the snake was allowed to exit of its own accord. Trials ended when the test snake exited the arc of the semicircle. A unique test snake was used for each trial. Trials in which the test snake failed to exit the opaque box after 10 min or trials in which the test snake exited out the back of the semicircle were eliminated (<6% of trials completed). The exit location on the arc of the semicircle was marked and the angle of exit was
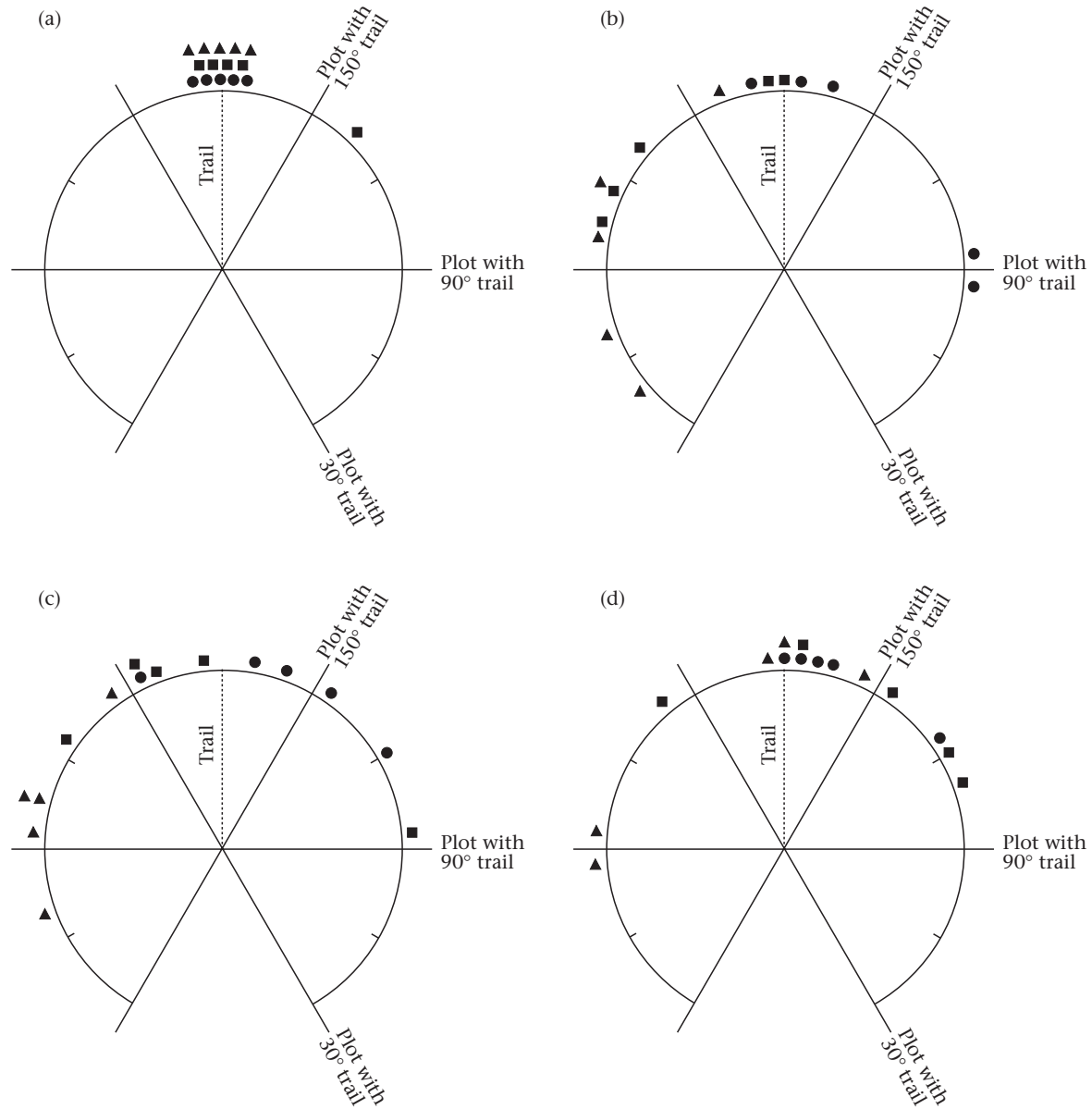
Figure 2. Results of spring trailing experiment showing (a) males with female trails, (b) males with male trails, (c) females with male trails and (d) females with female trails. Snakes were tested on plots with trails at either 30° (●), 90° (■) or 150° (▲) and their exit points were marked to the nearest 5° on the semicircle. Plots have been rotated so that the trail exits are identical for all plots in a treatment.

recorded to the nearest 5° for each trial. We also noted whether the test snake displayed a trail contact response (TCR), an overt response characterized by careful investigation of the substrate by the snake with short, rapid tongue-flicks followed by subsequent investigative movement along the pre-existing trail (Brown & MacLean 1983). Trail contact responses are commonly observed in snakes actively trailing and are used by some investigators to define when an individual is trailing (e.g. Lillywhite 1985).

We performed 15 trials for each treatment in the spring experiment with five trials conducted at each of the three angles. We performed 10–13 trials for each

treatment in the autumn experiment with the trials spread systematically over the three angles.

Statistics

We examined relationships between the stimulus trail angle and the angle of exit for the test snakes through chi-square tests of independence utilizing contingency tables (3×3 tables; columns: stimulus trail angles of 30, 90, 150°; rows: exit angle of test snakes, within the range of 0–60, 61–120, 121–180°; Zar 1984). Level of significance was set at $P < 0.05$.

Table 1. Occurrence of trail contact response (TCR) by adult red-sided garter snakes, *Thamnophis sirtalis parietalis*, during spring and autumn trailing experiments

Condition	Observations of TCR	
	Spring (N)	Autumn (N)
Males with female trails	15 (15)	0 (13)
Males with male trails	0 (15)	0 (13)
Females with male trails	0 (15)	0 (10)
Females with female trails	0 (15)	0 (10)

RESULTS

Spring Treatments

During the breeding season, males responded significantly to female trails, exiting within 5° of the female trail in 14 of the 15 trials performed ($\chi^2_4=25.000$, $P<0.001$; Fig. 2a). All 15 males displayed TCRs immediately upon first exiting the box (Table 1) including the one male not exiting near the female trail. Males did not, however, show a preference for male trails ($\chi^2_4=2.250$, $P=0.690$; Fig. 2b) and did not exhibit TCRs. The same was true for females, which appeared to exit randomly in all trials and showed no TCRs when presented with male trails ($\chi^2_4=6.800$, $P=0.147$; Fig. 2c) or female trails ($\chi^2_4=4.267$, $P=0.371$; Fig. 2d).

Autumn Treatments

During the autumn migration, males randomly exited the semicircle when tested with a female trail ($\chi^2_4=4.956$, $P=0.292$; Fig. 3a) and did not display TCRs at any point during the trials (Table 1). Similar results were observed for males tested with male trails ($\chi^2_4=5.316$, $P=0.256$; Fig. 3b) and females tested with female trails ($\chi^2_4=1.306$, $P=0.860$; Fig. 3d). Females also did not display TCRs to male trails, nor exit near the trails. However, there was a statistically significant relationship between the angle of the trail and the exit angle of the test females ($\chi^2_4=10.889$, $P=0.028$; Fig. 3c) because none of the females exited within 30° of a male trail.

DISCUSSION

The results from this study demonstrate that adult red-sided garter snakes are able to detect and respond to conspecific trails when presented in the natural environment. We observed both sexual and seasonal variability in the response to pheromone trails. Male garter snakes displayed trail contact responses and followed trails laid down by females during the breeding season, while neither sex displayed conspecific trailing behaviour during the period of autumn migration back to the hibernacula. These results offer support for the hypothesis that adult red-sided garter snakes use pheromone trails for locating potential mates, but do not support the hypothesis that adult garter snakes use pheromone trails as the primary mechanism for locating overwintering hibernacula.

Our results from the spring treatments confirm prior investigations of conspecific trailing in snakes during the breeding season (reviewed in Ford 1986; Mason 1992; Mason et al. 1998). In particular, laboratory studies have demonstrated that adult male garter snakes will detect and follow female trails during the breeding season (Noble 1937; Ford 1978, 1981, 1982), while females in general do not trail either sex (Ford 1986; Mason 1992). The ability of male snakes to detect and follow female trails during the breeding season is believed to be an adaptation that allows males, limited by visual and auditory cues, to locate potential mates over long distances (Ford 1986). This hypothesis is supported by field observations at our study hibernacula where male snakes actively following female trails will immediately initiate courtship behaviour upon encountering the trail producer (M. P. LeMaster, personal observation).

The lack of response of test snakes to pheromone trails during the migratory period suggests that adult red-sided garter snakes do not rely primarily on pheromone trails for navigating to winter hibernacula. Our result contrasts with previous laboratory-based studies evaluating conspecific trailing behaviour during the autumn for adult garter snakes (Ford 1981; Halpern & Heller 1981; Constanzo 1989). Specifically, Constanzo (1989) found that adults of both sexes from a communally denning population of the common garter snake, *Thamnophis sirtalis*, followed pheromone trails when presented in the laboratory during autumn, concluding that this population of garter snakes uses pheromone trails for locating hibernacula.

We believe that the difference in observed autumn behaviour between our study and previous studies could arise from two fundamental differences in experimental design. First, we conducted our experiment with adult snakes observed to be actively migrating at the time of collection. Many garter snake species using overwintering hibernacula undergo a period of autumn mating before returning to the hibernacula (Rossman et al. 1996), including the red-sided garter snake (Mendonca & Crews 1989). It is not clear whether previous studies used actively migrating snakes or snakes that may still have been primarily concerned with seeking out and courting potential mates. Second, we conducted our experiment in the field, compared to previous studies conducted in the laboratory. Laboratory experiments, conducted under controlled conditions, determine whether an animal possesses the ability to respond to a particular stimulus (Smith 1997). Field experiments, in contrast, allow for the evaluation of behavioural decisions made by an animal when influenced by prevailing environmental conditions. Thus, while garter snakes may be able to respond to pheromone trails when presented in isolation during the autumn, additional factors coexisting in the natural environment may lessen, or eliminate, the response. In support of this hypothesis is evidence that adult red-sided garter snakes from our study population do respond to pheromone trails during the period of autumn migration when presented under laboratory conditions (M. J. Greene, personal communication).
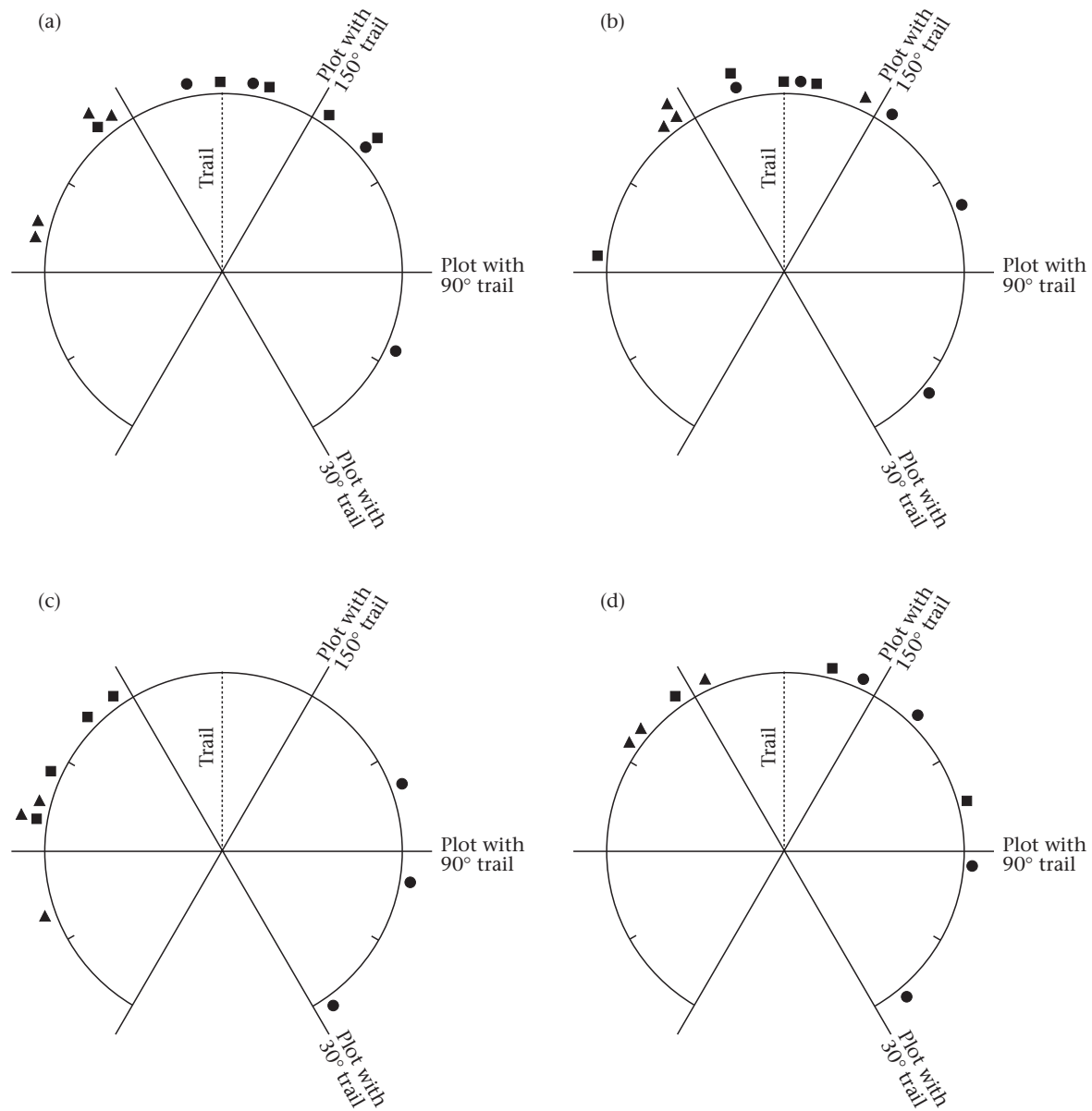
Figure 3. Results of autumn trailing experiment showing (a) males with female trails, (b) males with male trails, (c) females with male trails and (d) females with female trails. Snakes were tested on plots with trails at either 30° (●), 90° (■) or 150° (▲) and their exit points were marked to the nearest 5° on the semicircle. Plots have been rotated so that the trail exits are identical for all plots in a treatment.

We suggest two plausible explanations for how environmental factors might mediate the response of red-sided garter snakes to pheromone trails. First, conditions in the environment might dilute chemical cues contained within the trail to the point where they are no longer detectable (Magurran et al. 1996). Alternatively, additional stimuli in the environment (e.g. visual cues) may override a snake's ability to detect and process chemical cues located in trails. Most migrating vertebrates are known to rely on multiple cues for orientation, often arranged in a hierarchical structure (Able 1991); red-sided garter snakes may preferentially seek other cues for orientation and only respond to chemical cues when the additional cues are absent. Solar cues, the most

commonly used source of information for navigation by diurnally migrating animals (Able 1980; Shöne 1984), offer a likely source of additional information for red-sided garter snakes. In fact, studies have demonstrated that migratory species of garter snakes are capable of orienting with respect to both solar azimuth position (Lawson 1989, 1994) and polarized light (Lawson & Secoy 1991). A dependence on solar cues could explain why we observe red-sided garter snakes mainly migrating under sunny skies, although thermal constraints placed on snakes may also be responsible for this observation (Peterson 1987).

While we did not observe conspecific trailing behaviour during the autumn treatments, we did find a

significant trend for females to exit the experimental plots well distant of trails produced by males. Trail avoidance has previously been observed among snakes (Burger 1989; Burger et al. 1991), but these studies are limited to snakes discriminating between trails of predatory (ophiophagous) snakes and those of nonpredatory (nonophiophagous) snakes. Female red-sided garter snakes may avoid male trails near the hibernacula in an effort to escape vigorous autumn courtship, occasionally displayed by some males at the hibernacula (M. P. LeMaster, personal observation). It is unknown why a small subset of males continue to actively court females well after the period of autumn mating, but such harassment by these males could lead to increased mortality in females due to increased predation risk and energy expenditure (e.g. Weigensberg & Fairbairn 1994; Clutton-Brock & Langley 1997). Alternatively, the observed avoidance may be an artefact of the experimental design. Additional studies designed to test specifically for trail avoidance behaviour need to be performed to evaluate the importance of the observed result.

Acknowledgments

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