

PHEROMONES, SEARCH PATTERNS, AND OLD HAUNTS: HOW DO MALE TIMBER RATTLESNAKES (*CROTALUS HORRIDUS*) LOCATE MATES?

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ABSTRACT: During the mating period male rattlesnakes generally locate females only after traveling and searching long distances, whereas current evidence suggests that females do not actively search for mates. Here I discuss three hypotheses concerning long-distance mate location by male snakes: (1) scent trailing of pheromones laid down by females, (2) use of prior knowledge of female locations, and (3) use of efficient search patterns. I report on movements of four radiotracked male Timber Rattlesnakes (*Crotalus horridus*) prior to and following their accompaniment of females, and relate these movements to the three above hypotheses. In general, males made long distance, straight-line movements prior to locating a female, and retraced those movements following interaction with the female. In specific cases, movements suggested for or against one or more of the hypotheses. No single hypothesis, however, appears to explain all the data. Snakes might use multiple methods of mate location, separately or in combination, and mate location strategies likely vary within and among individuals, populations, and species.

INTRODUCTION

Early studies (Blanchard and Finster, 1933; Hirth et al., 1969) suggested that snake movement was unpredictable and likely consisted of random wanderings. With the advent of radiotelemetric techniques the resolution for studying snakes has greatly improved, and our understanding of patterns of snake movement has increased accordingly. When studied at this resolution, snake movement is not a random phenomenon. Many factors have been suggested to be involved in determining movements of snakes, including location of prey (Duvall et al., 1990; Madsen and Shine, 1996), mates (Slip and Shine, 1988; Duvall and Schuett, 1997), oviposition sites (Plummer, 1990) and birthing rookeries (Graves and Duvall, 1993), and migrations between summer ranges and winter hibernacula (Brown, 1993). However, even when we see the pattern and can infer the “why,” the “how” is often elusive.

With few exceptions (e.g., mating “balls” of garter-snakes at dens in spring; see citations in Rossman et al., 1996), instances of courtship and copulation in snakes in the field are difficult to observe without the aid of radiotelemetry. Little is known, for example, about the specific cues and mechanisms used by male snakes to locate females over long distances, or how females might attract males.

Here I detail movements made by eight (4 males, 4 females) Timber Rattlesnakes (*Crotalus horridus*) that came into contact or close proximity with each other and with five (3 males, 2 females) other individuals. I discuss three hypotheses of how male snakes might locate females over long distances, and relate them to my observations of *C. horridus* in southern Ohio.

MATERIALS AND METHODS

I performed a radiotelemetric study of *C. horridus* in Vinton Co., Ohio from fall 1994 through spring 1996. The data discussed in this paper were collected in the 1995 field season. The study site is an oak-hickory (*Quercus-Carya*) forest in steep foothills of the Appalachian Mountains. I used standard radiotelemetric techniques (Reinert and Cundall, 1982; Reinert, 1992) with minor modifications (Coupe, 1997). The time between collection of animals for radiotracker implantation and their release ranged from 5 to 10 days ($\bar{x} = 6.8$). While in captivity snakes were kept individually in nylon cloth bags in picnic coolers. I sexed snakes by probing for hemipenes (Schaefer, 1934). Snakes were released at the exact location where they were collected. During the time of this study, the average interval between locations of individual snakes was 1.37 days. This interval includes an instance where I was unable to locate a male for 27 days. Removal of this outlier results in an average tracking interval of 1.27 days. I marked locations with pin flags, and later recorded them with a Trimble Navigation (Sunnyvale, California) Pathfinder Pro XL Global Positioning System (GPS). Differential corrections, to correct for government scrambling of the satellite signals read by the GPS were made using Pfinder 3.0 software (Trimble Navigation, Sunnyvale, California). Corrected coordinates are accurate to within 3 m with some exceptions outside this range (L. Iverson, pers. comm.). Distances greater than 1 m are rounded to the nearest meter, and those under 1 m are visual estimates.

RESULTS

Animal DM3

In early July 1995, a radiotagged male, DM3, made five short, daily movements ($\bar{x} = 28$ m, range 8–44 m,

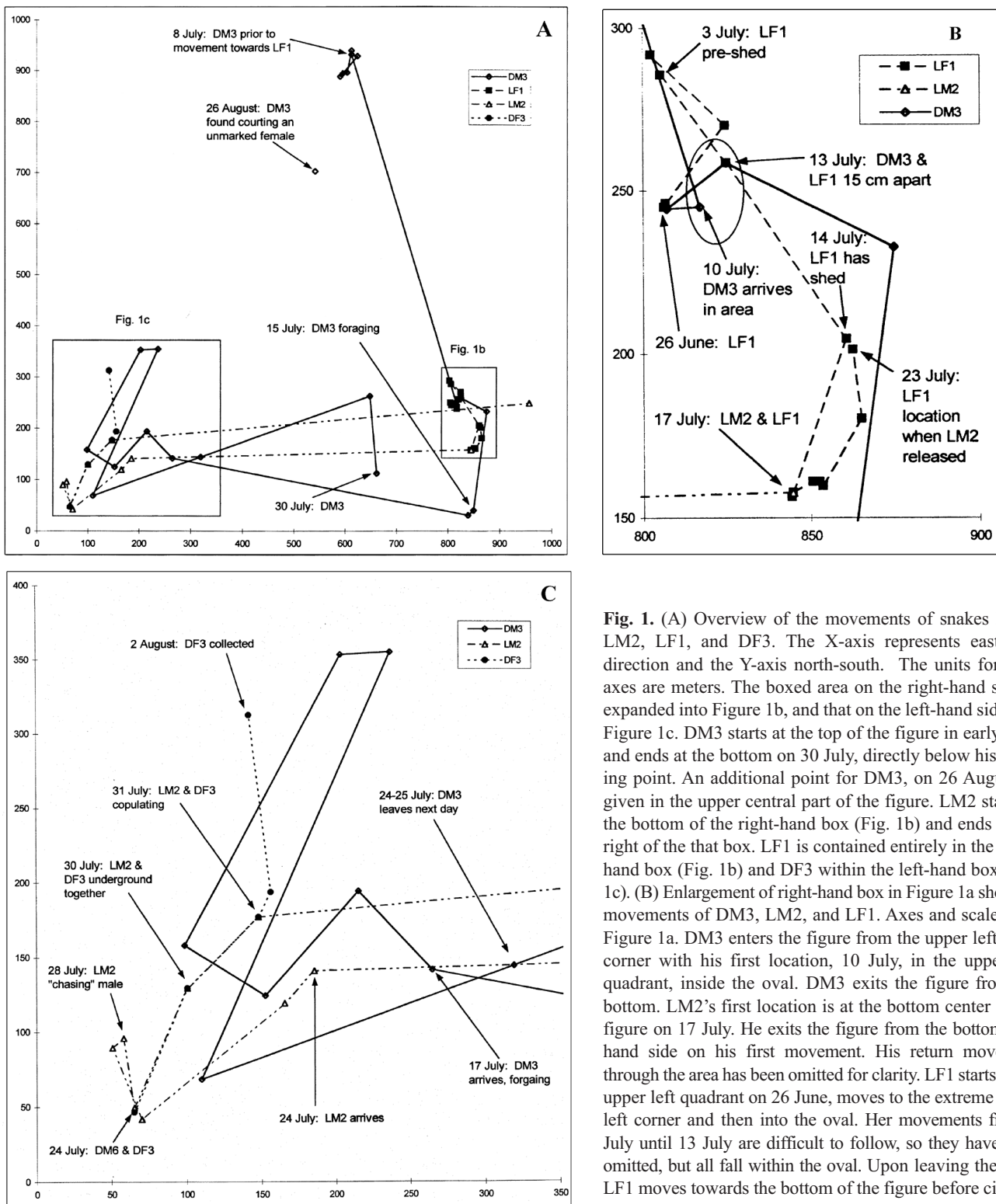


Fig. 1. (A) Overview of the movements of snakes DM3, LM2, LF1, and DF3. The X-axis represents east-west direction and the Y-axis north-south. The units for both axes are meters. The boxed area on the right-hand side is expanded into Figure 1b, and that on the left-hand side into Figure 1c. DM3 starts at the top of the figure in early July, and ends at the bottom on 30 July, directly below his starting point. An additional point for DM3, on 26 August, is given in the upper central part of the figure. LM2 starts at the bottom of the right-hand box (Fig. 1b) and ends to the right of the that box. LF1 is contained entirely in the right-hand box (Fig. 1b) and DF3 within the left-hand box (Fig. 1c). (B) Enlargement of right-hand box in Figure 1a showing movements of DM3, LM2, and LF1. Axes and scale as in Figure 1a. DM3 enters the figure from the upper left-hand corner with his first location, 10 July, in the upper left quadrant, inside the oval. DM3 exits the figure from the bottom. LM2's first location is at the bottom center of the figure on 17 July. He exits the figure from the bottom left-hand side on his first movement. His return movement through the area has been omitted for clarity. LF1 starts in the upper left quadrant on 26 June, moves to the extreme upper left corner and then into the oval. Her movements from 4 July until 13 July are difficult to follow, so they have been omitted, but all fall within the oval. Upon leaving the oval, LF1 moves towards the bottom of the figure before circling back. (C) Enlargement of left-hand box in Figure 1a showing

movements of DM3, LM2 and DF3. Axes and scale as in Figure 1a. DM3 enters the figure from the right-hand side, and his first location is on 17 July. He exits the figure from the same side with his last location on 25 July. LM2 also arrives from the right with his first location in the lower center of the figure on 24 July, also near the center, prior to exiting from the right-hand side. DF3 is first located on 24 July at the bottom left of the figure. She and LM2 follow the same path as they move together toward the center of the figure and separate by 1 August. DF3 then moves towards the top of the figure where she was collected on 2 August.

Fig. 1a) followed by a 716 m movement over two days to arrive in the vicinity of a radiotagged female, LF1, by 10 July (Table 1, Figs. 1a, 1b). At this time LF1 was pre-shed. On 11 July, DM3 was 17 m from LF1 and less than 1 m from LF1's locations for 26 and 27 June (Fig. 1b). On 13 July, DM3 was 15 cm from LF1. By 14 July LF1 had shed and moved 65 m. DM3 had moved 56 m in the same general direction, but was 32 m away.

DM3 was observed in a typical ambush foraging posture (Reinert et al., 1984) on 15 July, 195 m from his location on 14 July (Fig. 1a). He had moved 14 m by the next day, 16 July. On 17 July, he was again foraging after a movement of 585 m (Fig. 1c). Over the next six days he made shorter movements totaling 797 m (\bar{x} = 133 m, range 34–313 m; Table 1, Fig. 1c). On 24 July, he was 222 m from his location on 23 July, and appeared to be moving back to the area where he had been with LF1. He remained in the same location on 25 July (Fig. 1c), but on 26 July was found 350 m away moving in the same direction (Fig. 1a). I was unable to locate his signal again until 30 July. By that time he had moved 150 m south. His signal was lost again, and he was not found for 27 days, at which point he was located 602 m north of his last known location and was courting an unmarked female (Fig. 1a). He was on top of her and performing a "tail-search copulatory attempt" (Gillingham, 1987).

Animal LM2

By 17 July, LF1 had moved 52 m and was found being courted by a large, previously unmarked male, LM2 (Table 1, Fig. 1b). LM2 was collected, implanted with a radiotransmitter and then released on 23 July. By that time LF1 had moved five times (\bar{x} = 11 m, range 2–24 m; Fig. 1b), and was 47 m from where she had been in association with LM2. These two snakes were not observed together again. On 24 July, within 24 hours after his release, LM2 was located 659 m away in the same area that DM3 was leaving on 24 July (Figs. 1a, 1c). I suspected that the two males had moved to the same area to pursue a female, and so I made a search of the area. Within 30 min I found two previously unmarked snakes, a male (DM6) and a female (DF3), within 10 cm of each other, 153 m from LM2, and 50 m from DM3's location from the previous day, 23 July (Fig. 1c). DM6 and DF3 were collected for implantation of radiotransmitters. In the intervening time, LM2 made two movements (29 m and 123 m) directly toward the capture location of the new snakes, and on 26 July LM2 was located 7 m

Table 1. Dates in 1995 when specific males were observed in contact with or close proximity to specific females.

Male	Female	Approximate dates of association
DM3	LF1	10–14 July
	DF3	19–23 July
LM2	LF1	17 July
	DF3	24–31 July
DM4	DF4	29 July
	DF5	29 July
DM5	DF4	3–6 August
	DF5	3–6 August

from their capture location. LM2 then made two short movements (51 m and 10 m), and on 28 July was seen moving toward a much smaller unmarked male that was moving away from him. By the time DF3 and DM6 were released on 29 July, LM2 had returned (47 m) to 3 m from the pair's capture/release site.

On 30 July at 1045 h, the day after her release, DF3 was located with LM2 underground, 90 m and 87 m away from their respective locations on 29 July (Table 1, Fig. 1c). At 1705 h of the same day DF3 and LM2 were above ground at the same location. She was tightly coiled and he was loosely draped around her. They were not copulating, and my presence disturbed them. DF3 rattled and moved a few meters away. LM2 followed, and I left so as to minimize the disturbance.

The next day, 31 July, LM2 and DF3 were located copulating 67 m from their previous location. They were observed from 1242 h to 1340 h, stretched out in opposite directions. The female kept her tail up the entire time, and the male appeared to initiate movement by lifting his. When he raised his tail she would move forward and he backward. LM2 and DF3 would move like this for a few centimeters then stop, and start again when LM2 lifted his tail. The pair remained in copulo at 1800 h. Following copulation, DF3 made two additional movements before her radiotransmitter emitted a whine indicating impending failure. She was recollected on 2 August.

The day after copulation, LM2 was located 811 m east (Fig. 1a). He then made many short movements (N = 19, \bar{x} = 66 m, range < 1–419 m; not shown in the figures) as he shed his skin followed by a large movement on 25 August, which resulted in loss of radio contact. I was unable to relocate LM2 until 31 August, six days later, when he was located by helicopter. At that time LM2 was 1031 m north of his last known

location. He then made two short movements (17 m and 89 m) in the same direction before disappearing again; I was unable to locate him again by any means. On 3 September, an unmarked animal was observed 312 m from LM2's 31 August location, the terminus of his 1031 m movement. The unmarked snake's location was roughly along the line of LM2's long movement, but by this time LM2 had moved farther away, and it is impossible to know if they came in contact. The unmarked snake evaded capture, but judging from the snake's body size and relative tail length it was probably a female (Brown, 1993).

Animal DM4

On 23 July, in a different part of the study site (Fig. 2a), DM4 was released after implantation of a radiotransmitter. He made three relatively short movements (\bar{x} = 110 m, range 62–201 m) before moving 604 m to his location on 27 July (Fig. 2a). DM4's locations on 28 and 29 July took him 80 m and 311 m, respectively, in the same direction. At 1240 h on 29

July, he was located with an unmarked male and a previously unmarked female, DF4 (Table 1, Fig. 2b). Both new snakes were collected. At 1852 h of the same day DM4 was relocated. He had moved 107 m and was coiled 2 m from another previously unmarked female, DF5 (Table 1, Fig. 2b), who was moving away. The two new females were implanted with radiotransmitters and the male was marked for identification. DF5 was in a pre-shed state when she was collected, and shed on the day of her release. DF5 and the new male were released on 5 August. The new male was never recaptured. DF4 shed while she was in captivity, and was released on 6 August. DM4 had moved 76 m by 30 July, and by 1 August had moved 973 m back to where he had been released (Fig. 2a).

Animal DM5

Another male, DM5, had been released after implantation with a radiotransmitter on 30 July (Fig. 2a), and made four long movements (\bar{x} = 496 m, range 315–779 m) on consecutive days in a generally south-

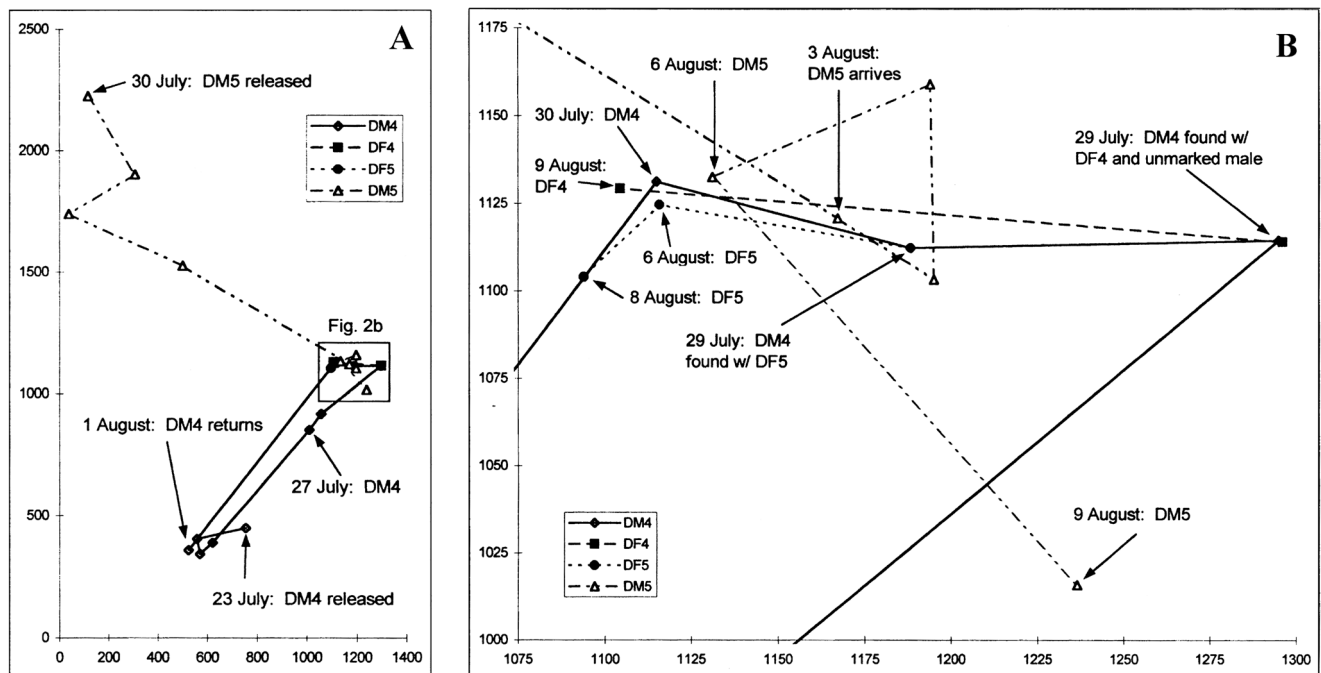


Fig. 2. (A) Overview of the movements of snakes DM4, DM5, DF4, and DF5. Axes and scale as in Figure 1a. The boxed area is expanded into Figure 2b. DM4 starts at the bottom of the figure on 23 July. He then moves to the box (Fig. 2b) in the middle of the right-hand side before returning to the bottom middle. DM5 begins at the upper left-hand corner and moves to the box (Fig. 2b). The movements of DF4 and DF5 are contained within the box (Fig. 2b). (B) Enlargement of boxed area in Figure 2a showing movements of DM4, DM5, DF4 and DF5. Axes and scale as in Figure 1a. DM4 enters the figure from the bottom with his first location on 29 July on the right-hand side of the figure. He then moves to the left-hand side where his last location before exiting from the middle of the left side is 30 July. DM5 enters the figure from the upper left-hand corner with his first location near the center on 3 August. He then moves in a circle and his last location is in the bottom right on 9 August. DF4 is first located in the upper right at DM4's first location. She then moves to the left where she is located on 9 August. DF5 is first located in the center of the figure on 29 July. She moves to the left-hand side by 8 August.

easterly direction. DM5's long movements ended on 3 August, 11 m from the location where DF5 was collected (Table 1, Fig. 2b). DM5's next three movements (33 m, 56 m, and 68 m), on consecutive days ending on 6 August, circled DF5's capture/release location, and placed him 17 m from her location on 6 August. On 6 August, DF4 was released 166 m to the east (Table 1, Fig. 2b). DF5 was not relocated on 7 August, but on 8 August she was 47 m from DM5's location on 6 August. DF4 and DM5 were not located again until 9 August, at which time DF4 had moved 192 m west, and DM5 157 m southeast (174 m apart) on his way out of the area. DF4 and DF5 continued to move west-northwest, the direction from which DM5 had come, to their den sites. DM5 continued southeast, making much shorter movements than those that had brought him in the vicinity of DF4 and DF5. Although DM5 was not seen with either DF4 or DF5, they were in close proximity and it is possible that they came in contact.

DM6 and other Males

After DM6 was released (29 July with DF3; Fig. 1c), he remained in the same general area but was not observed in association with other snakes. His largest recorded movement was 81 m. Four other males were radiotracked during this study, but none were ever observed with a female. Only one made a single movement > 500 m, which brought him close to his den site, so it is unlikely that it was associated with mate location.

DISCUSSION

The data I have presented illustrate what could be a common movement pattern exhibited by male *C. horridus* when locating females. In general, males make long linear movements (> 500 m) over 1–3 days, which bring them into contact with a female. They then make short movements associated with accompaniment and courtship, and following courtship (either ending in copulation or not) they make long movements back to the area where they originated. Currently, I am aware of three hypotheses that could explain how males locate females over long distances: scent trailing, prior experience, and efficient searching.

Scent Trailing

Scent trailing is the most widely assumed hypothesis (reviewed by Ford, 1986). Ford and Low (1984) describe a mechanism by which males could follow female scent trails. Ed McGowan (pers.

comm.) suggested that sexually receptive female *C. horridus* make long, linear movements, leaving scent trails that potentially attract males. Additionally, Brown (1995) suggested that male *C. horridus* might follow the scent trails of other males to females.

Scent trailing is a strategy used by males to locate females. It remains to be demonstrated, however, whether scent trailing is used by males over long distances to locate mates. In order to answer this question, data on long-term movements (at least one mating season) of pairs engaged in reproductive behavior are needed. If the paths overlap over long distances, scent trailing can be inferred. Ed McGowan (pers. comm.) observed a male *C. horridus* that had located a female the day before, following that female's exact path as she moved approximately 20 m ahead of the male. Presumably, the male followed the female in this manner over the 383 m that separated the animals' locations over the two days. McGowan also recorded other incidents where pairs of snakes were observed at the beginning and end points of long movements (up to 800 m) over short periods. Slip and Shine (1988) noted similar behavior in the Diamond Python (*Morelia s. spilota*), over distances of approximately 100 m.

Prior Experience

As many snakes can be long lived (≥ 25 years in *C. horridus*; Brown 1993; Martin, this volume), males that have found females in past years might simply return to those areas where they were successful in reproductive activities (e.g., mate location, courtship, copulation). In many snake species, individuals show some degree of home range fidelity, and return to the same areas year-to-year (Reinert, 1993). Shine (1987) suggests that Red-bellied Blacksnakes (*Pseudechis porphyriacus*) are familiar with the landscape and move directly between shelter locations. Thus, females might be spatially and temporally predictable, and males could use this information when locating mates. Ed McGowan (pers. comm.) suggested that male *C. horridus* locate females at specific rock outcroppings (which was not the case in aggregations I observed, perhaps because that type of habitat is not common at my study site). If females consistently use these or other locations year-to-year, then prior experience could greatly affect male movements associated with mate location. In order to support this hypothesis, the data must, at a minimum, show that female home ranges are stable across sexually active years or that sexually attractive females are consistently found at

specific locations (or specific types of habitats) during the mating season. The data should also show that males spending time in these home ranges, localities or habitats return to them in subsequent mating seasons.

Based on movement patterns observed in a population of Common Gartersnakes (*Thamnophis sirtalis*), Larson (1987) stated that the snakes appear to have "complex orientational capabilities" but did not speculate on the mechanisms of orientation. Mechanisms of orientation and navigation in snakes are poorly understood (reviewed by Gregory et al., 1987); thus, it is difficult to predict a movement pattern for males acting on prior experience. If snakes are able to locate themselves and a female's home range on an internal map, and they have some sort of compass sense (Landreth, 1973; Newcomer et al., 1974), then straight-line movement would be predicted. However, if snakes do not have an internal map and a compass sense, then one would expect them to move along the path previously used in finding (or returning from) the female.

Efficient Searching

Duvall and Schuett (1997) suggested that males use efficient search patterns when locating females. They argued that, for a given spatial distribution of females, males would locate females most efficiently by using a specific search pattern. They support this idea with data from their study on a Wyoming population of Prairie Rattlesnakes (*Crotalus viridis*). Males that located females were more likely to move in the predicted straight-line pattern over successive movements than those that did not.

If males are efficiently searching for females over long distances, the data need to show that they move in the predicted pattern (which could vary depending on the spatial distribution of females in the habitat; Duvall et al., 1994). The data must also eliminate the scent trailing and prior experience hypotheses. The data in Duvall and Schuett (1997) show that males moved in the predicted pattern, but the data are not incompatible with the other two hypotheses. The movement pattern that males would use if moving on prior experience might also be a straight-line, and if a female moves for a long distance in a straight-line the scent-trailing hypothesis also gives the straight-line prediction.

Current Work and Future Research

Multiple kinds of data are needed to sort out these hypotheses, but the most important will be those from

long-term (multiple year) radiotelemetric data on individuals of both sexes, and the spatial distribution of females in the habitat during the mating season. The former will provide data on the simultaneous movement patterns of males and females, and the latter can be used to discern the males' optimal search strategy. If tracings of male and female movements prior to accompaniment overlap for long distances, then scent trailing is likely. If locations of individual females are fairly stable from year-to-year or only shift slightly, the prior experience hypothesis might play a significant part in mate location by males. If tracings do not overlap and females are not located in the same places from year-to-year, then efficient searching is likely.

There is no reason to think that only one of these hypotheses is correct or mutually exclusive. Different species, different populations within a species, and different individuals within a population might use different methods of mate location. Individual males could use different strategies in different years or at different times of the mating season. Young males entering their first mating season with little experience might follow scent trails or search efficiently until they have learned the location of individual female home ranges, specific locations used by sexually receptive females, or the location of female preferred habitat. In species where males go through a prolonged period before achieving sexual maturity, young males that encounter females before sexual maturity might be selected to remember those locations for their first and subsequent mating seasons.

Older, experienced males could use any of the three strategies in locating mates, although particular strategies might be more successful than others, depending on variables such as population density and relative mortality rate. In dense populations, knowledge of a particular female's location might not be crucial in mate location, as the probability of encountering a female by chance, scent trailing, or efficient searching could be relatively high. Low population density might favor scent trailing and prior experience as these strategies provide reliable clues for the location of mates in an environment where mates are rare.

In populations with high female mortality, prior experience is not likely to be prevalent because this method of mate location requires stability in female spatial predictability across years. If female survivorship is low between mating seasons, their spatial predictability erodes and prior experience will only be useful if females aggregate in specific locations or habitats during the mating season. Conversely, prior

experience might be the preferred method in species with high female survivorship, as female locations in these species could be highly predictable. Of course, in order for males to use prior experience, they too must have a high probability of survival so they will have an opportunity to use their experience.

Last, it is also likely that multiple mechanisms could be used simultaneously. While it seems unlikely that an individual male could be efficiently searching and at the same time using prior experience (a male should search if he does not know where a female is, but if he knows a female's location he should move toward her rather than search), it is likely that he will be checking for scent trails while using either method.

Some aspects of the data I have presented might be instructive about the strategies that male *C. horridus* use to locate mates. The area that DM3 departed when he made his long movement toward LF1 (Fig. 1a) is an area where LF1 was not observed during 1995, when the two snakes were seen together, nor when she was tracked in 1994 (late summer and fall). Thus, it is unlikely that DM3 was following LF1's scent trail when he initiated movement toward her. This movement could support either the efficient searching hypothesis or the prior experience hypothesis. However, because the area where this pair came into contact was ca. 105 m from LF1's den site and adjacent to where she was located the previous fall, the prior experience hypothesis seems likely, given that DM3's den site was 20 m from LF1's. It seems possible, though, that DM3 used LF1's scent trail on his final approach, as he was located less than one meter from two of LF1's earlier locations (Fig. 1b). If DM3 was following LF1's scent trail on his final approach, then it is possible that scent trails are useful for long durations because LF1 used those locations two weeks prior to his arrival, and it rained (~2 cm) during the interim.

LM2 made a long movement to exactly the same area (Fig. 1a) where DM3 had moved to previously. As both snakes left from the same general area, it is possible that LM2 was scent-trailing DM3. If male-male scent trailing to females occurs (Brown, 1995), there could be two different scent-trailing strategies among males. An individual could be a "finder" or a "follower." In species where male-male combat is important for priority of access to females, and because size confers an advantage in combat (Madsen et al., 1993; Schuett, 1997), I would expect followers to be relatively large and likely be able to defeat males they are following. Male *C. horridus* engage in combat (Martin, 1992), and LM2 was the largest snake

observed at my study site. Alternatively, in species where male-male combat is absent or uncommon, followers might be younger, inexperienced males who are not yet proficient at finding females.

It is not known how long scent trails last in the field, but it has been suggested that snakes use scent trails laid down in the spring to guide them back to their den sites in the fall (Graves et al., 1986). The interaction between DM3 and LF1 suggests that scent trails might last at least two weeks. In his long movements (Fig. 2a) DM5 moved directly through the area that DF3 and DF4 subsequently occupied as they approached their den sites. If scent trails are long lasting then it is possible that DM5 was following DF4's or DF5's scent trail from earlier in the year as he approached them.

Brown (1995) observed that female *C. horridus* are commonly found in some stage of the shedding cycle during the mating season. Macartney and Gregory (1988) similarly noted that female Northern Pacific Rattlesnakes (*Crotalus viridis oreganus*; for taxonomic changes in this group, see Douglas et al., this volume) usually had shed < 48 h prior to being found in reproductive aggregations. Pheromones released during ecdysis likely induce reproductive behavior in snakes (Mason, 1992). Recently-shed females might leave more attractive scent trails. My data also support this idea, as three of five females observed with males were in a shedding cycle.

The interesting pattern emerging from my study is that of males moving to where they encounter a female and then back from whence they came. Reinert and Zappalorti (1988: Fig. 3b) tracked an individual male *C. horridus* that showed a similar pattern, executing it three times in a month (August). More data need to be collected before definitive statements can be made about this behavior, but it is possible that males are seeking females from a central location and returning to that location to minimize the possibility of becoming lost.

In their analyses, Duvall and Schuett (1997) only included snakes that had been located daily during the mating season. When testing for a correlation between the linearity of movements and mate location success, they only used animals for which "at least six successive and lengthy movements (> 50 m/day), during the breeding season" were recorded. Duvall and Schuett's (1997) specific criteria for ascertaining straight-line movements would eliminate all snakes that I tracked, because I was either unable to locate snakes daily during the mating season, or individuals

did not make six successive movements > 50 m. Thus, a direct comparison cannot be made between the two studies. However, the movement patterns described in both studies are similar in that males locating females made long-distance, short-term, linear movements prior to doing so, and this could represent a general pattern.

Differences in the importance of male-male combat among snake populations could affect the mechanisms used by males in locating females as a result of the trade-off between handling time (including male-male combat) and search time (Duvall et al., 1992, 1993; Arnold and Duvall, 1994). Presence or absence of male-male combat could be governed by factors such as phylogeny, food availability (affecting the proportion of receptive females), length of the active season (affecting the urgency in mate location), and population density (affecting the probability of finding another female), all of which might vary intra- or interspecifically (Schuett et al., 2001). Additionally, the form or length of combat might vary and is more likely to be observed in some populations than others, and this variation could affect our interpretation of the importance of combat. After an 11-year study, Duvall and Schuett (1997) concluded that male combat is likely not common in the mating system of *C. viridis* at their field site, as multiple males were rarely observed in the presence of females. I did not see combat in the *C. horridus* I tracked, but in one year I observed two instances where multiple males and at least one female were in close spatial and temporal proximity. Brown (1995) details a number of similar instances during a 12-year study of *C. horridus* in New York. I also observed three instances where multiple males were close to the same female in rapid temporal succession. I expect that in populations where male handling time of females is prolonged, the selection pressure on males to gather information about where to find females would be stronger than in populations where handling times are short. Thus, prior experience might be a better strategy in populations where male-male combat is important than in populations where combat is rare or absent. The efficient searching strategy might show the opposite trend.

While the resolution of radiotelemetric data is higher than that of capture-mark-recapture, typically it results in only one location every one to two days. This tracking interval does not allow researchers to record the actual path of movement an individual used between successive daily locations. Until technology progresses to allow implantation of miniature GPS

units, this is likely the best we can do for most species of snakes. The alternative is to significantly decrease sample size and shorten the tracking interval, which could also increase the disturbance of animals to an undesirable level.

The particular behavioral and habitat characteristics of some species of snakes make them amenable to extremely high-resolution studies of their movements. Secor (1992, 1994) detailed the exact movements of Sidewinders (*Crotalus cerastes*) between successive telemetry locations by mapping tracks left in the soft sand of his study site. *Crotalus cerastes* and other sidewinding species of vipers (Gans and Mendelssohn, 1971) that leave directional tracks in soft substrates could be useful in addressing questions regarding mate location, as it would be possible to map the exact path of movement individuals take during the mating season. When a pair of snakes is found in association, courtship, or copulation, it would be possible to assess the distance their tracks overlap prior to discovery. Track overlap data of this nature would provide a concrete measure of the importance of scent trailing in mate location. By providing information on how often males visit the same areas (and the same females) in different mating seasons, long-term tracking of individuals would allow for examination of the extent to which prior experience is used. Additionally, recording the exact movement paths that individuals use to arrive in the same areas in different years would provide information about the navigational abilities and strategies snakes have and use. Last, the resolution resulting from mapping the movement paths of individual snakes would allow researchers to know precisely how those paths fit straight-line or other possible efficient movement patterns.

Because sample sizes in my study are too small for meaningful statistical analyses (see Duvall and Schuett, 1997), the data pose more questions than they answer. In doing so, however, they direct our attention to an area of snake biology in need of further study. Data that definitely illustrate the mechanism(s) used by male snakes in locating females are rare. Further, mechanisms and strategies of mate location used by males appear to be many and varied within and among individuals, populations, and species. The elucidation of these mechanisms will require long-term studies on individuals in the field at a higher resolution than is typically available. Studies collecting these types of data will be instructive of the selective forces involved in shaping snake mating systems (Duvall et al., 1992, 1993).

Acknowledgments.—I enthusiastically thank Bethany Reisberger (who observed the copulation detailed herein, and the description is based on her field notes and conversations) and Vince Marshall for their work in the field. I also thank Doug Wynn for advice and support, Chris Caprette for discussions on the topic, Louis Iverson for help with the GPS, and the veterinary staff of the Columbus Zoo for performing implantation surgeries. John Clemm and Joe Barber of the Ohio Department of Natural Resources, Ohio Division of Wildlife (ODNR/ODW) helped in locating missing snakes from the air. I am grateful to (in alphabetical order) Nancy Anderson, Chris Caprette, David Duvall, Cory Fincher, Thomas Hetherington, Raksha Kink, Ed McGowan, Deni Porej, and Gordon Schuett for providing valuable comments on early drafts of this manuscript. The comments of an anonymous reviewer greatly improved the final draft. I thank Gordon Schuett for giving me the opportunity to participate in Biology of the Vipers Conference, for organizing it with Mats Höggren, and both of them and Michael Douglas and Harry Greene for editing this volume. I thank the United States Forest Service (USFS) for allowing me access to the field site and for use of the GPS unit. This project was funded by grants from the American Museum of Natural History, the Ohio Chapter of the Nature Conservancy, the USFS, and by a joint grant from Ohio State University (OSU) and the Columbus Zoo. All work was performed under an endangered wild animal permit granted by the ODNR/ODW, and I appreciate their cooperation. This work was conducted under OSU Institutional Laboratory Animal Care and Use Committee protocol # 95A0040.

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