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# Spatial learning of an escape task by young corn snakes, *Elaphe guttata guttata*

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Spatial learning is critical to most animals for many behaviours necessary to survival. In vertebrates, most studies on spatial learning and memory have been conducted in mammalian and avian species with few studies on reptiles. We examined spatial learning in the corn snake *Elaphe guttata guttata* by training 17 young snakes to find the one open shelter in an eight-hole arena, where the entrance was not visible from the arena surface. Over a 16-trial, 4-day training period, snakes showed (1) a significant decrease in the mean latency to the goal, (2) a significant decrease in the mean total distance travelled, (3) a significant increase in the percentage of the total distance travelled in the quadrant containing the goal, and (4) a significant increase in movement in the goal quadrant above chance. Although no differences were found in the number of errors made over the training period, snakes made fewer errors on all days than expected by chance. This study shows that snakes can learn rapidly a spatial-escape task that is relevant behaviourally and suggests that entering a shelter reinforces this learning. Mechanisms of orientation for the task described are discussed.

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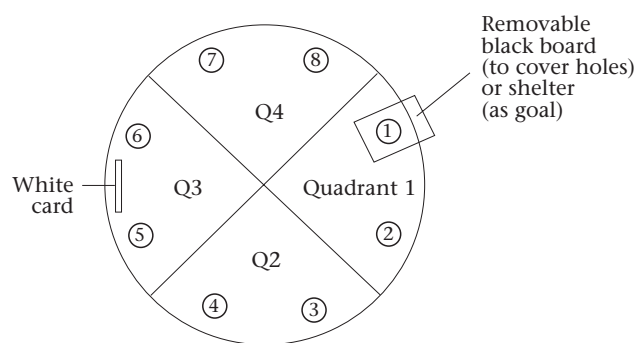
To generate general theories of learning and memory, it is important to study a broad range of species (Bingman 1992). Spatial learning is necessary for most animals to survive in their natural environment. Spatial problems encountered by animals in nature are relatively constant across species, such as returning home or going to and from a food source (Grobéty & Schenk 1992). The localization of food and shelter are among the tasks that are facilitated by spatial learning. Among amniotic vertebrates, studies of spatial learning and memory have been conducted primarily in mammals and birds (see Olton et al. 1979; Bingman 1990, 1992; Sherry et al. 1992; Benhamou & Poucet 1996). Although there have been some studies on spatial learning in reptiles, primarily in turtles and tortoises (reviewed in Burghardt 1977; and see Lenhardt 1981; Grisham & Powers 1990; Ishida & Papini 1997), very few spatial-learning studies

have used squamate reptiles (reviewed in Burghardt 1977).

Field studies strongly suggest that reptiles can learn and remember spatial tasks encountered in the wild, including orientation, homing and the localization of mates, shelter and foraging areas (crocodilians: Murphy 1981; Rodda 1985; chelonians: DeRosa & Taylor 1982; Yeomans 1995; Graham et al. 1996; Lohmann & Lohmann 1996; lizards: Adler & Phillips 1985; and snakes: Landreth 1973; Newcomer et al. 1974; Parker & Brown 1980; Lawson 1989; King & Duvall 1990; Weatherhead & Robertson 1990; Lawson & Secoy 1991; Durner & Gates 1993; see reviews by Owens et al. 1986; Gregory et al. 1987; Ford & Burghardt 1993). Most laboratory studies related to spatial learning in reptiles have used temperature or food as a reward (reviewed in Burghardt 1977; and see Grisham & Powers 1989, 1990; Day et al., in press). While many studies show that learning occurs, it is unclear whether subjects are learning based on spatial cues or learning to follow a trail, such as from chemical cues or a thermal gradient. In addition, laboratory studies on spatial abilities in reptiles have not been fruitful probably due to the use of tasks designed primarily for rodents (Burghardt 1977).

In the present study, we examine whether snakes can learn a behaviourally relevant spatial task when the goal

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**Figure 1.** Behavioural training arena (183 cm in diameter with a rim 61 cm high). Each of the eight holes was 7.68 cm in diameter and evenly spaced along the outer edge, 15 cm inside the outer perimeter. Snakes were placed in the centre of the black arena and trained to find an open hole (goal, see Methods for details). An inverted black shelter was placed under the goal. Only one hole was used as a goal for a given quadrant (e.g. even numbered holes in figure). The other seven holes were closed from underneath the arena by removable black boards. A large white card (60 × 30 cm) was placed on the wall of the arena in quadrant 3, with the lower edge of the card 15 cm above the floor of the arena. A video camera was suspended from the ceiling directly above the centre of the arena. A black sheet encircled the entire arena from ceiling to floor to minimize visual cues from outside the arena. Q: quadrant.

is not evident until it is reached. We developed a behavioural assay based on the ecology of snakes to address mechanistic hypotheses concerning spatial learning and memory. We hypothesized that snakes could learn an open-field escape task rapidly. We trained corn snakes to find an escape shelter through one of eight holes present in an open, brightly lit arena. Learning was indicated by changes in latency and path length to the goal and in a spatial preference for the arena quadrant with the goal. The results of this study support the results of previous orientation studies and show that snakes can learn a spatial task in a highly controlled environment.

## METHODS

### Subjects

We purchased 20 captive-born corn snakes (age 4–6 months; snout–vent lengths: 30–55 cm), from the Ophidian Research Colony (University of Texas at Tyler, Texas). Snakes used in the present study were of mixed sex and from six different litters. Snakes were housed individually in clear plastic sweater boxes at 27°C in our colony (12:12 h light:dark cycle) from the first week of birth and handled daily for the first month of life. Snakes were fed dead mice once a week and provided water *ad libitum*.

### Apparatus

A circular black arena (183 cm in diameter and 61 cm high) was used for training (Fig. 1). We cut eight holes (7.68 cm in diameter) in the bottom of the arena, evenly spaced along the outer edge and positioned 15 cm inside the outer perimeter. The arena consisted of a wooden

base and plastic rim around the perimeter of the base. The entire interior of the arena was painted black, using spray paint (Krylon, Columbus, Ohio). We secured a black plastic shelter beneath the hole opened for escape, and sealed off all other holes from beneath the arena (see Procedures below). We taped a large white cue card (60 × 30 cm) to the wall of the arena in quadrant 3, with the lower edge of the card 15 cm above the floor of the arena. Seven spotlights (250 W within a reflector) were situated evenly above the arena to enhance contrast for automated tracking and provide a bright open area. Generally, snakes of the genus *Elaphe* avoid bright, open areas (Fitch 1963; Durner & Gates 1993; D. A. Holtzman, personal observation), and juvenile corn snakes appear to be crepuscular (Burghardt 1978). We attempted to configure the environment to motivate snakes to search for shelter.

To minimize outside cues and experimenter interference, we hung black curtains around the arena from the ceiling to the floor. In addition, we used a Panasonic CCTV camera, mounted directly above the centre of the arena and connected to a computerized tracking system, HVS Water (HVS Image, Hampton, U.K.), for automated tracking of snakes. The HVS Water tracking system functioned with a DOS-based personal computer.

## Procedures

We trained 17 of the 20 snakes (chosen randomly from different litters and for each sex) to locate an open hole within the arena. We randomly chose one hole to remain uncovered (the goal) for each snake and placed a black plastic shelter beneath it with crumpled paper towels to provide a dark haven for escape from the arena. We submerged the opening of the goal 2.5 cm. Therefore, the goal could not be seen by snakes within the arena until they reached it. We covered the other seven holes from underneath the arena (2.5 cm below the surface) using pieces of posterboard painted black. No snakes were assigned to a goal hole within the same quadrant as a previous snake within the arena (i.e. goal holes were separated by at least one other hole for each successive snake placed in the arena).

Prior to their introduction into the arena, we placed the snakes in a styrofoam box. We then covered the box with a piece of cardboard and, holding it in place, inverted the box and placed it in the centre of the arena. We approached the arena from different directions around the arena for each trial and each snake. We pulled the cardboard out from under the box, leaving the snake on the floor of the arena and surrounded by the box. We allowed the snakes to remain under the box for 20 s before beginning a trial. To begin a trial, we lifted the box out of the arena and allowed the snake to move freely. At the time of release, we activated the automated tracking system. Trials lasted 15 min or until the snakes found the goal. When the goal was found, we allowed the snakes to remain in the goal shelter for 1.5 min. If a snake had not found the goal after 15 min, we gently guided the snake to the goal entrance and allowed it to stay in the escape shelter for 1.5 min.

We trained snakes individually in three groups of four and one group of five snakes. We conducted four trials/day for 4 days for each snake. We used four trials/day to optimize the efficiency of collecting data over many trials. Preliminary studies have shown that corn snakes learn the task described in this study faster with four trials/day than with one or two trials/day (unpublished data). We maintained intertrial intervals (from the beginning of one trial to the beginning of the next) at 80 min for each snake. We ran successive trials only after each snake within a group had finished the previous trial(s); that is, all first trials were run before second trials, etc. To avoid any effects of conspecific odours on subsequent behaviour, we cleaned the arena and the painted hole covers with a damp, soaped sponge following each trial, wiped them clean with water, and dried them. For each trial, we also washed the goal shelter with soap and water and dried it, and we changed the paper towels within the goal. We performed each set of trials for each group at the same time of day, between 1200 and 1700 hours.

For the 17 snakes trained in the arena, we recorded the following variables: (1) latency (in seconds) to reach the goal; (2) total distance (cm) travelled during the trial (used as a quantitative measure of path length to the goal); (3) the percentage of total distance spent in each quadrant (see Fig. 1) of the arena (used as a quantitative measure of spatial preference); and (4) errors made. We defined errors as every instance that a snake's head crossed the edge of a closed (nongoal) hole. We recorded a correct response when the snake's head crossed the edge of the goal hole, and we ended the trial if the snake found the goal.

We conducted extinction trials to determine whether access to an open hole reinforces the learned behaviour. We ran extinction trials on three snakes that showed learning based on decreases in latency to enter the goal shelter and increased movement in the goal quadrant (see Results). Immediately following the initial 4-day training period, we covered the goal along with all other holes. We then ran trials for 15 min as described above. We ran four extinction trials/day for each snake for 6 consecutive days following training. We obtained two measures for extinction trials, the latency to cross the formerly opened goal and the percentage of distance travelled in the former goal quadrant.

The three snakes, which had not been used previously, were treated identically to the trained snakes, except that all eight holes were covered for the 4-day training period. At the end of each 15-min trial, we returned these controls to their home cages. To quantify locomotor activity and identify any quadrant preferences within the arena, we determined the mean total distance travelled within the entire arena and the percentage of total distance travelled within each quadrant for each of the three control snakes.

## Statistics

We analysed the mean latency to the goal, total distance travelled, percentage of distance travelled in the goal quadrant, and number of errors over the 4 training days by a two-way (trials  $\times$  day) repeated measures analy-

ses of variance (ANOVA). To determine whether the snakes performed better in certain trials each day, we used post hoc *t* tests to determine whether there were significant decreases in latency and total distance travelled from the first to fourth day for each trial. We also compared the percentage of distance travelled in the goal quadrant and number of errors made to responses that would be predicted by chance, using two-tailed one sample *t* tests on the mean responses for each day. If snakes were moving randomly, 25% of the total distance travelled would be expected in the goal quadrant. Assuming a subject could make between zero and seven errors before finding the goal, a mean of 3.5 errors is predicted if snakes were investigating holes randomly. Although snakes could return to the same nongoal hole more than once (i.e. make many more than seven errors), we used 3.5 errors as the most conservative measure of chance performance (random movement with more potential errors would give a predicted value of more than 3.5).

For snakes used in extinction trials, we used nonparametric Friedman ANOVAs to test for differences between days in the latency to the goal and in percentage of distance travelled in the former goal quadrant. We also used Friedman ANOVAs to test for differences between days in the total distance travelled by the controls, which were never given an open hole. We used post hoc Wilcoxon signed-rank tests to test for differences between data from different days for the extinction trials. We performed all statistical tests using Statview and SuperANOVA (Abacus Concepts, Berkeley, California). Statistical significance was set at  $\alpha=0.05$  for all tests.

## RESULTS

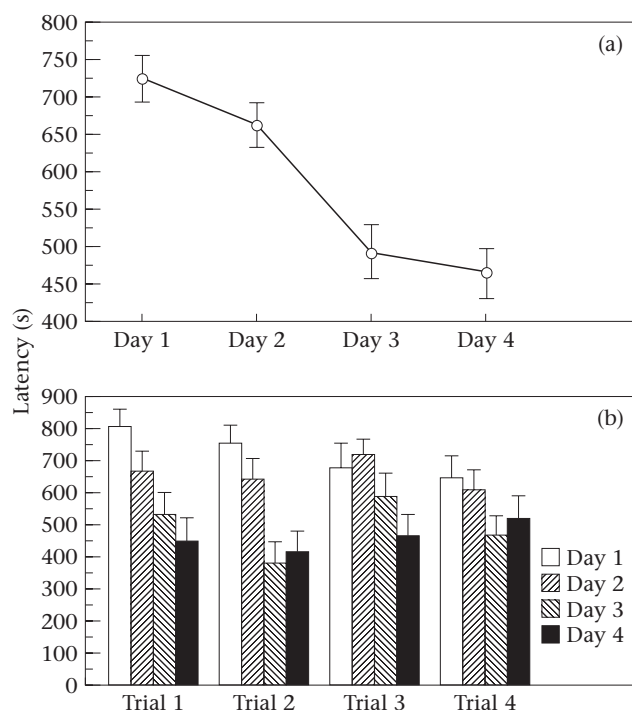
### Latency

There was a significant decrease in latency over the 4-day training period ( $F_{3,16}=13.79$ ,  $P<0.0001$ , Fig. 2a), with latencies decreasing steadily from the first day of training (mean  $\pm$  SE latency =  $723.56 \text{ s} \pm 31.04 \text{ s}$ ) to the fourth day of training ( $463.46 \pm 33.79 \text{ s}$ ; Fig. 2a). There were no significant differences between trials ( $F_{3,16}=1.44$ ,  $P>0.05$ ), nor was there a significant interaction between days and trials ( $F_{9,48}=1.46$ ,  $P>0.05$ ; Fig. 2b). Post hoc *t* tests showed significant decreases between the first and fourth day for the first trial ( $t_{16}=4.76$ ,  $P<0.0001$ ), second trial ( $t_{16}=4.43$ ,  $P<0.0001$ ), and third trial ( $t_{16}=2.84$ ,  $P<0.005$ ; Fig. 2b).

### Movement

#### Total distance travelled

There was a significant decrease for the total distance travelled/trial over the 4-day training period ( $F_{3,16}=10.45$ ,  $P<0.0001$ ), from  $1706.17 \pm 130.62 \text{ cm}$  on day 1 to  $850.80 \pm 103.17 \text{ cm}$  on day 4 (Fig. 3a). There were also significant differences between trials in the distance travelled ( $F_{3,16}=6.54$ ,  $P<0.001$ ), with the distance travelled in trial 2 ( $1138.64 \pm 108.29 \text{ cm}$ ) being less than that in trials 1 ( $1555.42 \pm 125.23 \text{ cm}$ ), 3



**Figure 2.** Mean ( $\pm$ SE) latencies (s) to enter goal. (a) By day; and (b) trial by day. See text for statistically significant differences.

(1700.73  $\pm$  132.76 cm), and 4 (1550.58  $\pm$  120.50 cm; Fig. 3b). There was also a significant interaction between trials and days ( $F_{9,16}=2.28$ ,  $P<0.02$ ; Fig. 3c), with significant decreases between the first and fourth day for every trial (trial 1:  $t_{16}=4.11$ ,  $P<0.0001$ ; trial 3:  $t_{16}=2.41$ ,  $P<0.02$ ; trial 4:  $t_{16}=2.28$ ,  $P<0.03$ ), except in trial 2 ( $t_{16}=-1.31$ ,  $P>0.05$ ; Fig. 3c).

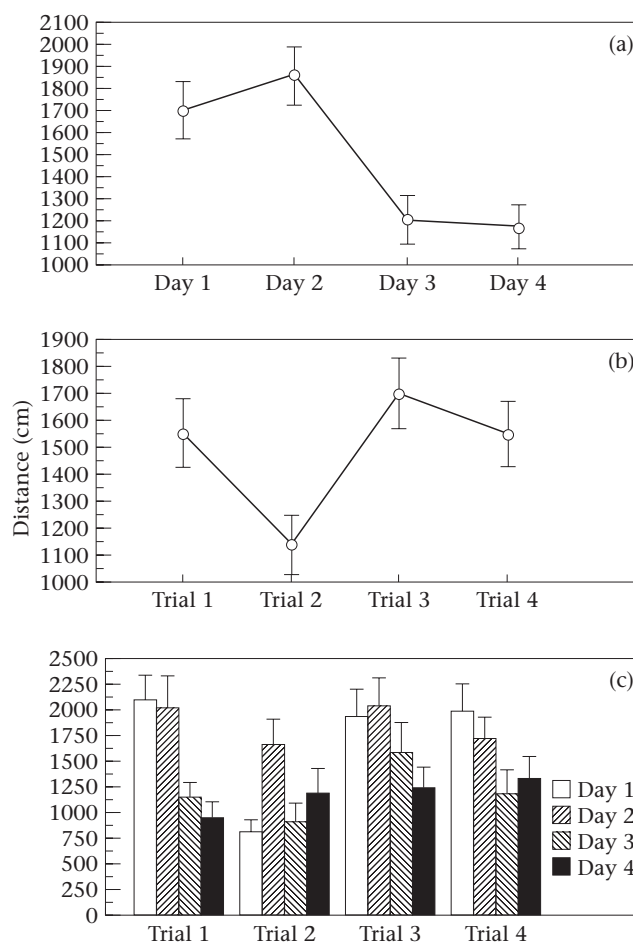
#### Percentage of distance travelled in goal quadrant

There was a significant increase in the percentage of distance travelled in the goal quadrant over the training period ( $F_{3,16}=5.56$ ,  $P<0.002$ ), from day 1 (27.13  $\pm$  1.77%) to day 4 (37.88  $\pm$  3.07%; Fig. 4). Snakes moved into the goal quadrant significantly more often than predicted by chance on the third ( $t_{16}=3.74$ ,  $P<0.002$ ) and fourth ( $t_{16}=3.20$ ,  $P<0.006$ ) days. There were no differences from chance movement in the goal quadrant for the first and second days (Fig. 4).

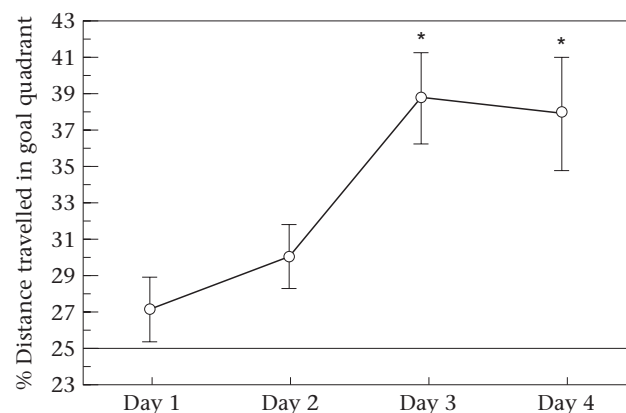
Changes in the percentage of distance travelled in the goal quadrant are reflected by the actual paths taken (Fig. 5). Snakes were more likely to take circuitous routes to the goal during the first day of training, staying mostly against the wall of the arena. With continued training, snakes took more direct paths to the goal (Fig. 5).

#### Errors

There were no significant changes in the number of errors made over the training period ( $F_{3,16}=1.95$ ,  $P>0.05$ ; Fig. 6), between trials ( $F_{3,16}=1.53$ ,  $P>0.05$ ), nor was there a significant interaction between days and trials ( $F_{9,48}=1.66$ ,  $P>0.05$ ). However, fewer errors were made



**Figure 3.** Mean ( $\pm$ SE) total movement (cm) within arena. (a) By day; (b) by trial; and (c) trial by day.



**Figure 4.** Mean ( $\pm$ SE) percentage of distance travelled in the goal quadrant for each day of training. Line at 25% indicates level of chance response (see text for details and analysis). \*Significantly higher than chance responses ( $P<0.05$ ).

than expected by chance for all days (day 1:  $t=-5.10$ ,  $P<0.0002$ ; day 2:  $t=-7.69$ ,  $P<0.0001$ ; day 3:  $t=-10.69$ ,  $P<0.0001$ ; day 4:  $t=-7.74$ ,  $P<0.0001$ ;  $df=16$  for all; Fig. 6). The mean ( $\pm$ SE) number of errors remained between 1.85  $\pm$  0.23 for the first day and 1.38  $\pm$  0.27 on the fourth day.



## Extinction

Figure 7 shows the latencies over the 4-day training period and for the 6 days of extinction trials. There were significant changes in latency to find the goal over the training and extinction trials ( $\chi^2_9=50.32$ ,  $P<0.0001$ ; Fig. 7). As for the entire group, the three snakes in the extinction trials showed significant decreases in latency to locate the goal from day 1 to day 4 of the training period ( $818.75 \pm 42.85$  s versus  $256.25 \pm 18.64$  s,  $P<0.05$ ; Fig. 7). Although there was no significant change in latency to locate the goal between the last day of training and the first day of extinction ( $256.25 \pm 18.64$  s versus  $240.08 \pm 17.63$  s,  $P>0.05$ ; Fig. 7), there was a significant increase in latency from the first day of extinction to the sixth day of extinction ( $240.08 \pm 17.63$  s versus  $627.75 \pm 66.73$  s,  $P<0.05$ ; Fig. 7).

There were also significant changes in the percentage of distance travelled in the former goal quadrant over the training and extinction periods ( $\chi^2_9=42.00$ ,  $P<0.0001$ ; Fig. 8). The percentage of movement in the goal quadrant increased significantly from day 1 to the day 4 of training ( $21.70 \pm 1.12\%$  versus  $45.41 \pm 5.56\%$ ,  $P<0.05$ ; Fig. 8), but there was no significant change between the last day of training and the first day of extinction ( $45.41 \pm 5.56\%$  versus  $48.92 \pm 5.33\%$ ,  $P>0.05$ ; Fig. 8). However, there was a significant decrease in the percentage of movement in the goal quadrant from the first day of extinction to the sixth day of extinction ( $48.92 \pm 5.33\%$  versus  $27.13 \pm 1.84\%$ ,  $P<0.05$ ; Fig. 8).

## Controls

There were no significant differences between controls in the distance travelled in the arena or within each quadrant over the 4-day period ( $\chi^2_3=6.00$ ,  $P>0.05$ ; Fig. 9). However, one snake showed a preference for quadrant 3 (with the white cue card) from day 2 through to day 4.

## DISCUSSION

Previous studies on the spatial learning abilities of snakes have suggested that this group performs poorly in maze tests (reviewed in Burghardt 1977). The present study shows that snakes can rapidly learn a spatial task that is relevant to their natural behaviour. Qualitative differences in behaviour were noted between individual snakes. During the first day of trials, most snakes tended to travel quickly around the arena wall (thigmotaxis) once they began moving (see Fig. 5), as shown for lizards (L. B. Day, personal communication). Over subsequent trials, some subjects continued to move quickly while others moved more slowly. These differences could indicate that slower moving subjects were more comfortable within the arena (i.e. had less motivation to escape) or were less motivated to explore than those that moved more quickly. Investigatory behaviour in snakes has been shown to decrease with increased familiarity of an environment (Chiszar et al. 1976). However, the data from the present experiment suggest that snakes may

increase exploratory behaviour with repeated trials during the same day (see Fig. 3b). Although both sexes and individuals from different litters were used, we did not test for sex and litter effects, which could contribute to the variation observed for corn snakes in the task used in the present study. No reliable differences have been found between the sexes in the size of home ranges for snakes (reviewed in Gregory et al. 1987). Litter effects have been shown for other behaviours in snakes, such as feeding responses (see Burghardt 1978).

## Latency

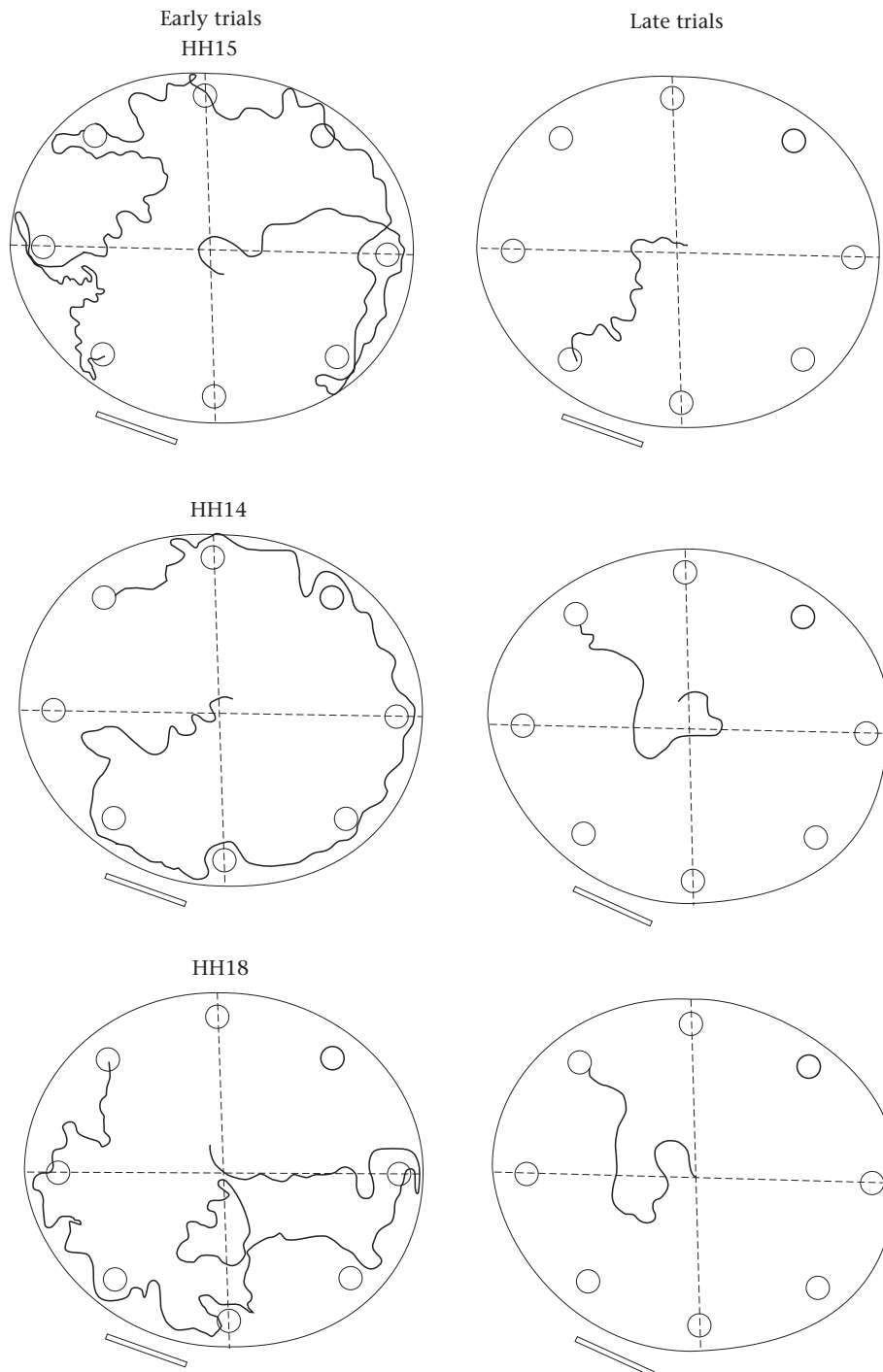
Changes in latency, and the lack of changes in latency, have been noted in other studies involving spatial learning in snakes (reviewed in Burghardt 1977). In the present study, latency to find the goal decreased significantly over the 4-day training period (Fig. 2a). Significant decreases occurred over the training period for all trials except the fourth (Fig. 2b), suggesting that the snakes did not perform as well during the fourth trial. This result may have been due to increased exploratory behaviour during the fourth trial, as described above.

Differences were also noted between some individuals in the latency to first movement at the beginning of each trial. On the first day of trials, all snakes remained at the release point, in the centre of the arena, for 1–5 min. Some snakes continued to remain stationary at the centre of the arena upon release for the subsequent trials, and others tended to move as soon as they were released. As mentioned above, individual differences in performance may be due to differences in motivation for escape in this task.

## Movement

The amount of total distance travelled decreased significantly over the 4-day training period (see Fig. 3a). Snakes travelled less during the second trial than for all other trials (Fig. 3b). For the first, third and fourth trials, there were significant decreases in the total distance travelled from the first to fourth days, but no changes were seen in the total distance travelled from the first to fourth days during the second trial of each day (see Fig. 3c). These results suggest that more direct paths were taken over time in each of the trials, except the second trial, where snakes appeared to perform well each day.

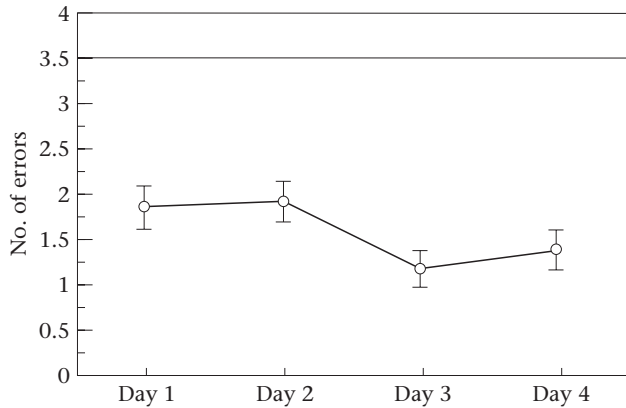
The snakes also showed a preference for the goal quadrant by the third day of training (Fig. 4). Increases in the percentage of movement within the goal quadrant correspond with movement above chance observed in that quadrant by the third day. Together, the movement data suggest that snakes acquired a preference for their goal quadrant. Although quadrant 4 was selected randomly as the goal quadrant for eight snakes, it is unclear whether snakes learned better when trained to this quadrant, based on fewer numbers trained in other quadrants. While the snakes' performance varied for the movement measures, individuals did show preferences for other goal quadrants. In addition, control snakes showed no preference for any quadrants, with the exception of one that



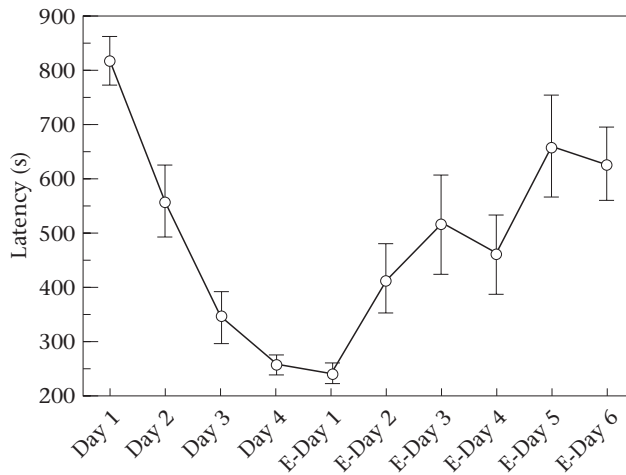
**Figure 5.** Paths taken by three corn snakes during early and late training trials. Notice the circuitous paths taken before reaching the goal during early trials. Paths taken to reach the goal were much more direct during later trials. For snake HH15, the early trial was the second trial of day 1, and the late was the third trial of day 4; for snake HH14, the early trial was the first trial of day 2, and the late trial was the fourth trial of day 4; and for snake HH18, the early trial was the first trial of day 1, and the late was the third trial of day 4. The rectangle in the lower left represents the position of the card on the wall in quadrant 3. Quadrant 1 is in the upper right.

showed a preference for quadrant 3 (with the cue card, see below). Although the data suggest that there were no consistent cues that facilitated learning the task in quadrant 4, we cannot exclude differences in the performance of individual snakes based on assignments to different quadrants.

The paths taken to the goal became much more direct with experience (Fig. 5). These results show that new paths were formed and that finding the goal was not achieved using a simple strategy, such as circling. M. Kunka, I. G. Bernstein and J. L. Kubie (unpublished data) found that Plains garter snakes, *Thamnophis radix*,



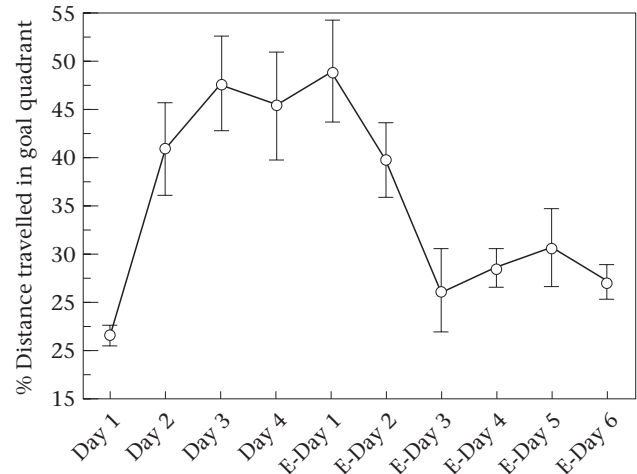
**Figure 6.** Mean ( $\pm$ SE) number of errors made prior to locating the goal. An error was recorded whenever a snake's head crossed the edge of a nongoal hole. The line at 3.5 indicates the level of chance response (see text for details and analysis). All points were significantly lower than chance responses ( $P < 0.05$ ).



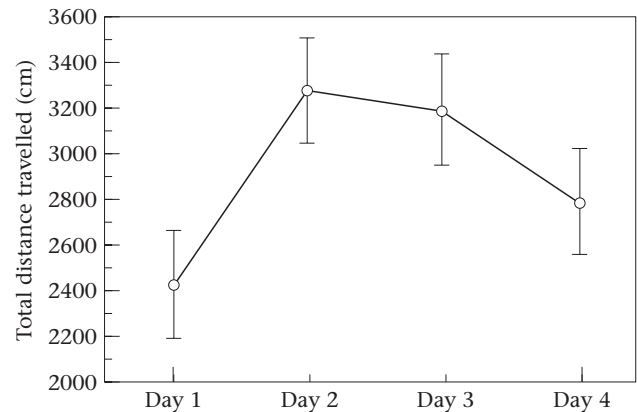
**Figure 7.** Mean ( $\pm$ SE) latencies (s) for three snakes during the 4-day training and 6-day extinction (E) periods.

performed better than chance in finding food rewards in four- and eight-arm radial mazes, and that the snakes did not use circling as a strategy. These data suggest that snakes form spatial memories and may use different mechanisms to orient (see Mechanisms of Orientation below).

A qualitative difference was noticed in the paths taken by individuals. Initially, all snakes moved directly to the arena wall. By the end of the fourth day of trials, some snakes made a random choice of path, while others were more consistent in their choice of direction. Importantly, the direction chosen by individuals appeared to be different, such that different snakes moved in different directions. These results suggest nonrandom movement, which is supported by the preference for goal quadrants. Nonrandom orientation has been described in snakes (Landreth 1973; Newcomer et al. 1974; Parker & Brown 1980; Gregory et al. 1987; Lawson 1989; King & Duvall 1990; Lawson & Secoy 1991; Durner & Gates 1993; Ford & Burghardt 1993), with discussion of mechan-



**Figure 8.** Mean ( $\pm$ SE) percentage of distance travelled in the goal quadrant by three snakes during the 4-day training and 6-day extinction (E) trials.



**Figure 9.** Mean ( $\pm$ SE) total movement (cm) within the arena for three control snakes during a 4-day period. There were no significant differences between days ( $P > 0.05$ , see text for details).

isms of orientation (see Mechanisms of Orientation below).

Most snakes travelled extensively in one quadrant adjacent to the goal quadrant, as well (data not shown). These results suggest that our distinction of quadrants may not have been representative of areas that snakes used as 'goal quadrants'. That is, the separation of the arena into four quadrants was made arbitrarily by the tracking software. The snakes' representation of the arena may have included adjacent quadrants as areas associated with the goal.

## Errors

Decreases in (and the lack of changes in) the number of errors have been noted in other studies involving spatial learning in snakes (reviewed in Burghardt 1977). Theoretically, the snakes in our studies could have made more than seven errors (as predicted; see Methods) before finding the goal by returning to nongoal holes



encountered previously. Snakes did return to nongoal holes before going to the goal, but no more than seven errors were made during a single trial. There were also no changes observed in the number of errors made over the 4-day training period (Fig. 6). However, fewer errors (approximately 1.5 errors on average) were made than expected by chance (3.5 errors) on all days. These results suggest that snakes may be learning the task extremely quickly. M. Kunka, I. G. Bernstein and J. L. Kubie (unpublished data) calculated a spatial memory of two to three arms in experiments using garter snakes in four- and eight-arm radial mazes. However, no changes in latency to find a food reward were observed in their experiment.

In the present study, snakes may have been able to find the goal but chose to investigate one to two other holes before entering the goal. The consistency in the number of errors made is interesting in light of the observed decrease in path length to reach the goal over the training period. This result suggests that the investigation of nongoal holes is an important behaviour given that it was maintained throughout training. Snakes may be looking for other escape routes within the environment and/or demonstrating a natural tendency to explore.

## Extinction

The results of the extinction trials showed that corn snakes can locate the goal hole without an opening present, but entering the goal is necessary to reinforce learning. The snakes' ability to find the goal in the absence of an opening strongly suggests that they do not need a direct cue from the goal in order to find it. When entry into the goal shelter was blocked, the snakes showed an increase in latency to locate the goal (Fig. 7) and a decrease in distance travelled in the goal quadrant in subsequent trials (Fig. 8). The inverse relationship between latency to locate the goal and distance travelled in the goal quadrant are thus tightly correlated with entering the goal.

During the training period, individuals moved consistently in specific directions from the start, with each snake going in a different direction (as mentioned above). During extinction trials, all three snakes moved directly towards the white card. This result suggests that the snakes may have travelled in relation to the white card during the training period, but in the absence of a goal, they used the white card as a beacon for directed movement.

## Controls

Control snakes showed no significant differences in the distance travelled in the arena or in each quadrant over the 4-day period. The slight preference by one snake for the quadrant containing the white card further supports the idea that the white card may have functioned as a cue for directed movement in the absence of an open hole, as in the extinction trials. The lack of preferences for quadrants (other than the one containing the white card) suggests that the snakes' behaviour was not influenced by the arena itself.

## Mechanisms of Orientation

Mechanisms of orientation were not tested explicitly in the present study. Several results suggest that snakes were not moving randomly in the arena. Consistent, directed movements were made to the goal. When snakes were denied access to the goal, they changed their directed movements to the white card on the arena wall. A previous study from our laboratory has shown that adult snakes trained in a circular arena with visible goals will rotate their responses when the card is rotated (Holtzman 1998). Interestingly, some of these snakes also rotate their behaviour with arena rotation, suggesting use of tactile cues on the arena floor or some other intra-arena cue not obvious to us. Landreth (1973) suggested that rattlesnakes may use tactile cues for orientation and goal learning in the field. Although the visual cue afforded by a card on the arena wall is obvious, we cannot discount the presence of a distinct odour emanating from the card. The use of olfactory cues for orientation has been suggested for snakes and other reptiles (reviewed in Owens et al. 1986; Ford & Burghardt 1993).

Ongoing studies with snakes of the same size and age have shown that orientation will shift with card or arena rotation (D. Holtzman, A. Jain, W. Amaya & T. Nyberg, unpublished data). However, some individuals do not appear to be affected by either manipulation, suggesting use of some other cue, probably outside the arena. The use of solar cues is well documented in snakes (Landreth 1973; Newcomer et al. 1974; Lawson 1989; Lawson & Secoy 1991); the most convincing evidence comes from clock-shift studies and predicted behavioural rotation (Newcomer et al. 1974; Lawson 1989). It should be noted that it is unclear what aspects of solar radiation are used by snakes. Lawson & Secoy (1991) hypothesize that polarized light may be used for orientation in garter snakes, as described for the desert lizard *Uma notata* (Adler & Phillips 1985). It is unknown whether snakes can use stellar or lunar cues, as suggested for alligators (Murphy 1981). In the present study, snakes could have used a 'celestial' cue outside the arena such as the array of overhead lamps. Alternatively, other cues could have been used, such as vibrational cues as described for a lizard (Hetherington 1989), acoustic cues as described for a turtle (Lenhardt 1981), or geomagnetic cues as described for sea turtles (Lohmann & Lohmann 1994, 1996) and alligators (Rodda 1984). Snakes probably use a number of cues available to them as demonstrated in other animals (Able 1991).

We suggest that movements by trained snakes within the arena were not made by using the cue card as a beacon and travelling towards it. This hypothesis is supported by the development of more direct paths used by the end of the training period. If a beacon alone were being used, we would expect movement towards a specific place, with specific turns made afterward. For example, snakes could have learned to go to or away from the cue card and then make a specific turn to get to the goal. By the end of the training period, fairly direct routes were taken to the goal (see Fig. 5). It appears that the snakes were using the cue card as a landmark. Preliminary studies have shown that snakes trained identically to those in the present study move directly to the goal when

released from a novel location within the arena (D. Holtzman, A. Jain, W. Amaya & T. Nyberg, unpublished data). Rats are capable of solving a spatial problem without the use of direct cues from the goal (Morris 1981). A later study showed that spatial learning is facilitated by landmark stability and associated context cues (Biegler & Morris 1996). Obviously, these factors would be beneficial to any animal in its natural environment. Taken together, results with snakes suggest that snakes use a configuration of cues to learn the location of a goal. Alternatively, path integration may be used by the snakes to make more direct paths to the goal over time (Bennett 1996).

Species differences in snakes are evident in the amount of time or number of trials needed to learn spatial tasks (Newcomer et al. 1974; Burghardt 1977). However, these studies are difficult to compare because different methods and criteria were used to establish learning. A recent report suggests that spatial learning in lizards differs from that of rodents (Day et al., in press). We are currently investigating the specific cues used by snakes to solve spatial tasks. We have obtained preliminary evidence for differences in learning for snakes of different ages and species using the same task described for the present study (Holtzman 1998; D. Holtzman, A. Jain, W. Amaya & T. Nyberg, unpublished data). By comparing results from a variety of snake species with different natural histories and phylogenetic relationships, we hope to test hypotheses of the relationships between spatial ability, ecology and phylogeny, as well as the mechanisms used by snakes for spatial learning and memory.

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