Orientation Abilities and Mechanisms in Nonmigratory Populations of Garter Snakes (Thamnophis sirtalis and T. ordinoides)

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I tested the navigational abilities in nonmigratory populations of garter snakes (*Thamnophis sirtalis* and *T. ordinoides*) from Spectacle Lake Provincial Park on Vancouver Island, British Columbia, Canada. Displacement studies were carried out from 1986–88 to determine the level of orientational abilities present in each species and to examine potential orientation cues. Snakes were displaced from their home range and tested in an arena under a variety of conditions. The results demonstrated that nonmigratory *T. sirtalis* possessed advanced navigational abilities. Advanced abilities may be absent in *T. ordinoides*. *Thamnophis sirtalis* demonstrated time-compensated solar orientation as determined by 6-h phase-delayed tests. Pheromone trails produced by gravid females, but not by males, may also provide an orientation guide for *T. sirtalis* under some conditions. *Thamnophis ordinoides* did not respond in a discernible way to either solar or pheromonal cues. The findings of this study were compared with similar tests performed on a migratory population of *T. sirtalis*. Navigational skills vary little between migrating and nonmigrating populations of the same species but may be poorly developed in nonmigratory species.

A NIMALS that migrate long distances presumably have well-developed orientational abilities that allow them to locate widely separated goals rapidly and accurately. Griffin's (1952) studies on orientation in birds provided a useful system for categorizing orientation behavior. In its simplest form, Type I orientation (random wandering or piloting by using familiar landmarks as guides) allows an animal to locate goals. Type II orientation includes the ability to select a specific compass direction regardless of where it leads. Type III orientation, or navigation, is more complex in that it includes a map component in addition to a compass sense. Navigation allows an animal to fix its present location relative to that of a distant goal in relation to, or as a function of, the existence of such a map.

Snake movements range from short, erratic wanderings (e.g., Blanchard and Finster, 1933; Hirth et al., 1969; Fitch and Shirer, 1971) to long, unidirectional migrations (e.g., Madsen, 1984; Macartney, 1985; Larsen, 1987). I have previously reported on advanced navigational abilities in a northern migratory population of the common garter snake, *Thamnophis sirtalis* (Lawson, 1989). Gregory et al. (1987) suggested that snakes would display different degrees of orientation ability in relation to their normal patterns of movement behavior. However, prior to the present study, that hypothesis had not been examined.

This paper presents the findings of orientation studies performed on two populations of nonmigrating garter snakes—*Thamnophis sirtalis*, the common garter snake, and *T. ordinoides*, the northwestern garter snake—from the same study site on Vancouver Island, British Columbia, Canada. In conjunction with Lawson (1989), I address the hypothesis that orientational abilities in snakes differ according to normal movement behavior. By comparing both migratory and nonmigratory populations of *T. sirtalis*, phylogenetic and physiological differences are minimized, thus allowing a more accurate examination of the effect of ecological variation on orientational abilities. Phylogenetic differences, on the other hand, can be ex-
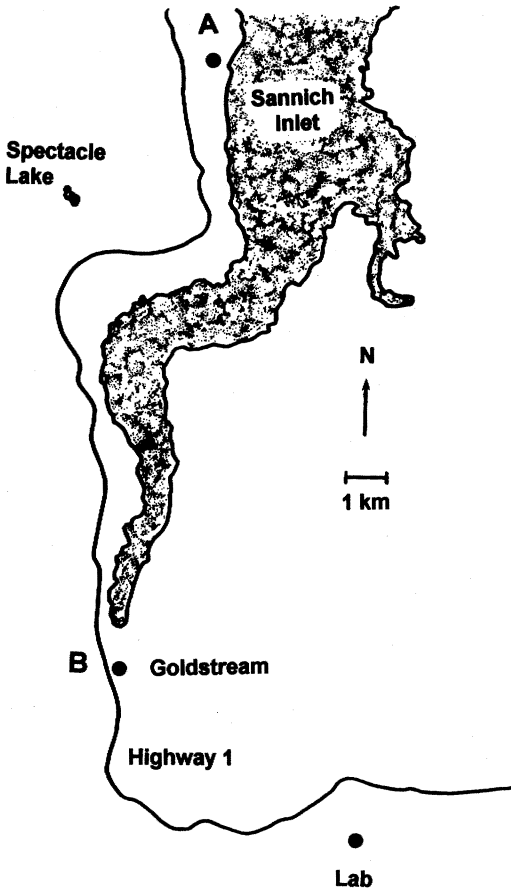
Fig. 1.   Location of test sites A and B and the laboratory relative to Spectacle Lake.

plored by comparing orientational behavior of different species living in the same environment.

Snakes demonstrating either Type II or Type III orientation must possess a compass sense. Chemosensory (Fitch, 1960; Brown and Parker, 1976; Lawson, 1989) and solar cues (Landreth, 1973; Newcomer et al., 1974; Lawson and Secoy, 1991) have been suggested or demonstrated as orientation guides for migrating snakes. The possible use of these reference systems was examined for the nonmigratory Vancouver Island snakes. Phase-shifting tests involving resetting the internal clocks of the subjects and conspecific pheromone trails were used to examine these potential cues.

Finally, orientation capabilities of neonates was considered. Young snakes of migratory populations are often born at some distance from communal hibernacula; and their ability to locate a suitable den, whether one used by the adults or a different one, has often been questioned. Scent trailing has been suggested as an

important cue used by neonates to achieve this (Brown et al., 1982; King et al., 1983; Duvall et al., 1985), yet only a few studies have dealt specifically with this question (Brown and MacLean, 1983; Reinert and Zappalorti, 1988). The ability of neonates to orient using solar cues alone has not been examined previously.

METHODS

Study area and general procedures.—Most snakes used in the study were collected from Spectacle Lake Provincial Park (SLPP) (48°34′N, 123°34′W) on southern Vancouver Island, British Columbia, Canada (Fig. 1). Some tests involved snakes collected from Goldstream Park (site B, Fig. 1). Spectacle Lake Provincial Park is largely forested and occupies approximately 83 ha. The climate is generally mild throughout the year with a winter rainy season.

Two snake species are common at SLPP—*T. sirtalis* and *T. ordinoides*. No large communal dens have ever been noted at SLPP, and suitable hibernation sites appeared to be abundant. Prey items (primarily frogs, salamanders, and worms for *T. sirtalis* and exclusively slugs and worms for *T. ordinoides*; Gregory, 1984; pers. obs.) were common throughout the study area. Long-distance movements of snakes apparently do not occur (unpubl.).

Snakes were captured by hand and given individual identification marks by removing unique combinations of subcaudal scutes (Blanchard and Finster, 1933). Larger snakes were sexed by probing for hemipenes (Schaefer, 1934), and small snakes were sexed by attempting to evert the hemipenes (Gregory, 1983). Snout–vent lengths (SVL) were determined to the nearest 5 mm.

Movements.—Movement patterns of snakes were determined from the recapture of marked snakes. Maps of SLPP were made using aerial photo enlargements (scale 1:33). Distances and directions were calibrated by ground survey. Consecutive capture points of snakes were mapped, and directions and distances of movements were determined from the maps.

To determine whether the members of each population moved in a common direction, i.e., displayed population directionality, only movements of 10 m or more were considered for analysis. I examined directionality for three periods: (1) movements occurring during spring (1 March–31 May); (2) movements occurring during summer (1 June–31 Aug.); and (3) movements in which the snake was first captured in the spring and captured for the second time in

the summer. Autumn movements were not examined because of insufficient sample sizes. Data were examined for both unimodal and bimodal tendencies with the latter case indicating an axis of travel rather than a single direction. Directionality of movements of the SLPP populations were analyzed by circular statistics (see below).

Orientation test procedures.—Orientation testing of adults was performed in the spring and summer of 1987 and 1988. Unless otherwise indicated, tests were performed on either clear days or on partially cloudy days while the sun was visible. Except for the phase-shifting tests, snakes were collected and tested on the same day. Snakes were transported to the test site in wire mesh cages that permitted a view of the sky between the time of capture and testing.

Two test sites were selected (A and B; Fig. 1), approximately 6 km in roughly opposite directions from Spectacle Lake. All snakes were tested singly to prevent the actions of any one snake influencing those of another. Each snake was placed in a release box in the center of the test area, a 6 m diameter, 1 m high octagonal arena made with eight sheets of styrofoam insulation board. The arena was placed over a level gravel substrate. After a 5-min adjustment period, the box was raised by a string attached to the box. The movement of the snake was monitored by an observer standing still outside the arena, and the point of contact with the arena wall was recorded as the directional choice of the snake. Preliminary tests demonstrated that, as long as there was no movement by the observer, the presence of the observer did not influence the snake's directional choice. The substrate was raked between trials to disperse any odors that might have been deposited during a trial (see Pheromone trailing).

Testing primarily involved adults although some neonates were also tested. To obtain neonates, some gravid females were captured and kept in cages, some at SLPP and others at the laboratory (Fig. 1); no wild-born neonates were used in orientation tests. Three categories of captive-born neonates were tested: (1) born outside at SLPP; (2) born outside at the laboratory; and (3) born inside at the laboratory and kept inside until testing. In the last category, no attempt was made to mimic natural light conditions. These categories were selected to test the hypothesis that neonates imprint upon solar cues present at the birth site.

The testing procedure described above was the protocol for the basic orientation tests. Results of these tests were used to determine the orientation type (Type I, II, or III).

Solar orientation.—Phase-shifting was used to identify the use of time-compensated azimuth position as an orientation guide. In all but one phase-shift test, snakes were removed from the field and subjected to a 6-h delayed LD shift by keeping them in indoor cages under an artificial photoperiod (one 60-W incandescent bulb). "Sunrise" was delayed 2 h/day from true sunrise for the first three days of captivity, and the snakes were maintained under the 6-h delay for an additional day. No attempts were made to mimic ambient temperatures, and room temperatures were approximately 20 C over the course of the phase-sifts. One group of SLPP *T. sirtalis* was subjected to a 6-h phase-advance. A control test, in which the animals were removed from the field but kept under natural light conditions for four days prior to testing was also performed for SLPP *T. sirtalis*. Males and females were housed together during the phase-shift. Phase-shift tests were carried out for the SLPP *T. sirtalis* at both test sites but only at test site B for *T. ordinoides*.

Pheromone trailing.—Pheromone trails were produced by directing a conspecific along a 40 cm corridor inside the arena prior to a test. The direction in which the trail was laid was outside the 95% confidence interval of the mean direction selected by snakes in the basic orientation tests. Occasionally, however, a stimulus snake was allowed to select its own direction. Such a trail was used as a stimulus only if it was outside the 95% confidence interval of the mean direction from the basic tests. Trail tests were performed on both clear and cloudy days. All trailing tests were performed at test site B.

Trailing tests involved males and females as both stimulus and subject snakes. Only gravid females were used as stimulus snakes to reduce the possible occurrence of reproductive trailing. Tests involving stimulus trails produced by males preceded female-produced trail tests, again to reduce the possibility of reproductive trailing.

Analysis.—Results were analyzed by circular statistics described by Batschelet (1981). A significance level of $\alpha = 0.05$ was selected for all tests. The mean angle, ϕ, of each test series was calculated as was its length, r. The length serves as a measure of the concentration of the sample points about the mean direction and has a maximum value of 1.0 when all sample points lie at the same position. Mean angular deviations, s, were calculated and mean vectors are presented as $\phi \pm 1$ s. Confidence intervals at the 95% level were determined from published charts (Bat-
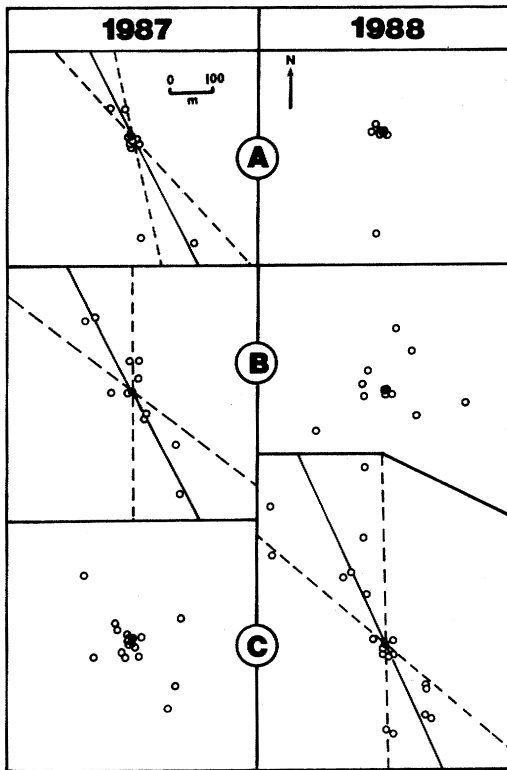
Fig. 2. Seasonal directionality exhibited by SLPP *Thamnophis sirtalis*. (A) Movements occurring during spring. (B) Movements occurring from spring to summer. (C) Movements occurring during summer. Open circles represent the distance and direction moved by an individual between successive captures. First captures of each snake within each time category have been standardized to a common starting point (closed circle). Solid lines indicate significant directionality in the indicated direction. Dashed lines represent the 95% confidence interval around that direction.

schelet, 1981) and are shown on the polar diagrams as dotted lines.

In all tests a "homeward" direction was predicted a priori. For SLPP snakes, Spectacle Lake was the predicted direction in basic orientation tests. The exceptions were neonates born at the laboratory, for which the direction toward the laboratory served as the predicted direction, and snakes collected from Goldstream Park, which was the predicted direction for these snakes.

With the sun moving across the sky at an average rate of 15°/h over a 24-h period, phase-shift tests altered the predicted direction by 90° clockwise (for phase-delayed tests) or counterclockwise (for phase-advanced tests). Pheromone trailing test results were analyzed by considering two predicted directions—the homeward direction as described above and the direction of the trail.

The deviation of the mean vector from the predicted direction, v or "homeward component," was calculated (Batschelet, 1981). Its value ranges from -1.0 to a maximum of 1.0 when all animals move exactly homeward. Significant directionality, versus a null hypothesis of randomness, was tested by the V-test. The V-test was used to detect clustering around a predicted direction; however, it cannot be used to detect significant deviations from this direction (Aneshansley and Larkin, 1981). For this purpose, I used 95% confidence intervals (Batschelet, 1981). A significant deviation of the mean vector from the predicted direction was concluded when the predicted direction was outside the confidence interval.

In some cases, the polar diagrams suggested strong directionality but not in the predicted direction. In these instances, significant directionality was tested by Rayleigh's test, which is based on the value of r and the sample size. Critical levels are given in charts in Batschelet (1981). For a unimodal sample, significance by this test indicates a concentration of the sample points about the mean. This test also was used to test the significance of axial data, that is, when it appeared that snakes selected two directions that differed by 180°. To examine this response, angles were first doubled (Krumbein, 1939) and reduced *modulo* 360° to obtain r_2, ϕ_2, and s_2. Halving these values produced r, ϕ, and s. A significant value of r established that the snakes were orientated along an axis rather than in a single direction.

I found no precedent for analyzing trailing responses in circular arenas; therefore, I examined this response by determining the significance of the homeward component, using both the trail and the homeward direction as predictions. In cases in which stimulus snakes were allowed to select their own direction, angles were rotated by an appropriate amount so that the trail was standardized at 0°.

RESULTS

Directionality of movements.—Figure 2 and Table 1 present the analysis of seasonal directionality in *T. sirtalis*. In no case were *T. sirtalis* oriented in a single common direction, but in all three time periods (spring 1987, spring to summer 1987, and summer 1988) significant movement along a northwest-southeast axis occurred that ran parallel to the shore. However, the lake did not act as a barrier to movements, and it was not uncommon to see snakes in the water.

Seasonal directional patterns in *T. ordinoides*

TABLE 1. SEASONAL DIRECTIONALITY IN SLPP SNAKES. * indicates bimodal rather than unimodal directionality. The larger r value of the two is given below. The mean vector (ϕ) is given only if significant directionality was evident. SS = sample size too small to calculate mean vector; ϕ = mean vector; s = 1 angular deviation; r = length of mean vector; Sp = spring; Su = summer.

Season of 1st/2nd capture	Year	n	No. snakes	$\phi \pm s$	r	P	95% C.I.
				T. sirtalis			
Sp–Sp	1987	5	4	333 ± 30	0.89*	<0.05	315–345
	1988	3	3	SS	—	—	—
Sp–Su	1987	11	11	333 ± 27	0.56*	<0.05	306–360
	1988	12	12	—	0.33*	>0.05	—
Su–Su	1987	18	15	—	0.26	>0.05	—
	1988	20	16	336 ± 24	0.66*	<0.001	312–360
				T. ordinoides			
Sp–Sp	1987	11	9	—	0.32*	>0.05	—
	1988	3	3	SS	—	—	—
Sp–Su	1987	7	7	333 ± 21	0.74*	<0.05	312–354
	1988	11	11	—	0.39*	>0.05	—
Su–Su	1987	22	16	—	0.09	>0.05	—
	1988	7	6	323 ± 37	0.79	<0.01	286–360

were examined in the same manner and are presented in Table 1 and Figure 3. Significant movement along the northwest-southeast axis during movements occurred between the spring and summer of 1987 and in a northwest direction in the summer of 1988.

Orientation.—The results of orientation tests performed on Vancouver Island are summarized in Tables 2 (*T. sirtalis*) and 3 (*T. ordinoides*). Tests on neonates are summarized in a separate section.

SLPP *T. sirtalis* demonstrated homeward orientation at both test sites (Fig. 4A–B) under clear skies. One group of nine *T. sirtalis* from Goldstream Park (test site B) was also tested at site A while the sun was obscured on a day with 95% cloud cover (Fig. 4C). Orientation was directed toward Goldstream Park. *Thamnophis ordinoides* were homeward oriented at site B (Fig. 4E) but showed random orientation at site A (Fig. 4D).

Solar orientation.—Directions selected by phase-delayed *T. sirtalis* were oriented in the predicted direction (direction to SLPP + 90°) at both sites (Fig. 5A–B) as were those selected by the phase-advanced group (direction to SLPP—90°; Fig. 5C). *Thamnophis ordinoides* displayed oriented behavior but not in the predicted direction (SLPP + 90°) nor toward Spectacle Lake (Fig. 5D).

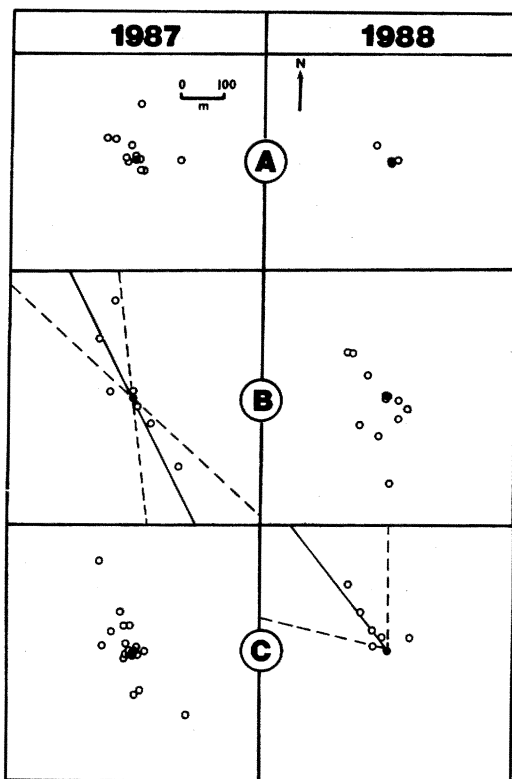*Pheromone trailing.*—*Thamnophis sirtalis* did not trail conspecific males under cloudy skies (Fig.

Fig. 3. Seasonal directionality exhibited by SLPP *Thamnophis ordinoides*. (A) Movements occurring during spring. (B) Movements occurring from spring to summer. (C) Movements occurring during summer. See Figure 2 for explanation of figure symbols.

TABLE 2. COMPONENTS OF THE MEAN VECTORS OF ORIENTATION TESTS FOR *Thamnophis sirtalis* AND DEGREE OF HOMEWARD ORIENTATION. Snakes were collected from SLPP unless otherwise indicated. ϕ = mean vector; s = 1 angular deviation; r = length of mean vector; v = homeward component; u = V-test statistic; θ = predicted direction. All tests were performed under clear skies unless otherwise indicated. *** Confidence limits outside the range of published charts.

Condition	Site	n	$\phi \pm s$	r	v	u	P	θ	95% C.I.
I. Basic									
Spring	A	14	263 ± 52.5	0.58	0.46	2.42	<0.01	225	223–303
Summer	B	11	17 ± 36.2	0.80	0.74	3.48	<0.0001	355	351–43
Summer Cloud (Goldstream snakes)	A	9	211 ± 44.4	0.70	0.63	2.67	<0.005	185	173–249
II. Phase—shift									
Spring phase—advanced	A	12	125 ± 38.9	0.77	0.76	3.71	<0.0001	135	98–152
Spring phase—delay	A	11	323 ± 40.5	0.75	0.74	3.48	<0.0001	315	293–353
Spring phase—delay	B	9	101 ± 53.1	0.57	0.55	2.32	<0.01	85	47–153
III. Neonates—basic									
Autumn Clear, born lab indoors	B	10	67 ± 78.6	0.06	0.03	0.12	>0.05	130	***
IV. Pheromone trailing									
A. Male trails									
Summer Cloud									
To home	B	8	109 ± 66.8	0.32	−0.13	−0.52	>0.05	355	***
To trail	B	8	109 ± 66.8	0.32	−0.21	−0.84	>0.05	240	***
B. Gravid female trail									
Summer Clear and Cloud									
To home	B	18	229 ± 63.3	0.39	−0.23	−1.37	>0.05	355	***
To trail	B	18	229 ± 63.3	0.39	0.38	2.34	<0.01	240	***
Clear skies									
To home	B	8	190 ± 69.2	0.27	−0.26	−1.04	>0.05	355	***
To trail	B	8	190 ± 69.2	0.27	0.17	0.69	>0.05	240	***
Cloudy skies									
To home	B	10	243 ± 54.4	0.55	−0.21	−0.92	>0.05	355	193–293
To trail	B	10	243 ± 54.4	0.55	0.55	2.46	<0.01	240	193–293

6A). Orientation in this group was random. Some trailing of gravid females did occur although there was considerable variation in response (Fig. 6B), with results on clear and cloudy days combined. When distinguished by sky condition, significant trailing was noted only under cloudy skies (Fig. 6C). Females appeared to demonstrate a stronger trailing response. Under clear skies, orientation was random (Fig. 7D). In no case did snakes orient toward SLPP. *Thamnophis ordinoides* showed no tendency to cluster around either the trail or the homeward direction when either male (Fig. 6E) or female trails (Fig. 6F) were present.

Neonates.—Neonates were tested during autumn 1988. Unfortunately I had poor success obtaining neonates for testing, either from the field or captive litters, especially for *T. sirtalis*. Nevertheless, preliminary tests were run, and their results are presented in Table 3.

I performed one set of tests of *T. sirtalis* neonates involving seven snakes born in captivity at the laboratory and kept indoors until the day of testing. When tested at site B in the autumn of 1987, these snakes were randomly oriented (Fig. 7A) under clear skies.

Basic tests of neonate *T. ordinoides* resulted in an oriented response on one occasion but not on another. Snakes from a captive-born litter from Spectacle Lake tested under full cloud were randomly oriented (Fig. 7B). Snakes born outdoors at the laboratory and kept under natural light conditions did orient toward the laboratory, their birth site (Fig. 7C), when tested under clear skies. However, littermates of the first group tested on the same day did show clustering around the trail produced by the mother (Fig. 8A). An outdoor, laboratory-born group showed no evidence of orienting either toward their mother's trail (Fig. 8B) or toward the laboratory when tested under clear skies.

TABLE 3. COMPONENTS OF THE MEAN VECTORS OF ORIENTATION TESTS FOR SLPP *Thamnophis ordinoides* AND DEGREE OF HOMEWARD ORIENTATION. ϕ = mean vector; s = 1 angular deviation; r = length of mean vector; v = homeward cmoponent; u = V-test statistic; θ = predicted direction. All tests were performed under clear skies unless otherwise indicated. *** Confidence limits outside the range of published charts.

Condition	Site	n	$\phi \pm s$	r	v	u	P	θ	95% C.I.
I. Basic									
Spring	A	14	294 ± 56.7	0.51	0.18	0.97	>0.05	225	248–340
Summer	B	10	21 ± 30.3	0.86	0.77	3.46	<0.0001	355	4–38
II. Phase—shift									
Spring phase—delay	B	11	157 ± 30.3	0.86	0.27	1.25	>0.05	85	136–178
III. Neonates—basic									
Autumn Clear, born lab outdoors	B	10	131 ± 54.4	0.55	0.55	2.46	<0.01	130	81–181
Autumn Cloud, born SLPP outdoors	B	7	256 ± 60.6	0.44	−0.07	−0.23	>0.05	355	***
IV. Pheromone trailing									
A. Male trails									
Summer Clear									
To home	B	10	37 ± 67.8	0.30	0.23	1.01	>0.05	355	***
To trail	B	10	37 ± 67.8	0.30	−0.28	−1.23	>0.05	240	***
B. Gravid female trail									
Summer Clear and Cloud									
To home	B	12	59 ± 72.0	0.21	0.09	0.45	>0.05	355	***
To trail	B	12	59 ± 72.0	0.21	−0.21	−1.02	>0.05	240	***
Summer Clear									
To home	B	6	95 ± 64.8	0.37	−0.06	−0.22	>0.05	355	***
To trail	B	6	95 ± 64.8	0.37	−0.30	−1.05	>0.05	240	***
Summer Cloud*									
To home	B	6	36 ± 16.7	0.83	**	**	=0.009	355	***
V. Neonate trailing									
Mother Trail/Autumn Cloud, born SLPP outdoors									
To home (SLPP)	B	7	339 ± 32.4	0.84	0.81	3.01	<0.001	355	***
To trail	B	7	339 ± 32.4	0.84	0.84	3.13	<0.001	340	***
Mother Trail/Autumn Clear, born lab outdoors									
To home (lab)	B	7	172 ± 55.0	0.54	0.40	1.50	>0.05	130	***
To trail	B	7	172 ± 55.0	0.54	0.20	0.76	>0.05	240	***

* Examined for bimodality. Results are for axial rather than unimodal directionality. Level of P for Rayleigh's test.
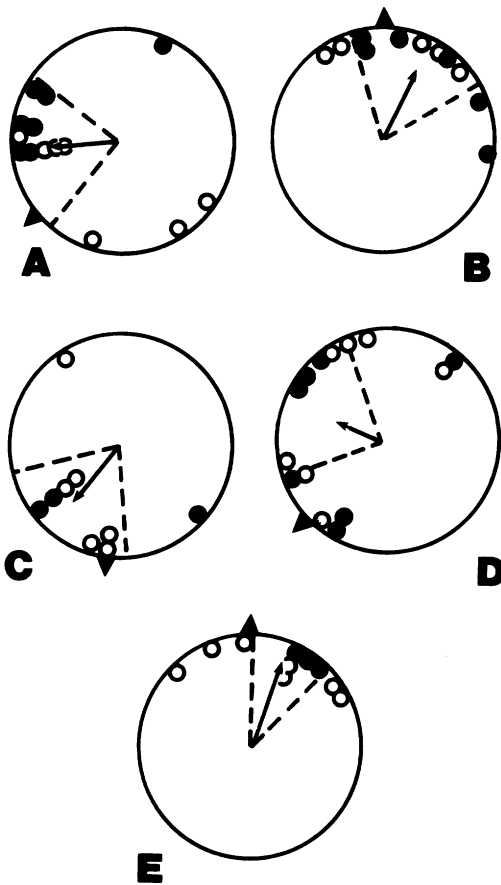
DISCUSSION

Thamnophis sirtalis from Spectacle Lake selected directions that led to the lake from both test sites, suggesting Type III navigation. However, it is necessary to view these directional selections in relation to the normal movement pattern of snakes in this population. If the direction leading toward home from the test site is the same as directions taken by animals during their normal movements, the possibility of Type II orientation cannot be discounted. That is, the animals may not be aware of being displaced and are, instead, displaying normal movement behavior in a particular direction.

Movements at Spectacle Lake by this species were usually irregular, although significant directionality running parallel to the lake did occur (unpubl.). Certain prey items, particularly amphibians, which comprise the majority of the diet of *T. sirtalis* at SLPP, may be more abundant along the shore, which would account for the directionality (along the long axis of the lake) occasionally recorded. Madsen (1984) noted that *Natrix natrix* displayed unidirectional movements resulting from foraging along stone fences. Comparative statistical techniques for circular measures require several restrictive assumptions that were not met; therefore as an approximate indicator of differences, I exam-

Fig. 4. Basic orientation tests. (A) *Thamnophis sirtalis* from SLPP tested at site A under clear skies. (B) *Thamnophis sirtalis* from SLPP tested at site B under clear skies. (C) *Thamnophis sirtalis* from Goldstream tested at site A under 95% cloud cover. (D) *Thamnophis ordinoides* from SLPP tested at site A under clear skies. (E) *Thamnophis ordinoides* from SLPP tested at site B under clear skies. Closed circles = males; open circles = females. The center of the diagram represents the release point within the arena, and the outer margin represents the arena walls. Individual test scores, measured as angles, are represented by dots along the circumference of the circle. For basic and phase-shift tests, north, 0°, is lcoated at the top of the diagram. For pheromone trail tests, the trail direction is at the top of the diagram. The predicted direction (θ) is indicated by a triangle outside the circle. Arrows inside the circles represent the mean direction (ϕ); the length of the arrow indicates the degree of clustering around the mean direction (r). Dashed lines represent the 95% confidence interval of the mean vector. No arrow is drawn if both Rayleigh's test and the V-test found orientation to be random.
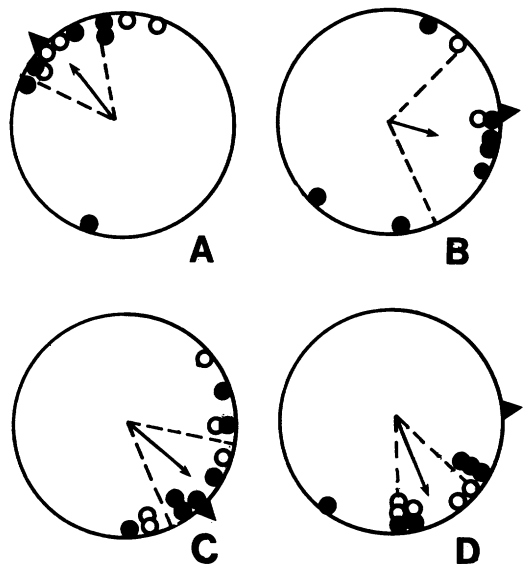
Fig. 5. Phase-shift orientation tests. (A) *Thamnophis sirtalis*, site A, phase-delayed. (B) *Thamnophis sirtalis*, site B, phase-delayed. (C) *Thamnophis sirtalis*, site A, phase-advanced. (D) *Thamnophis ordionides*, site A, phase-delayed. See Figure 4 for explanation of figure symbols.
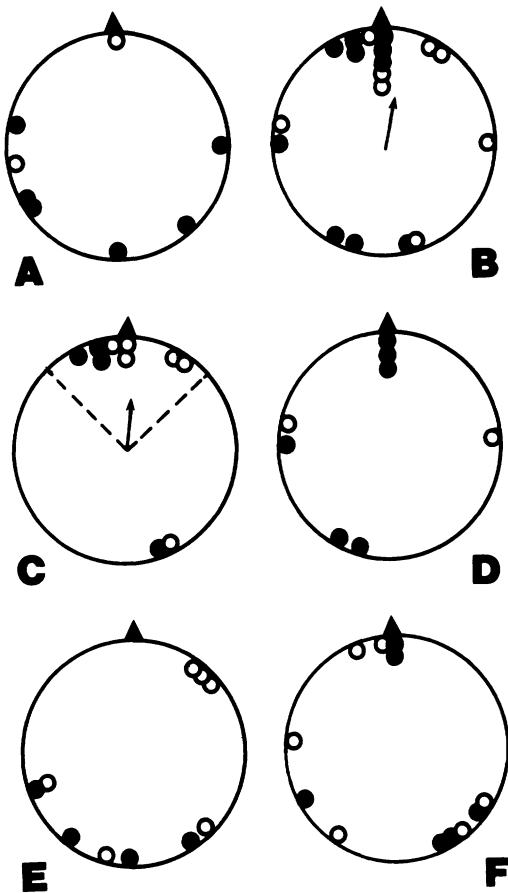
Fig. 6. Pheromone trailing tests. (A) *Thamnophis sirtalis*; trails produced by males. (B) *Thamnophis sirtalis*; trails produced by gravid females. (C) *Thamnophis sirtalis*; trails produced by gravid females; cloudy skies. (D) *Thamnophis sirtalis*; trails produced by gravid females; clear skies. (E) *Thamnophis ordinoides*; trails produced by males. (F) *Thamnophis ordinoides*; trails produced by gravid females. Triangles outside the circle represent the direction of the trail. See Figure 4 for explanation of additional figure symbols.
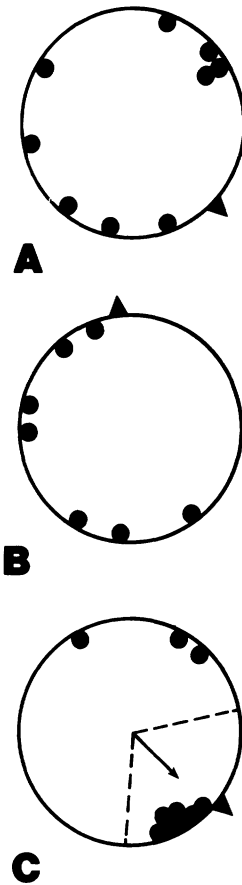

Fig. 7. Basic orientation tests of neonates. (A) *Thamnophis sirtalis* born and kept indoors at laboratory and tested under clear skies. (B) *Thamnophis ordinoides* born outdoors in captivity at SLPP and tested under cloudy skies. (C) *Thamnophis ordinoides* born outside at laboratory and tested under clear skies. Scores not distinguished by sex. See Figure 4 for explanation of figure symbols.

ined overlap between the 95% confidence intervals of angles selected during arena test and angles of movements occurring at Spectacle Lake. For both test sites, there was some overlap; thus, the possibility existed that snakes were exhibiting Type II orientation. That is, the snakes may not have been correcting for displacement and were continuing to orient as if they had not been displaced. Yet, orientation by snakes at SLPP was always directed along an axis rather than in a single direction, whereas the arena tests never suggested bimodality. The results of the phase-shift tests gave further evidence that these snakes displayed Type III navigation.

Mixed results were obtained for *T. ordinoides*. Although homeward orientation was observed at one test site, snakes were randomly oriented at the second. It is possible that snakes were attracted to some cue outside the arena at this second site and were thus not motivated to home, but I was not able to determine this. At the first test site, overlap between the 95% C.I. of the selected direction and the spring-to-summer directionality noted in 1987 did exist, again raising the possibility that snakes were orienting in accordance with normal movement patterns rather than toward home. Definite conclusions regarding their level of orientational ability could not be reached from these data.

Thamnophis sirtalis from Spectacle Lake are capable of orienting with respect to solar azimuth position as demonstrated by the phase-
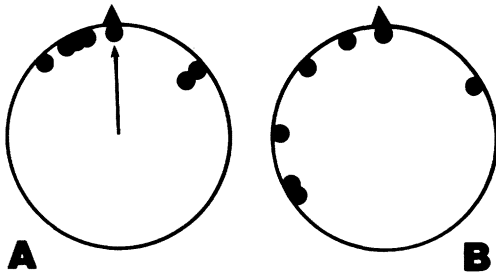
Fig. 8. Pheromone trailing tests of *Thamnophis or-dinoides* neonates. (A) Born outdoors in captivity at SLPP and tested under cloudy skies. (B) Born out-doors at laboratory and tested under clear skies. Out-er triangle represents the direction of the trail pro-duced by the mother. Scores not distinguished by sex. See Figure 4 for explanation of additional figure sym-bols.

shifting tests. Celestial guides (solar azimuth po-sition predominantly, but also polarized light patterns) have been identified as the most com-monly used guides by diurnally migrating ani-mals (Able, 1980; Shöne, 1984). Because of the consistent nature of solar cues and presumably their ease of perception, this hypothesis has much merit. Only a few studies, however, have specifically examined whether snakes are ca-pable of using solar cues. Aside from this study, solar orientation has been examined and dem-onstrated in snakes by Landreth (1973) for *Cro-talus atrox*, Lawson (1989) for *Thamnophis sir-talis*, Lawson and Secoy (1991) for *Thamnophis radix*, and Newcomer et al. (1974) for *Nerodia sipedon* and *Regina septemvittata*. Phase-shifting tests, which are required to validate the use of the sun as an effective compass because animals must be able to compensate for the sun's move-ment across the sky, have previously been per-formed only by Newcomer et al. (1974) and Lawson (1989).

Pheromone trails laid by gravid females, but not by males, also appeared to be effective ori-entation cues for nonmigratory *T. sirtalis*. Sim-ilar findings were reported for migratory *T. sir-talis* from WBNP tested during the vernal dispersal phase (Lawson, 1989). In the migra-tory population, these findings suggested the hypothesis that females, who generally begin migrating toward the summer range prior to the males, produce trails that are eventually fol-lowed by the males, at least during the initial stages of their migration. In this sense, females are acting as migratory "leaders." This appears to be the case for nonmigratory *T. sirtalis* as well.

Trailing abilities appeared to be slightly en-hanced under cloudy conditions, suggesting that

solar cues are more important orientation guides. Neither solar cues nor pheromone trails were effective as orientation guides for adult *T. ordinoides*.

Unfortunately I had poor success in acquiring neonates for testing so I am unable to draw conclusions about the ontogeny of orientation behavior in these animals. Not unexpectedly, neonate *T. sirtalis* that had no prior exposure to the sun demonstrated random orientation. Tests of neonate *T. ordinoides* suggested that they might imprint on solar cues at the birth site, similar to Galligan and Dunson's (1979) suggestion that neonate *Crotalus* imprint on den odors and Carr's (1967, 1972) hypothesis that turtle hatchlings imprint on cues characteristic of their natal beach. In the absence of solar cues, *T. ordinoides* apparently will follow pheromone trails produced by the mother. This supports the hypothesis proposed by Brown and Parker (1976) and Brown and MacLean (1983) that ne-onates that hibernate in a communal den during their first winter use adult pheromone trails as orientation guides.

Snakes have critical resources that they must locate—food, mates, and overwintering sites being among the most important—and the dis-tribution of these resources relative to one an-other determines overall movement patterns of snakes. When geographic and environmental conditions exist that limit the availability of these resources and shorten the time available to search for these resources, an effective means of locating them presumably becomes critical. The migratory population of *T. sirtalis* from Wood Buffalo National Park (WBNP) in north-ern Alberta exemplies this (Larsen, 1987). Ad-vanced navigational skills for WBNP *T. sirtalis* are, therefore, expected and have been dem-onstrated (Lawson, 1989). However, the exten-sive diversity of movement patterns of snakes suggests no discernible cut-off point at which navigational abilities would become superflu-ous, at least within a species. Therefore, non-migratory *T. sirtalis* have equal navigational abilities to migratory *T. sirtalis*.

The same may not be true between species, however. *Thamnophis ordinoides* have received very little attention in terms of ecological stud-ies, and I am not aware of any other research that has specifically examined its movement pat-terns. Because it appears to forage almost ex-clusively on slugs and earthworms throughout its restricted range in relatively mild climates (thus hibernating sites near or within feeding ranges are likely abundant), it would not be sur-prising if no long-distance migratory popula-tions existed. Because migrations do not appear

to be important in their history, sufficient evolutionary time and the lack of requirement for longer movements may have either resulted in the loss of advanced navigational skills, assuming that these skills were present in the ancestral form, or the failure of them to evolve at all. Thus a case may be made for differences in orientational abilities between migrating and nonmigrating species but not between migratory and nonmigratory populations of a species.

The presence of redundant cues and of navigational abilities does not imply that these systems are used extensively during the normal movements of individuals. Route memorization and the use of visual or olfactory landmarks, both within a limited home range and during longer migrations, probably play dominant roles under normal conditions. According to Baker's (1978) least-navigational hypothesis, when an animal possesses a navigational repertoire, cues that permit movements with a minimum time investment in locating goals will be used, but the most effective cue may vary according to circumstances.

I was able to add little to the understanding of ontogenetic development of orientation in snakes, but the results lend support to the hypothesis that neonates locate hibernacula by trailing adults. It is also possible that newborn snakes imprint on solar cues available at the birth site. Further research in this area is essential to properly explore this possibility.

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Molecular Systematics and Radiation of the Haplochromine Cichlids (Teleostei: Perciformes) of Lake Malawi

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Mitochondrial DNA (mtDNA) restriction fragment length polymorphisms were assayed among 40 species of Lake Malawi haplochromines (Cichlidae) including representatives of ecologically divergent genera. Six distinctive mtDNA lineages were distinguished, two of which were major clades, represented by a large number of species. The other four lineages were each represented by a single species with a divergent mtDNA haplotype. One of the two major clades was composed of the shallow-water, rock-dwelling mbuna species, whereas the other included a diverse array of sand-dwelling and pelagic species. A number of taxa, found to be firmly embedded within the mbuna clade, are quite distinct in morphology and generally inhabit deeper, sediment-rich areas rather than the rocky habitats typical of other mbuna. The mbuna group is generally thought to be a monophyletic assemblage, but these results suggest that it is actually paraphyletic. In contrast to the high morphological diversity among Malawi haplochromine species, mtDNA sequence divergence was found to be remarkably low. This finding underscores the unprecedented rapidity of speciation and evolutionary plasticity in this fish species flock.

Beginning with the earliest collections and descriptions of Malawi haplochromines, taxonomists have been challenged and frustrated by attempts to reconstruct the phylogenetic history of this fauna. Two primary obstacles have confounded this reconstruction. First, a paucity of shared derived traits often prevented identification of sister-group relationships (though many autapomorphic traits are present). Second, an abundance of parallelism has made it difficult to assure that shared traits are actually synapomorphic (Eccles and Trewavas, 1989). Early work on the Malawi ichthyofauna revealed a large number of new spe-