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Choices of Neonate *Thamnophis elegans vagrans* Between Conspecific, Congeneric, and Heterogeneric Odors

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ABSTRACT.—Responses of snakes to pheromones of other conspecific individuals or of heterospecifics vary among species. Most colubrid snakes choose substrates marked by conspecifics over those marked by heterospecifics and over "clean" (unmarked) substrates. In such cases, snakes presumably are using chemical signals from other individuals as clues about suitable habitat. In this study, neonate *Thamnophis elegans vagrans* were tested in a series of two-choice shelter tests to examine their reactions to odors of conspecifics, *T. sirtalis* (a congeneric), *Charina bottae* (a heterogeneric), and an unmarked control. In addition, we tested whether or not neonate *T. elegans* would discriminate between conspecific neonates and adults. Based on previous studies, we predicted that the snakes would choose conspecifics over heterospecifics and over unmarked substrates, and that there would be no difference in reactions to conspecific adults and neonates. However, the snakes chose the other odors over the conspecific odor, and generally chose the odor of another neonate over that of an adult *T. elegans*. It is possible that neonates avoid conspecific odors, especially adult odors, because larger *T. elegans* may eat smaller snakes and thus pose a threat of predation.

Aggregation behavior for various apparent purposes is well documented in snakes (Gregory et al., 1987) and is mediated by the vomeronasal system (Heller and Halpern, 1982). Lab-

oratory studies have demonstrated that certain species of snakes tend to hide under cover objects (Burghardt, 1983), especially under shelters that previously were occupied by conspe-

cifics rather than under clean shelters (Dundee and Miller, 1968; Heller and Halpern, 1982). Most of the species of colubrid snakes that have been tested associate with conspecific odors rather than occupy clean areas or associate with heterospecifics (Scudder et al., 1980; Heller and Halpern, 1981; Burghardt, 1983).

In the field, aggregations may be based on attraction of the individuals to a common site, or attraction of the individuals to each other (Gregory et al., 1987). In the latter case, individuals may "trail" other individuals (e.g., Brown and MacLean, 1983). Aggregating and trailing behavior may facilitate learning of den location (Brown and MacLean, 1983; Graves et al., 1986; Reinert and Zappalorti, 1988), foraging (Arnold and Wassersug, 1978), defense (Graves, 1989), and short-term reduction of heat loss (Aleksiuk, 1977; Graves and Duvall, 1987) or water loss (Graves et al., 1986).

Most of the above advantages could as easily be attained in interspecific as well as intraspecific aggregations; although mixed-species aggregations of snakes are known (e.g., Gregory, 1975; Brown and Parker, 1976), studies of aggregating and trailing behavior nevertheless have shown that several species of snakes can, and do, differentiate between conspecific and heterospecific (both congeneric and heterogeneric) scents (Scudder et al., 1988). Presumably, snakes tend to aggregate intraspecifically because conspecifics have similar requirements.

In this study, we test responses of neonate garter snakes, *Thamnophis elegans*, to odors of conspecific, congeneric heterospecific, and heterogeneric snakes. In particular, we test the hypothesis that neonate *T. elegans* will preferentially associate with the odor of conspecifics over those of other species. Furthermore, because closely related species may have similar odors (cf. Brown, 1979 for mammals), we test the hypothesis that *T. elegans* will be more attracted to odors of close relatives (congenerics) than distant relatives (heterogenerics).

MATERIALS AND METHODS

Neonate *Thamnophis elegans vagrans* from three populations (Keremeos, Creston, and Island View, British Columbia), were born in the laboratory on 14 and 15 August 1991. They were separated and placed into individual containers between 20 and 23 September 1991, and were fed live guppies or frozen smelt to satiation. The possibility of the snakes detecting each other was kept to a minimum by thorough washing of anything that came in contact with the snakes or their bedding, including the feeder's hands during feeding. The test containers and shelters were washed thoroughly with soap and warm water before each test. The snakes could see

each other from their respective cages only through the plastic walls of the cages.

To test odor preference, we placed each snake individually into a test container in the late afternoon or evening and left it undisturbed for at least 14 h to allow it time to explore and become accustomed to the container. The test containers (35 cm × 15 cm × 25 cm) held two shelters made of overturned aluminum shells 6 cm in diameter and with a hole about 2 cm wide cut in one side. These were placed at opposite corners and lightly taped to the adjacent wall to prevent movement.

Under each shelter we placed a piece of paper towel, about 6 cm square, either with the feces of one of the snake species on it or clean, as a control. The snakes used for sources of scent were adult, year-old, and neonate *T. elegans* that were not used as test snakes, neonate *T. sirtalis* (a sympatric congeneric), and adult *Charina botatae* (a sympatric heterogeneric). The piece of paper towel was used immediately after removal from the snake's cage; the feces were no more than two days old. We used paper with feces to guarantee that the snake had been on that section of paper, so the odors present were probably a mixture of fecal odor and skin pheromones. A water dish was placed in the center of each container.

The position of the snake was observed every ten minutes for an hour, in the first series of tests, and 15 times over a 3 h period in subsequent tests. Care was taken not to disturb the snake while observing it. Each snake was scored a "1," a "2," or a "0," depending on its position at the time of each observation. The first two numbers indicate the number of the shelter with which the snake was associated (i.e., inside, on top of, curled up beside, or half the body length inside). The "0" indicated that the snake was not in or on either shelter. After the test, we returned the snake to its particular container and treated it as before. Three separate experiments were run.

The snakes were initially housed together an average of 38 d before they were isolated. They spent an average of 41 d isolated before Experiment 1, 100 d apart before Experiment 2, and 136 d apart before Experiment 3.

The positions of the shelters in the test containers (relative to the front or the back of the shelf on which the containers rested) were selected randomly in each test to eliminate any effect that position might have. We picked the snakes for testing in the order in which their cages were kept on the shelf. In subsequent experiments, we chose snakes in such a way as to avoid using an individual in the same test twice, but there was otherwise no systematic bias in our selection.

The number of times an individual was scored in association with a certain shelter was calculated as a proportion of the number of times it was associated with either shelter, and individuals tested in the same category in the same experiment were pooled to obtain an overall proportion and variance. The formula we used to calculate the proportion was:

$$p = \frac{\sum a_i}{\sum m_i}$$

where a_i = total number of choices of one shelter made by snake i , m_i = total number of times that snake i was observed associated with either shelter, and with variance calculated by:

$$V(p) = \frac{1}{n\bar{m}^2} \left[\frac{\sum a_i^2 - 2p \sum a_i m_i + p^2 \sum m_i^2}{n - 1} \right]$$

where n = number of snakes in the sample and \bar{m} = average number of observations per snake (after Mendenhall and Schaeffer, 1971). Approximate 95% confidence limits on p were calculated as $2 V(p)$. We used this approach to account for heterogeneity among individuals and to give greater weight to data from individuals for which we had more observations. The significance of variation among individuals in a given experiment was tested by heterogeneity chi-square (Zar, 1984), using a null hypothesis of no choice ($P = 0.5$) for each individual. That overall null hypothesis of no choice was tested on the pooled sample of all observations in a given experiment, using chi-square. The rejection level used throughout was $\alpha = 0.05$. These tests were one-tailed, given the directional predictions of choice in the initial hypotheses. Following Samuels (1989), probabilities for the one-tailed tests were obtained by dividing in half those read from the table.

Specific methods for each experiment are presented with Results below.

RESULTS

Experiment 1.—The first series of tests began on 25 October and ended on 8 November, 1991. Six combinations of scents were used: *T. elegans* vs. *T. sirtalis*; *T. elegans* vs. *C. bottae*; *T. elegans* vs. control; *T. sirtalis* vs. *C. bottae*; *T. sirtalis* vs. control; and *C. bottae* vs. control. Year-old and neonate *T. elegans* were used to produce the conspecific odors used. Five different snakes were tested in each category, for a total of 30 snakes tested. Each snake was observed 7 times, for 35 observations in each category (a total of 210 observations). Snakes were usually associated with a shelter (157 out of 210 observations), but the frequency of shelter use, and therefore sample size, varied greatly among categories (17 to 31 observations out of 35). Snakes moved

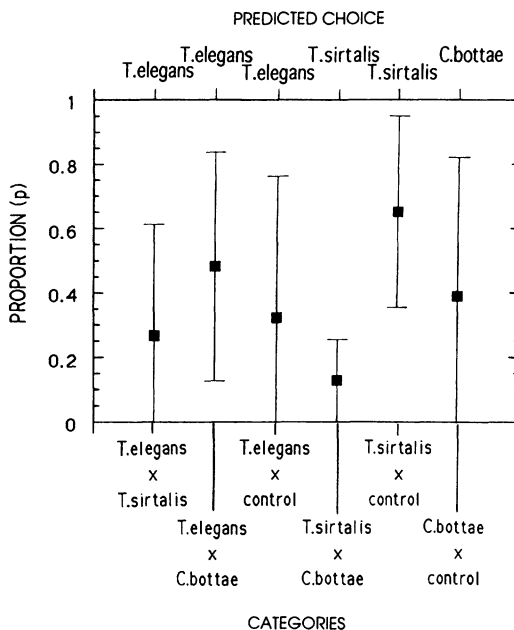


FIG. 1. Proportion of observations in specified shelter over total shelters chosen in Experiment 1. Vertical lines are approximate 95% confidence limits.

from one shelter to another and from a shelter into the open or vice-versa at various times during the experiment; for a short time after each snake was placed in a test container, we observed that it moved around the whole area, usually also entering both shelters.

The five snakes within each test category were pooled, and the estimated proportions are shown in Fig. 1. Based on the pooled samples in each category, *T. elegans* chose the odor of *T. sirtalis* and the control significantly more often than its own odor (Table 1); no other choices were significant. However, in most cases, there was significant heterogeneity of choice among individuals in a particular category (Table 2), reflected in the wide confidence intervals seen in Fig. 1. Unfortunately, the small number of observations prevented a separate test of $H_0: p = 0.5$ for each individual.

Experiment 2.—Because the results of Experiment 1 were unexpected, we conducted a second run with more observations. The same thirty snakes were tested, ten in each of three categories repeated from the first experiment: *T. elegans* vs. *T. sirtalis*; *T. elegans* vs. control; and *T. sirtalis* vs. control. These tests ran from 10 December, 1991 to 9 January, 1992. Each snake was observed 15 times, for 150 observations in each category (total of 450 observations). This time the scent for *T. elegans* shelters was obtained exclusively from an adult, as all other neonates and year-old snakes had been placed

TABLE 1. Departure of observations from $H_0: P = 0.5$ for Experiments 1 to 3. In each case, data from different individuals are pooled and tests are done on corrected (1 df) chi-square values. All tests except Experiment 3 are 1-tailed. * overall χ^2 is significantly different from $P = 0.5$, but in direction inconsistent with 1-tailed H_a ; therefore, H_0 is not rejected. A = $P < 0.0005$, B = $P < 0.001$, C = $0.0125 < P < 0.025$, D = $0.025 < P < 0.05$, E = $0.05 < P < 0.125$, F = $0.25 < P < 0.375$, G = $0.50 < P < 0.75$, H = $0.75 < P < 0.90$, I = $P = 1$.

Test	χ^2	Test	χ^2
Experiment 1 (df = 1)		Experiment 3 (df = 1)	
<i>T. elegans</i> × <i>T. sirtalis</i>	4.966 ^C	Adult × neonate <i>T. elegans</i>	56.011 ^B
<i>T. elegans</i> × <i>C. bottae</i>	0 ^I	Experiment 1 and 2 (df = 1)	
<i>T. elegans</i> × control	3.333 ^D	<i>T. elegans</i> × <i>T. sirtalis</i>	52.033 ^A
<i>T. sirtalis</i> × <i>C. bottae</i>	15.613 [*]	<i>T. elegans</i> × control	109.191 ^A
<i>T. sirtalis</i> × control	1.565 ^E	<i>T. sirtalis</i> × control	12.403 ^A
<i>C. bottae</i> × control	0.235 ^F		
Experiment 2 (df = 1)			
<i>T. elegans</i> × <i>T. sirtalis</i>	29.883 ^A		
<i>T. elegans</i> × control	113.618 ^A		
<i>T. sirtalis</i> × control	20.840 ^A		

in hibernation. The snakes were tested as above, with no individual snake being tested in the same category as in Experiment 1. Snakes were usually associated with shelters (331 out of 450; range among categories was 94 to 131 out of 150); again, there was no particular pattern of movement during the observation period.

This time, the test snakes clearly preferred *T. sirtalis* over *T. elegans*, the control over *T. elegans*, and the control over *T. sirtalis* (Fig. 2, Table 1). Again, however, there was generally heterogeneity among individuals in a particular test category (Table 2). The data for Experiments 1 and 2 pooled are shown in Fig. 2 and Table 1.

Experiment 3.—As the results for Experiment 2 were similar to, but more extreme than, those of Experiment 1, any variations in methods between the two were examined to determine any reason for the differences. In Experiment 2, we had used adult feces instead of juvenile feces for the *T. elegans* shelters, so we compared responses to adult vs. neonate *T. elegans*. Nine snakes were tested as before on 15 January, 1992, with the choice between adult and neonate *T. elegans* shelters. Feces from neonates were taken from experimental snakes other than the individual tested. They were each observed 15 times,

for 135 observations in total. Snakes were associated with shelters in 90 of 135 observations; there were no obvious patterns of movement.

The results of the analyses are shown in Tables 1 and 2. The snakes strongly preferred neonate over adult shelters (adult shelters were chosen 10% of the time). This result is underscored by the observation that in none of the 9 observations scored for the adult shelters were the snakes actually inside the shelter. However, the observations were not homogeneous among individuals (Table 2).

DISCUSSION

A foraging snake that detects the odor of a conspecific may find suitable food, and large numbers of similar snakes grouped together could confuse or saturate a predator to the point that only a few, or none, are caught (Gregory et al., 1987). In most cases, individual snakes presumably benefit in some way by responding positively to the odor of another of the same species, or to the odor of a related species.

In contrast, the main conclusions of this study were that (1) *Thamnophis elegans* chooses to associate with the odor of a congeneric over that of a conspecific; (2) that individuals of this spe-

TABLE 2. Heterogeneity chi-square analysis on observations from Experiments 1 to 3, under $H_0: P = 0.5$. A = $P < 0.0005$, B = $P < 0.001$, C = $0.0125 < P < 0.025$, D = $0.025 < P < 0.05$, E = $0.05 < P < 0.125$, F = $0.25 < P < 0.375$, G = $0.50 < P < 0.75$, H = $0.75 < P < 0.90$, I = $P = 1$.

Test	χ^2	Test	χ^2
Experiment 1 (df = 4)		Experiment 2 (df = 9)	
<i>T. elegans</i> × <i>T. sirtalis</i>	14.640 ^D	<i>T. elegans</i> × <i>T. sirtalis</i>	19.189 ^C
<i>T. elegans</i> × <i>C. bottae</i>	12.000 ^C	<i>T. elegans</i> × control	4.434 ^H
<i>T. elegans</i> × control	22.867 ^B	<i>T. sirtalis</i> × control	42.956 ^B
<i>T. sirtalis</i> × <i>C. bottae</i>	1.973 ^C	Experiment 3 (df = 8)	
<i>T. sirtalis</i> × control	8.680 ^D	Adult × neonate <i>T. elegans</i>	15.675 ^D
<i>C. bottae</i> × control	13.271 ^C		

cies show no preference between odors of a heterogeneric and any other odor; and (3) that neonate *T. elegans* strongly choose to associate with other neonate conspecifics over adult conspecifics.

Based on results for other snake species in the literature, *T. elegans* was expected to choose conspecifics over heterospecifics, and to choose either over an unmarked control. However, the results obtained from our first set of tests were in many ways opposite to those expected. The three nonsignificant tests in Experiment 1 were ambiguous, but in two of the other three cases, neonate *T. elegans* selected *against* the odor of their own species. In the final case, *T. elegans* selected a distant relative over a near relative. Moreover, in Experiment 2, neonate *T. elegans* not only preferred other odors over those of conspecifics, but also chose the control over a near relative. In other words, the choices were generally inverse to those predicted by degree of phylogenetic relationship. However, the significant heterogeneity among individuals in most tests indicates that other (unmeasured) factors also influence choice in this species.

The results of Experiment 2 were even more pronounced than those of Experiment 1. However, in Experiment 2, only adult *T. elegans* were used to condition the paper, as the juvenile and neonate *T. elegans* used in the first experiment had been placed in hibernation. The possibility that this affected the results was explored in Experiment 3, in which the scent of the adult was tested against that of neonates. Although these results were not homogeneous among experimental runs, there was a strong trend of avoidance of the shelters conditioned by adults.

Adult *T. elegans* are known to eat other snakes (Stebbins, 1966; Gregory, 1978; Butler, 1981; Kephart, 1982; Gregory and Campbell, 1987), including conspecifics (Woodin, 1950; White and Kolb, 1974), so it is possible that the neonates have an innate aversion to the scent of the adults that extends weakly to younger snakes, which are less of a threat because of their smaller size. Neonates could present a different odor than adults (cf. Brown, 1979), so the test snakes might be able to estimate the amount of threat a particular individual might pose by its scent alone. Other *Thamnophis* species apparently do not eat other snakes at all (e.g., Gregory and Campbell, 1987), so would not pose a threat to young *T. elegans*. However, as the scent of the congeneric (*T. sirtalis*) would presumably be more similar to the conspecific scent than the scent of a heterogeneric (*C. bottae*), the neonates would prefer to associate with the less similar scent.

The reactions of snakes to conspecific odors can vary between neonates and adults of the same species. Adult *Crotalus viridis* avoid substrates conditioned by conspecifics (King et al.,

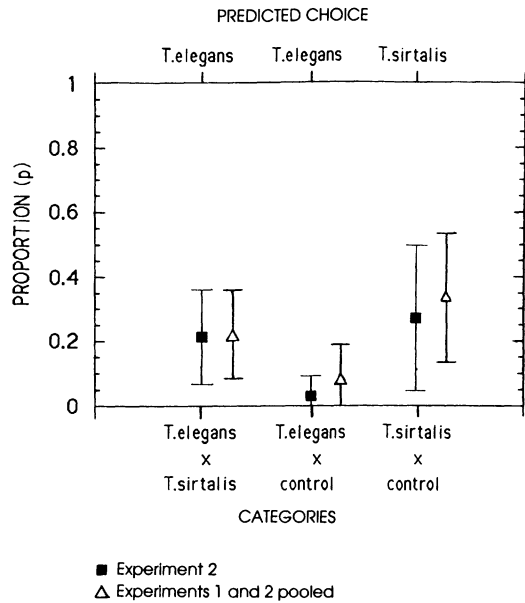


FIG. 2. Proportion of observations in specified shelter over total shelters chosen in Experiment 2, and in Experiments 1 and 2 pooled. Vertical lines are approximate 95% confidence limits.

1983), whereas neonates prefer substrates marked by conspecifics (Graves et al., 1986; Scudder et al., 1988). In contrast, the species of *Thamnophis* in which both neonates and adults have been tested showed similar results for both age groups (*T. radix*—Porter and Czaplicki, 1974; Graves and Halpern, 1988; *T. sirtalis*—Ford, 1978, 1982; Burghardt, 1980, 1983; Heller and Halpern, 1982). In the case of *T. elegans*, it is possible that an adult also would avoid other adults in most situations, as any snake larger than itself could still pose a threat. Conversely, an adult could be attracted to the scent of a neonate as a potential food item.

There are several factors in the methods that we and others used that could have affected the outcome of our experiments. For example, Heller and Halpern (1982) moved the snakes back to the center of the test arena after each observation, as they felt that animals left between observations may simply be staying where they are instead of actively choosing a shelter. However, staying in a shelter can be considered significant in itself, as it indicates that the snake has chosen to be there and is not merely passing through while exploring the area. Even when undisturbed completely, neonates will leave the shelters and move about (Burghardt, 1983; pers. obs.), so consecutive observations in one spot may have more significance than a single observation. Furthermore, moving, and therefore disturbing, an animal after each observation might condition it against the chosen shelter.

It is possible that the test snake conditioned the first shelter it entered with its own odor, and then chose to remain there. If this was the case, the results should have been random in all of the tests, as a particular snake has an equal chance of entering either shelter first. As the results did not show random choice, this apparently did not occur.

A final consideration is the possibility that an individual snake reacts differently to the scent of another snake than it would in an actual encounter with that snake. Burghardt (1983) states that the reaction to a site that another snake has conditioned is separate from the response to the presence of that snake. In our study, we concentrated on the reactions of *T. elegans* to the odors of other snakes, and we based our reasoning on studies that also primarily used scent as the stimulus.

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Salinity Relations of *Chelydra serpentina* in a Long Island Estuary

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ABSTRACT.—I examined the use of saline habitats by the common snapping turtle (*Chelydra serpentina*) in a Long Island estuary, where salinities range from fresh water (0 ppt) to approximately 70‰ seawater (100‰ seawater = 35 ppt). Movements, blood osmotic concentration, feeding habits, and leech infestation were monitored. Salinity data and field observations of distribution offer circumstantial evidence that snapping turtles are restricted to salinities hypoosmotic to the blood plasma (308 milliosmolal). Turtles were placed in enclosures at capture sites in a saline tidal creek in an attempt to test the possibility that other factors might be important in determining range extension into saline waters. These experiments showed that the turtles are unable to osmoregulate when forced to remain in relatively saline water (mean salinity = 13.9 ppt) over periods ranging from 11 to 27 d and offer conclusive evidence that water salinity is a dominant factor limiting snapping turtle distribution in estuaries.

The interaction of biotic and abiotic factors that limits a species' geographic range is a complex phenomenon. It is often difficult to assess the precise role a particular factor plays in determining an animal's distribution (Brown and Gibson, 1983). In areas characterized by steep gradients, such factors as temperature, salinity, pH, and oxygen concentration can be important in determining not only patterns of individual distribution, but also the structure of entire communities (Dunson and Travis, 1991; Matthews et al., 1992).

Dunson (1982, 1986), Lauren (1985) and Dunson and Mazzotti (1989) gathered distributional and physiological evidence to support the hypothesis that water salinity is a dominant factor limiting the distribution of fresh water reptiles in estuarine habitats. Of course, other physical factors such as nesting site availability, temperature, water depth and substrate, or biotic factors such as competition, predation, parasitism, or food availability or preference could be involved. In the present study, field observa-

tions were made with the objective of determining the use of saline habitats by snapping turtles (*Chelydra serpentina*) in a Long Island, New York estuary. I have previously shown that hatchling snapping turtles from this study area have a marked inability to grow in fresh water, as compared to an inland (New Jersey) group (Kinneary, 1992).

MATERIALS AND METHODS

Field data were collected along a 4.2 km section of the Carmans River estuary (Wertheim National Wildlife Refuge, Long Island, New York) beginning at the mouth of the river where it enters Bellport Bay (Fig. 1). Most of the field work was concentrated in Little Fish Creek (LFC) and a nearby fresh water (FW) impoundment. Little Fish Creek is the most seaward of the main tidal creeks. It had a steep horizontal salinity gradient (0 ppt to approximately 70‰ seawater over a distance of 750 m). The creek was marked at meter 0 (from its mouth), 100, 200, 300, 400, 500, 600, and 700 m. The stations were used as reference points for the various field data collected. Little Fish Creek terminates in a small pond about 750 m from its mouth. Aside from a small (FW) stream entering this pond,

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