Journal of Chemical Ecology, Vol. 17, No. 6, 1991

RESPONSE TO PREY CHEMICAL CUES BY HATCHLING PINE SNAKES (*Pituophis melanoleucus*): EFFECTS OF INCUBATION TEMPERATURE AND EXPERIENCE

JOANNA BURGER

Department of Biological Sciences
Rutgers University
Piscataway, New Jersey 08855-1059

(Received October 24, 1990; accepted February 4, 1991)

Abstract—The ability of hatchling pine snakes (*Pituophis melanoleucus*) to select and follow or avoid chemical odors of prey (mice, *Mus musculus*) on a shavings and paper substrate was investigated in Y-maze experiments, as a function of incubation temperature and experience. Incubation temperature affected behavior in the maze, and the maze choices of naive snakes, but not of snakes that had already eaten a mouse. The data indicate that snakes that have eaten, preferentially enter the arm bearing chemical stimuli from mice, whereas those that have not eaten show no preference.

Key Words—Chemical cues, incubation temperature, experience, predation, pine snake, *Pituophis melanoleucus*, mice, *Mus musculus*, learning, olfaction.

INTRODUCTION

Pheromonal communication, as demonstrated in controlled laboratory experiments on trailing of conspecifics or prey by chemical means, occurs in snakes (Brown and Maclean, 1983; Chiszar et al., 1986; Ford, 1982; Ford and O'Bleness, 1986; Gehlback et al., 1971; Heller and Halpern, 1981) and lizards (Cooper and Vitt, 1986a). Reptiles use chemical sensory abilities in several important contexts (Von Achen and Rakestraw, 1984; Mason 1991), including recognition of prey (Burghardt, 1973, 1980; Chiszar et al., 1986; Cooper, 1989, 1991; Cooper and Alberts, 1990; Cooper and Vitt, 1989; Krekorian, 1989), detection of conspecifics (Cooper and Vitt, 1984) and related congeners (Cooper and Vitt, 1986c,d), trailing of conspecifics to hibernacula (Brown and Maclean, 1983) or to mates (Ford and Schofield, 1984; Ford and O'Bleness, 1986), and recognition of ophiophagous snakes (Weldon and Burghardt, 1979; Weldon, 1982; Burger, 1989a). Reptiles often respond to chemical stimuli by increased tongue flicks (Cooper and Vitt, 1984, 1985, 1986b; Cooper et al., 1986). Most of the studies dealing with prey detection have relied on examinations of tongue-flicking (i.e., Cooper, 1989; Krekorian, 1989) rather than examination of choice behavior in individuals.

In this report I examine the behavior of hatchling pine snakes (*Pituophis melanoleucus*) experimentally exposed to shavings with and without the odor of mice (*Mus musculus*). I was particularly interested in whether hatchling snakes could discriminate between odors and no odors and whether incubation temperature or prior experience with live mice affected their responses. In nature, pine snake eggs experience differences in temperature similar to those used in this experiment (Burger and Zappalorti, 1986).

METHODS AND MATERIALS

Under appropriate state permits, pine snake eggs were collected from the Pine Barrens of southern New Jersey (Ocean, Cumberland, and Monmouth counties) in 1986 (247 hatchlings), 1987 (221 hatchlings), and 1988 (230 hatchlings). In 1986 the clutches from each female were divided in thirds; one third was incubated at 23°C, another at 28°C and a third at 33°C. In 1987 and 1988 all eggs were incubated at 28°C.

Date of hatching was noted. Snakes were maintained in individual plastic (30 × 15 × 19 cm) cages at 24-26°C. Cages contained paper for shelter. They were given the opportunity to drink water daily. Snakes were sexed by eversion of the hemipenes (Fitch, 1963; Gregory, 1983; Gutzke et al., 1985).

To determine the response of hatchlings to potential prey, I performed two experiments: one to examine the effect of both incubation temperature and experience on response (1986), and the other to examine the effect of experience alone (1987 and 1988). All experiments were conducted at 24-26°C.

In 1986 all hatchlings were exposed to a live mouse, whereas in 1987 and 1988 some hatchlings were exposed to a live mouse and others were not. Hatchlings exposed to a mouse either caught and ate the mouse or they did not. This design (Table 1) allowed evaluation of the effects of different types of experiences on hatchling response in the maze. Because incubation temperature affected behavior in the Y maze in 1986, all eggs were incubated at the same temperature in 1987 and 1988.

In 1986, hatchlings that had shed (15–20 days of age) were individually placed in an aquarium with a live laboratory mouse (12–18 g) for 20 min and

TABLE 1. EXPERIMENTAL DESIGN FOR HATCHLING PINE SNAKE EXPOSURE TO MOUSE ODORS—EXPOSURE TO LIVE MICE AND NUMBER OF HATCHLINGS IN EACH CATEGORY

Prior experience	1986	1987 and 1988
Exposed to live mouse		
Ate	96	130
Did not eat	151	75
Not exposed to mice (post-shed)[a]	—	202
Not exposed to mice (pre-shed)[b]	—	44

[a] Snake tested in maze after initial shedding.
[b] Snake tested prior to shedding.

were allowed to eat the mouse if it was caught within this time. Ten days following their exposure to a mouse, the hatchlings were tested in a Y-maze apparatus (after Burger, 1989a). The base arm of the Y maze was 1 m long and 15 cm wide with 15-cm-high wooden sides. The two experimental arms extended at a 45° angle from the base and were of the same dimensions as the base arm. Plexiglas was placed over the maze to prevent the hatchlings from escaping, but the ends of the maze were open, allowing snakes to crawl out. The base arm had shavings with no odor, the experimental arms had shavings with no odor on one side and shavings from a mouse cage in which three mice had lived for five days on the other. The floor of all three arms was covered with paper. After every test the paper with the shavings was removed, and the arm with the mouse shavings was switched (to avoid possible position effects).

In 1987 and 1988 all snakes were incubated at the same temperature, but only half the snakes were exposed to a live mouse prior to experimentation (Table 1). The remaining hatchlings were tested without exposure to a live mouse, either before shedding (10–12 days of age) or after shedding (25–30 days of age). Pine snakes normally do not eat until they have shed (Burger, 1989b). In 1987 and 1988 hatchlings were randomly assigned to condition (whether to be exposed to a mouse or not), but some hatchlings within each clutch were assigned to each of the exposure categories.

In all test experiments the hatchlings had a choice of selecting the experimental arm with shavings with no odor or the experimental arm with shavings from a mouse cage. We did not touch the shavings with our hands. Each snake was tested only once. Following experimentation all pine snake hatchlings were returned to their original nest sites in the field, together with their siblings and egg shells.

For each trial the hatchling was placed by hand into the base arm with its head facing the entrance. The hatchling was allowed to move freely up the base arm to the intersection, where it usually moved into one of the experimental arms. The trial ended when the hatchling left the Y maze through one of the experimental arms. Two experimenters were necessary to time various behaviors. The time each hatchling was in the base and experimental arm, time at the Y junction (where the two experimental arms diverge from the base arm), and the number of tongue flicks when the snake was in each location were recorded.

Contingency table χ^2 tests were used to determine differences in responses, and two-tailed Kruskal-Wallis χ^2 tests were used to determine differences in the distribution of response time and tongue flicks under several conditions. The percent of hatchlings that entered the arm with the mouse shavings as a function of experience did not differ significantly between 1987 and 1988 (contingency table χ^2 test), so these data were combined. Data are presented as means ± 1 SE. Probability levels of less than 0.05 were accepted as significant.

RESULTS

In the 1986 experiment, 71% (68 of 96) of the hatchlings that had eaten a mouse selected the experimental arm with mouse shavings ($\chi^2 = 16.6$, $df = 1$, $P < 0.001$), whereas only 33% (38 of 114) of those that had not eaten a mouse did so ($\chi^2 = 12.6$ $df = 1$, $P < 0.001$), In the above analysis, I tested the null hypothesis that there were no differences in response; thus, half the hatchlings should choose each experimental arm. Hatchlings that ate when exposed to a mouse selected the experimental arm with mouse odor significantly more often than did those that had not eaten ($\chi^2 = 29.2$, $df = 1$, $P < 0.001$).

Incubation temperature (28°C vs. 33°C) did not affect the frequency of mouse eating ($\chi^2 = 2.7$, not significant), but did affect Y-maze choices (Table 2). Hatchlings incubated at 28°C showed no significant difference in their response when they had eaten a mouse, but showed a significant difference when they had not previously eaten. Hatchlings incubated at 33°C showed the opposite response; significantly more hatchlings that had eaten chose the experimental arm with mouse shavings whereas there was no difference if they had not eaten (Table 2). I could not examine a sufficient sample incubated at 23°C in 1986 for a two-way analysis.

In the Y maze, hatchlings normally moved quickly down the base arm, stopped momentarily at the Y junction (called time motionless hereafter), explored in the junction by moving their head back and forth with rapid tongue flicking, and then moved down one of the experimental arms. The time hatchlings spent in the base arm and at the choice point in the Y junction, and the number of tongue flicks in the base arm varied significantly by incubation temperature (Table 3). Movement time in the base arm and time motionless were inversely related to incubation temperature.

The number of tongue flicks in the base arm was directly related to incu-

TABLE 2. EFFECT OF INCUBATION TEMPERATURE ON HATCHLING PINE SNAKE BEHAVIOR (1986)[a]

Presented with mouse	28°C	33°C
Ate mouse[b]		
Chose mouse shavings	24	44
Chose no-odor shavings	16	12
Contingency χ^2 (*P*)	1.6 (NS)	9.1 (0.001)
Did not eat mouse[c]		
Chose mouse shavings	13	25
Chose no-odor shavings	47	28
Contingency χ^2 (*P*)	19.2 (0.001)	0.8 (NS)

[a] Shown are number in each category. Snakes incubated at 22°C are not included because none initially ate a mouse.
[b] χ^2 for 28° vs. 33°C = 1.2 (NS).
[c] χ^2 for 28° vs. 33°C = 10.5 (0.001).

TABLE 3. BEHAVIOR OF HATCHLING PINE SNAKES AS FUNCTION OF INCUBATION TEMPERATURE. (MEANS ± SE; TIME IN SECONDS)

	Incubation temperature			Kruskal-Wallis
	23°C	28°C	33°C	χ^2 (*P*)
Number of Snakes	38	106	103	
Base arm				
Time	5.4 ± 0.6	4.1 ± 0.3	3.4 ± 0.3	9.71 (0.02)
Flicks	16.9 ± 0.3	17.9 ± 0.4	18.0 ± 0.5	9.91 (0.03)
Choice site				
Motionless				
Time	23.1 ± 5.6	12.4 ± 3.9	7.1 ± 2.2	7.79 (0.05)
Flicks	18.9 ± 1.6	17.1 ± 2.1	17.9 ± 2.6	0.86 (NS)
Explore				
Time	17.9 ± 7.9	9.8 ± 4.6	26.6 ± 14.3	0.49 (NS)
Flicks	2.3 ± 0.8	3.2 ± 1.2	3.9 ± 1.5	0.89 (NS)
Experimental arm				
Time	8.1 ± 3.4	5.6 ± 1.2	4.7 ± 1.3	3.99 (NS)
Flicks	15.6 ± 0.5	16.6 ± 0.4	16.9 ± 0.4	3.81 (NS)

bation temperatures. Although there were differences in the number of tongue flicks in the base arm, they were not large, and there were no differences in the number of tongue flicks in the other parts of the maze. These data may suggest that regardless of the time spent in different parts of the maze, the hatchlings

TABLE 4. RESPONSE OF HATCHLINGS AS FUNCTION OF EXPERIENCE (TIME IN SECONDS AND TONGUE FLICKS)

			Not exposed		Kruskal-Wallis
	Ate	Exposed	Shed	Preshed	χ^2 (*P*)
Number	130	75	202	44	
Base arm					
Time	4.5 ± 2.5	4.8 ± 2.1	9.9 ± 17.4	8.0 ± 14.5	43.9 (0.0001)
Flicks	16.8 ± 3.5	17.3 ± 3.9	17.0 ± 4.3	17.0 ± 3.9	7.2 (NS)
Choice site					
Motionless	4.9 ± 11.0	4.2 ± 8.1	10.4 ± 22.7	7.2 ± 17.0	11.6 (.02)
Flicks	3.2 ± 3.3	6.3 ± 4.3	6.3 ± 5.0	5.5 ± 4.7	42.7 (0.0001)
Explore					
Time	3.1 ± 8.2	2.1 ± 5.5	6.1 ± 15.4	5.0 ± 16.5	8.5 (0.07)
Flicks	10.8 ± 5.6	8.0 ± 6.1	12.0 ± 4.8	11.4 ± 5.4	7.3 (NS)
Experimental arm					
Time	6.1 ± 6.0	6.8 ± 4.4	12.4 ± 19.7	11.4 ± 17.3	66.3 (0.0001)
Flicks	16.4 ± 2.7	16.1 ± 3.0	16.4 ± 3.4	16.4 ± 3.3	0.5 (NS)
% Entered mouse choice arm	75.7	36.9	39.6	34.1	46.1 (0.0001)

used a similar number of tongue flicks to assay the situation when they encountered mouse odor.

There were significant differences in their choices as a function of experience ($\chi^2 = 46.1$, $df = 6$, $P < 0.001$). Over 75% of the hatchlings that had eaten chose the experimental arm with the shavings, whereas only 34–40% of the snakes with all other experiences (those exposed to mice but did not eat and those not exposed) did so.

Hatchling behavior in the maze also varied significantly with respect to experience (Table 4). The time in the various parts of the Y maze varied significantly (except for exploring in the Y junction), even though this was a novel situation for all hatchlings. In general, hatchlings exposed to live mice spent less time in every section than those not exposed.

DISCUSSION

Role of Experience. Pine snake eggs in the Pine Barrens normally hatch from late August to late September (Burger and Zappalorti, 1986). Most pine snakes travel to hibernacula in October, and by early November have entered the hibernacula or are near its entrance (Burger et al., 1988). Thus, pine snake hatchlings have only a few weeks to find food and a suitable hibernaculum.

Presumably, snakes that find food have higher overwintering success than those that do not find food. Thus, it would be adaptive to be able to recognize rodent runs or burrows by chemical means, increasing the likelihood of encountering prey. Field observations of hatchlings released in the New Jersey Pine Barrens indicate that 12 individuals encountered mouse runs and immediately changed their direction of movement, following them below ground (J. Burger, unpublished data). Indeed, in two cases the hatchlings found, caught, and ate *Peromyscus leucopus*.

I had initially predicted that hungry snakes (i.e., those that had not eaten) would show the highest preference for the mouse shavings. Yet the experiments indicate that experience with eating a mouse leads to the preference for prey odors. Hatchling pine snakes that have already eaten a mouse detect and follow the odor of mice, whereas those that have not eaten show no preference for a mouse trail.

Some hatchlings may never learn to forage, an experience amateur herpetologists and zoo keepers report for some snakes. With repeated exposure to live mice in the laboratory, about 15% of hatchlings fail to eat by 50 days of age.

Role of Incubation Temperature. In a variety of reptiles incubation temperature affects mortality and body structure (Burger et al., 1987; Deeming and Ferguson, 1989a; Gutzke et al., 1985; Vinegar, 1974), thermal selection (Deeming and Ferguson, 1989b, Lang, 1987; Lang et al., 1989), adult sexuality (Gutzke and Crews, 1988), secondary sex ratios (Burger and Zappalorti, 1988; Webb and Cooper-Preston, 1989), sexual differentiation (Charnier, 1966; Ferguson and Joanen, 1982; Yntema, 1976, 1979) and locomotion, agility, and antipredator behavior (Burger, 1989b, 1990). Thus it is no surprise that incubation temperature can affect chemoreception or feeding behavior.

In these experiments hatchlings incubated at 33°C showed a greater preference for the experimental arm with the mouse shavings than did those incubated at 28°C. These results suggest that hatchlings incubated at higher temperatures will respond more quickly to mouse trails or runs than those incubated at lower temperature. Even if these differences are developmental (i.e., in another week the 28°C hatchlings would behave similarly), the slight advantage suggested by these data for snakes that hatch from warmer nests may be enough to effect overall survival since hatchlings have only limited time to find their hibernacula before cold weather sets in.

Pine snake hatchlings incubated at low temperature (23°C) moved more slowly in the Y maze than did hatchlings from eggs incubated at higher temperatures. This corraborates my previous findings with pine snakes where locomotion was examined directly (Burger, 1989b). Similarly, black racer (*Coluber constrictor*) hatchlings incubated at 22°C moved more slowly than those incubated at 28°C (Burger, 1990).

More generally, however, the added time hatchlings incubated at low temperatures spend motionless or exploring at a decision point in nature may cause the difference between catching a mouse or not. That is, hatchlings hunt by searching for mouse burrows (J. Burger, unpublished data), and the extra time may allow prey to escape. Thus hatchlings from nests incubated at low temperatures may be at a disadvantage with respect to hunting compared to other hatchlings. In these experiments, previous experience with catching and eating a mouse affected responses to the chemical odor trials of mice, confirming that experience sharpens the hunting ability of pine snakes.

Acknowledgments—I thank R.T. Zappalorti for companionship in the field; M. Gochfeld, J. Sollazzo, M. Mikovsky, and B. Lauro for help with the experiments; and W. Cooper and M. Gochfeld for valuable suggestions on an earlier draft of the manuscript.

REFERENCES

BROWN, W.S., and MACLEAN, F.M. 1983. Conspecific scent-trailing by newborn timber rattlesnakes, *Crotalus horridus. J. Herpetol* . 39:430-436.

BURGER, J. 1989a. Following of conspecific and avoidance of predator chemical cues by pine snakes (*Pituophis melanoleucus*). *J. Chem. Ecol* . 15:799-806.

BURGER, J. 1989b. Incubation temperature has long-term effects on behavior of young pine snakes (*Pituophis melanoleucus*). *Behav. Ecol. Sociobiol.* 24:201-207.

BURGER, J. 1990. Effects of incubation temperature on behavior of young black racers (*Coluber constrictor*) and king snakes (*Lampropeltis getulus*). *J. Herpetol.* 24:158-163.

BURGER, J., and ZAPPALORTI, R.T. 1986. Nest site selection by pine snakes, *Pituophis melanoleucus*, in the New Jersey Pine Barrens. *Copeia* 1986:116-121.

BURGER, J., and ZAPPALORTI, R.T. 1988. Effects of incubation temperature on sex ratios in pine snakes: Differential vulnerabilities of males and females. *Am. Nat.* 132:492-585.

BURGER, J., ZAPPALORTI, R.T., and GOCHFELD, M. 1987. Developmental effects of incubation temperature on hatchling pine snakes *Pituophis melanoleucus. Comp. Biochem. Physiol.* 87A:727-732.

BURGER, J., ZAPPALORTI, R.T., GOCHFELD, M., BOARMAN, W.I., CAFFREY, M., DOIG, V., GARBER, S.D., LAURO, B., MIKOVSKY, M., SAFINA, C., and SALIVA, J. 1988. Hibernacula and summer den sites of pine snakes *Pituophis melanoleucus* in the New Jersey Pine Barrens. *J. Herpetol.* 22:425-433.

BURGHARDT, G.M. 1973. Chemical release of prey attack: Extension to naive newly hatched lizards, *Eumeces fasciatus. Copeia* 1973:178-181.

BURGHARDT, G.M. 1980. Behavioral and stimulus correlates of vomeronasal functioning in reptiles: Feeding, grouping, sex, and tongue use, pp. 275-301, D. Muller-Schwarze, and R.M. Silverstein (eds.). *in* Chemical Signals in Vertebrates and Aquatic Invertebrates. Plenum Press, New York.

CHARNIER, M. 1966. Action de la temperature sur la sex-ratio chez l'embryon d'*Agama agama* (Agamidae, Lacertilien). *Soc. Biol. Quest Afr.* 160:620-622.

CHISZAR, D., RADCLIFF, C., BOYD, R., RADCLIFF, A., YUN, H., SMITH, H.M., BOYER, R., ATKINS, B., and FEILER, F. 1986. Trailing behavior in cottonmouths (*Agkistrodon piscivorus*). *J. Herpetol.* 20:269-272.

COOPER, W.E. 1989. Strike-induced chemosensory searching occurs in lizards. *J. Chem. Ecol.* 15:1311-1320.

COOPER, W.E., 1991. Chemical detection of predators by a lizard, the broad-headed skink (*Eumeces laticeps*). *J. Exp. Zool.* In press.

COOPER, W.E., and ALBERTS, A.C. 1990. Responses to chemical food stimuli by an herbivorous actively foraging lizard, *Dipsosaurus dorsalis. J. Herpetol.* 46:259–266.

COOPER, W.E., and VITT, L.J. 1984. Detection of conspecific odors by the female broad-headed skink, *Eumeces laticeps. J. Exp. Zool.* 229:49–54.

COOPER, W.E., and VITT, L.J. 1985. Responses of the skinks, *Eumeces fasciatus* and *E. laticeps*, to airborne conspecific odors: Further appraisal. *J. Herpetol.* 19:481–486.

COOPER, W.E., and VITT, L.J. 1986a. Tracking of female conspecific odor trails by male broad-headed skinks (*Eumeces laticeps*). *Ethology* 71:242–248.

COOPER, W.E., and VITT, L.J. 1986b. Interspecific odor discrimination by a lizard (*Eumeces laticeps*). *Anim. Behav.* 34:367–376.

COOPER, W.E., and VITT, L.J. 1986c. Interspecific odor discrimination among syntopic congeners in scincid lizards (genus *Eumeces*). *Behavior* 97:1–9.

COOPER, W.E., and VITT, L.J. 1986d. Thermal dependence of tongue-flicking and comments on use of tongue flicking as an index of squamate behavior. *Ethology* 71:177–186.

COOPER, W.E., GARSTKA, W.R., and VITT, L.J. 1986. Female sex pheromone in the lizard *Eumeces laticeps. J. Herpetol.* 42:361–366.

DEEMING, D.C., and FERGUSON, M.W.J. 1989a. Effect of incubation temperature on growth and development of embryos of *Alligator mississippiensis. J. Comp. Physiol. B.* 159:183–193.

DEEMING, D.C., and FERGUSON, M.W.J. 1989b. The mechanism of temperature dependent sex determination in Crocodilians: A hypothesis. *Am. Zool.* 29:347–383.

FERGUSON, M.W.J., and JOANEN, T. 1982. Temperature of egg incubation determines sex in *Alligator mississippiensis. Nature* 296:850–853.

FITCH, H.S. 1963. Criteria for determining sex and breeding maturity in snakes. *Herpetologia* 16:49–51.

FORD, N.B. 1982. Species specificity of sex pheromone trails of sympatric and allopatric garter snakes (*Thamnophis*). *Copeia* 1982:10–13.

FORD, N.B., and O'BLENESS, M.L. 1986. Species and sexual specificity of pheromone trails of the garter snake, *Thamnophis marcianus. J. Herpetol.* 20:259–262.

FORD, N.B., and SCHOFIELD, C.W. 1984. Species specificity of sex pheromone trails in the plains garter snake, *Thamnophis radix. Herpetologica* 40:51–55.

GEHLBACK, F.R., WATKINS, J., and KROLL, J. 1971. Pheromone trail following studies of typhlopid, leptotyphlopid, and colubrid snakes. *Behavior* 40:282–294.

GREGORY, P.T. 1983. Identification of sex of small snakes in the field. *Herpetol. Rev.* 14:42–43.

GUTZKE, W.H.N., and CREWS, D. 1988. Embryonic temperature determines adult sexuality in a reptile. *Nature* 332:832–834.

GUTZKE, W.N., PAUKSTIS, G.L., and MCDANIEL, L.C. 1985. Skewed sex ratios of adult and hatchling bull snakes, *Pituophis melanoleucus*, in Nebraska. *Copeia* 1985:649–652.

HELLER, S., and HALPERN, M. 1981. Laboratory observations on conspecific and congeneric scent trailing in garter snakes (*Thamnophis*). *Behav. Neurol. Biol.* 33:372–377.

KREKORIAN, C.O. 1989. Field and laboratory observations on chemoreception in the desert iguana, *Dipsosaurus dorsalis. J. Herpetol.* 23:267–273.

LANG, J. 1987. Crocodilian thermal selection, pp. 301–307, *in* G.J.W. Webbs, S.C. Manolis, and P.J. Whitehead (eds.). Wildlife Management: Crocodiles and Alligators. Surry, Baetty and Sons, London.

LANG, J.W., ANDREWS, H., and WHITAKER, R. 1989. Sex determination and sex ratios in *Crocodylus palustris. Am. Zool.* 29:935–952.

MASON, R. 1991. Reptilian pheromones, *in* C. Gans and D. Crews (eds.). Biology of the Reptilia, Vol. 18. Academic Press, New York. In press.

VINEGAR, A. 1974. Evolutionary implication of temperature induced anomaly of development in snake embryos. *Herpetologica* 30:73–74.

VON ACHEN, P.H., and RAKESTRAW, J.L. 1984. The role of chemoreception in the prey selection of neonate reptiles, *in* Vertebrate Ecology and Systematics—A Tribute to Harry S. Fitch. R.A. Seigel, L.E. Hunt, J.L. Knight, L. Malaret, and N.L. Zuschlag (eds.). Museum of Natural History, University of Kansas, Lawrence, Kansas.

WEBB, G.J.W., and COOPER-PRESTON, H. 1989. Effects of incubation temperature on crocodiles and the evolution of reptilian oviparity. *Am. Zool.* 29:953–971.

WELDON, P.J. 1982. Responses to ophiophagous snakes by snakes of the genus *Thamnophis*. *Copeia* 1982:788–794.

WELDON, P.J., and BURGHARDT, G.M. 1979. The ophiophage defensive response in crotaline snakes: Extension to new taxa. *J. Chem. Ecol.* 5:141–151.

YNTEMA, C.L. 1976. Effects of incubation temperature on sexual differentiation in the turtle *Chelydra serpentina*. *J. Morphol.* 150:453–462.

YNTEMA, C.L. 1979. Temperature levels and periods of sex determination during incubation of eggs of *Chelydra serpentina*. *J. Morphol.* 159:17–27.