
INFLUENCES OF HIBERNACULUM MICROENVIRONMENT ON THE WINTER LIFE HISTORY OF THE GARTER SNAKE (*THAMNOPHIS SIRTALIS*)¹

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ABSTRACT. A communal hibernaculum in Portage County, Wisconsin, which was studied from 1981-1984, served as a winter refuge for 200 to 300 garter snakes (*Thamnophis sirtalis*). The den was an abandoned cylindrical cistern (about 100 cm diameter × 245 cm deep) constructed of stacked fieldstone in predominantly porous soils. Garter snakes approaching the den in October exhibited "trailing" behavior. This observation, coupled with significant differential arrival timing of small and larger snakes, supports the previously established contention that pheromone trails from conspecifics are important in den relocation. The hibernation period lasted from October to early April. During this time, the snakes were submerged in acidic (pH 5.5 — 6.0), hypoxic (dissolved oxygen = 2.9 ppm) well water. Sustained winter submergence provided a stable thermal regime, allowed the occupation of preferred thermal microsites, and prevented dehydration. The den depth-temperature gradient followed a pronounced, seasonally dependent cycle that was correlated with entrance and emergence behaviors and may have served as a stimulus for the onset and termination of dormancy. A cold temperature, anti-predator, defense behavior was demonstrated by newly emerged snakes and was characterized by cloacal elimination, dorso-ventral compression of the body, and mouth-gaping.

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INTRODUCTION

Hibernation is an important feature of the life histories of reptiles inhabiting regions that experience seasonal prolonged cold conditions and decreased food availability. The physiological, ecological, and demographic implications of reptilian hibernation have been the focus of numerous field and laboratory investigations. Gregory (1982) has recently summarized this literature.

Hibernating snakes inevitably must select subterranean dens that offer protection from predators and damaging temperatures. The maintenance of total darkness (Aleksiuk 1976) and availability of moisture (Gilles-Baillien 1974) may be conditions important to overwintering success. Although a number of snake hibernacula (e.g. loose soil, cover objects, animal structures, rock crevices, abandoned human structures;

Gregory 1982) have been identified, little is known about the internal physical structure and seasonal variation in microclimate within these dens. These data are scarce principally because many dens are inaccessible to investigators, too large or diffuse for intensive study, or destroyed by excavation upon discovery. The den described in this study provided a unique opportunity to examine relationships between some winter life-history aspects of a temperate-region reptile and its physical microenvironment.

METHODS AND MATERIALS

The study was carried out during 1981-1984 at a communal snake hibernaculum in Portage County (44°N, 90°W), Wisconsin. Garter snakes (*Thamnophis sirtalis*) approaching the den site were collected in October, 1981 with a nylon screen drift fence (63 cm high) circumscribing the den opening and with wire funnel traps. Beginning in late September, captured snakes were measured for snout-vent length (SVL) and marked prior to release inside the fence. These animals were subsequently recaptured inside the fence, recorded, and allowed to disperse from the den site after emerging in April. Snakes

captured at other times (October, 1982, 1983; April, 1983, 1984) were collected by hand, measured for SVL, weighed, and sexed by hemipenal eversion.

Measurements of ambient air temperature were made with maximum-minimum thermometers placed 1 m above the den during late September, 1981. Precipitation data were obtained from a weather station at the University of Wisconsin, (Stevens Point, Wisconsin) 18 km from the den site.

Temperatures within the hibernaculum were measured on eight occasions (April, August, September, October, November, and December) in 1983 and twice (March and April) in 1984 with a telethermometer (Yellow Springs Instrument Co., Model 44TD). Gradient measurements were taken in the center of the hibernaculum at 20-cm depth intervals from the ground surface. Relative humidity was measured in a similar manner with a portable psychrometer (Pscytron, Model 566).

Coecal temperatures of newly emerged garter snakes were measured in April, 1983 and 1984 with the telethermometer and a rectal thermistor probe. Insertion of the probe required minimal handling of the animal.

The pH of water in the hibernaculum was measured in April, 1983 with a Hach pH Kit (Hach Chemical Co., Ames, Iowa). Dissolved oxygen was measured in April, 1983 and 1984 with the Winkler method (Anonymous, 1978).

RESULTS

The hibernaculum was located in a small (1.0 ha), upland (352 m elevation) woodlot that was bounded on three sides by agricultural fields. Remnants of the stone foundation of a barn and farmhouse prevented this area from being tilled. Vegetation in the woodlot was dominated by mature box elder (*Acer negundo*) and black cherry (*Prunus serotina*) trees; small openings contained blackberry (*Rubus* spp.) thickets. A dense growth of grasses bordered the woodlot on all sides.

The hibernaculum was a small, cylindrical cistern of varying diameter (90-109 cm) and 245 cm deep. The walls, which were loosely constructed of stacked fieldstone, averaged 46.4 cm in thickness, creating a calculated total wall volume of 4.9 m³. Approximately 10 to 15% of this volume was crevice space, and was thus usable by hibernating snakes. The opening at the surface was bordered by a concrete collar (5 cm thick). A flat, metal sheet covered the opening and prevented precipitation from entering the well directly. It also excluded most incident light. Openings in the vegetation and a slight slope exposed the well to the southwest sky.

The soil adjacent to the den appeared to be well-drained; borings produced 15 cm of sandy loam overlying well-defined gravel and sand strata (11 cm and 31 cm, respectively). An impenetrable rock layer at 58 cm prevented further boring.

Water depths in the well followed a pronounced seasonal cycle. Maximal depths were attained in April (1983, 123 cm; 1984, 152 cm) owing to snowmelt and precipitation. The water level receded during June, and the well remained dry until autumn. In October, 1983, water (depth = 43 cm) was present in the well at the time of snake entrance. Subsequent precipitation consisted largely of snow; thus little additional filling of the well occurred during winter.

Well-water during April was cold (1.8°C), acidic (pH 5.5-6.0), and contained little dissolved oxygen (2.9 ppm). Although clear when undisturbed, the water was odoriferous owing to the decomposition of snake carcasses. Winter mortality was slight, however; only three dead snakes were found in the well during 1981-1984. Although one of these had multiple

rodent wounds along the dorsum, no definite determination of the cause of death could be made. Non-fatal rodent wounds were also observed on several newly emerged snakes.

Thermal gradients in the den, recorded at different times over the course of several days, showed that shallower regions experienced greater thermal fluctuations than deeper areas. Surface-to-bottom temperature differences were greatest during the summer, particularly in August (Fig. 1). Temperatures nearest the den opening fluctuated most rapidly in all seasons, and closely tracked changes in ambient temperature. Temperatures deeper inside the well were generally more stable. For example, den surface temperatures on 13 August (26.5°C) and 14 September (16.2°C), 1983 varied by 10.3°C; yet the difference at 120 cm was only 1.2°C. Temperatures (12.3°C) at the bottom of the well were identical.

Cooling of the den in autumn, 1983 was dependent upon prevailing air and substrate temperatures and was characterized by a gradual decrease in upper well temperatures. After cooling, the den became approximately isothermal at about 7°C (Fig. 1). Additional cooling of the upper well occurred in November. Subsequently, the well bottom represented the warmest portion of the den. Upper well temperatures presumably remained low (freezing or below) throughout the winter. In April, temperatures in the upper well region were again elevated above well bottom temperatures (Fig. 2) owing to the warming of air and substrate.

Temperatures in north, east, and southwest wall crevices were measured once at 20-cm intervals from the ground surface on 4 April, 1983 (Fig. 3). East and southwest wall crevice temperatures were warmer (0.1-0.8°C) than those on the north wall at all but one level. Preference by *T. sirtalis* for these slightly warmer microsites was not apparent; the snakes appeared to be distributed laterally in a random arrangement.

Relative humidity (78%, April, 1983; 83%, September, 1983) inside the well was considerably higher than ambient each time it was measured. On these dates, humidity subjacent to the metal cover was 16 and 21% higher than just above it and increased with depth to

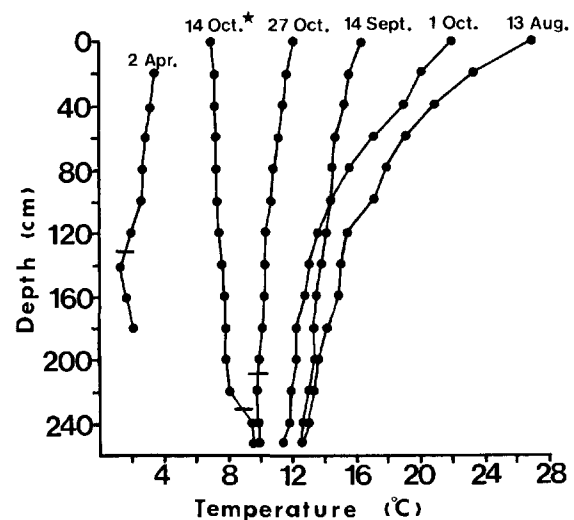


FIGURE 1. Depth-temperature curves recorded within the hibernaculum during 1983. The date of snake entrance is indicated by the star. Horizontal lines indicate water surface at sample time.

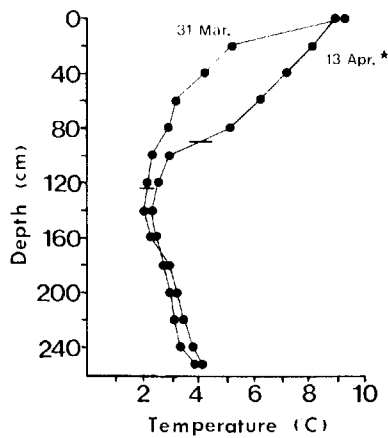


FIGURE 2. Depth-temperature curves recorded within the hibernaculum during spring, 1984. The date of snake emergence is indicated by the star. Horizontal lines indicate water surface at sample time.

near-saturation at 120 cm, regardless of whether water was present.

Although garter snakes were the most abundant species using the den in all years, fox snakes (*Elaphe vulpina*) and red-bellied snakes (*Storeria occipitomaculata*) also were observed hibernating in the den. Estimates of population size were based upon counts made each autumn in the vicinity of or within the hibernaculum. Accordingly, the den served as a winter refuge for 200 to 300 garter snakes. More fox snakes used the den in 1981 (N = 9) than in 1983 (N = 3). Use of the den by red-bellied snakes was uncommon (1981, N = 1; 1983, N = 2).

Unfortunately, no attempt was made in autumn, 1982 to systematically capture returning snakes that were marked in 1981. Thus, a calculation of den fidelity was

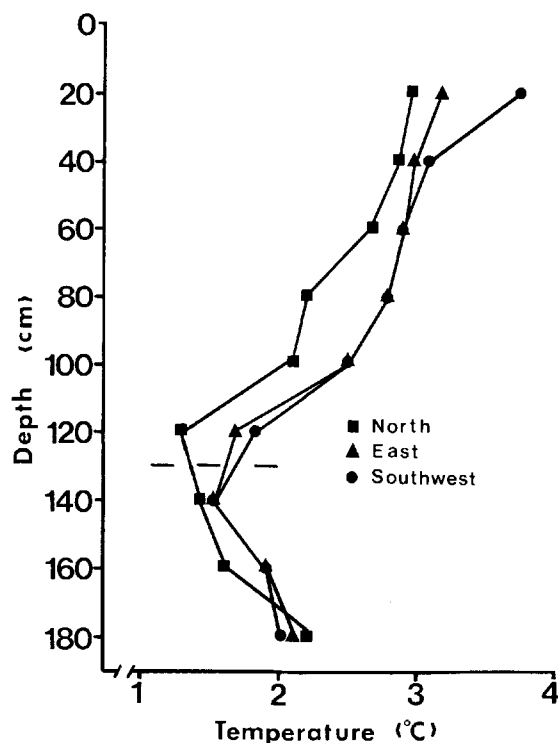


FIGURE 3. Temperatures in north, east, and southwest wall crevices recorded at 20-cm intervals within the hibernaculum on 4 April 1983. Horizontal lines indicate water surface at sample time.

not possible. However, many garter snakes observed in and around the den during the autumn of 1982 had ventral scutes marked the previous year. At least one garter snake bearing the 1981 mark was observed in the den during October 1983.

Arrival of garter snakes at the den site peaked in October, although the actual date varied annually (1981, early October; 1982, mid-October; 1983, late October). Migrating snakes usually approached the den from the southwest; few snakes were found to the north of the hibernaculum. Approaching snakes appeared to follow common and well-defined "travel lanes" through the underbrush. These routes did not appear to be associated with topographic features or landmarks, as they typically bisected homogeneous cover. Snakes within a 25-m radius of the den opening were observed frequently to enter the hibernaculum within a few hours. Although most snakes remained in the hibernaculum after entry, marked garter snakes were observed occasionally basking in the proximity of the den on warm days.

Drift-fencing and trapping during autumn, 1981 permitted an evaluation of the relationship between local weather conditions and the arrival of garter snakes at the den site. Arrival and entrance behaviors coincided with den isothermy and were independent of external temperature extremes, but inversely related to the occurrence of precipitation (Table 1). Also, snakes arriving earlier in the fall were significantly (Kruskal-Wallis test, $H = 9.34$, $P < 0.05$) larger than those arriving at other times (Fig. 4). Smaller *T. sirtalis* were not observed at the hibernaculum until relatively late in the migration. Length, weight, and sex ratio data for garter snakes using the den from 1981 to 1984 are presented in Table 2. Mean lengths (pooled = 49.5 cm SVL) and weights (pooled = 55.8 g) did not vary significantly over the study period. Assuming that the growth rate of Wisconsin new-born snakes is similar to that of conspecifics in Michigan, very few (N = 2) first-year *T. sirtalis* (17-28 cm SVL in October; Carpenter 1952) used the hibernaculum. The smallest male (37.0 cm SVL) and female (37.6 cm SVL), excluding the two first-year individuals, that used the Wisconsin den corresponded to second-year animals in Carpenter's (1952) study. The sex ratios for only October, 1982 (0.3:1) and April, 1983 (3.5:1) were significantly (Chi square test, $P < 0.05$) different from the expected 1:1.

TABLE 1

Dates of garter snake arrival and local weather conditions at a hibernaculum in Portage County, Wisconsin, September-October, 1981

Dates*	Number captured**	Temperature (°C)		Precipitation (cm)
		Max	Min	
28-29 Sep	26	—	7.0	0
30 Sep-1 Oct	1	13.9	4.0	snow, trace
2-3 Oct	18	14.4	-1.1	0
4-5 Oct	7	12.2	2.2	rain, 1.2
6-7 Oct	17	11.7	2.2	0
8-9 Oct	14	16.7	-2.2	0
10-11 Oct	25	13.3	—	0

*Field data were collected between 1530 and 1800 h at 2-day intervals.

**Values represent the total number of previously unencountered snakes arriving at the den during each sampling period.

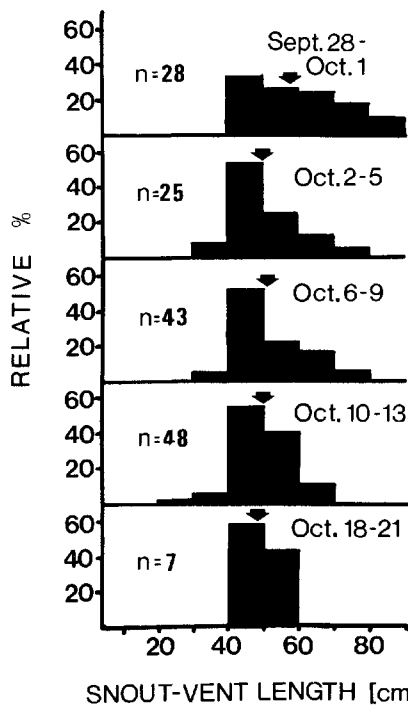


FIGURE 4. Relationship between the chronology of arrival (as relative % of the sample) at the hibernaculum and snout-vent lengths of garter snakes during 1981. Arrows indicate mean lengths.

Eighty-three snakes taken from the hibernaculum in October, 1982 and 1983 were killed and examined internally for the presence of food in the gastrointestinal tract. All stomachs and intestines were void of food indicating that *T. sirtalis* hibernate with empty guts.

Soon after they entered the hibernaculum in October, garter snakes appeared to be distributed randomly among the many cracks and crevices formed by the abutment of irregularly shaped stones. The heads of these animals frequently protruded from the spaces and were oriented toward the center of the well. Many snakes occupied crevices up to 80 cm below the water surface and anchored their bodies in place by wedging them between rocks. Garter snakes were occasionally observed swim-

ming from one side of the well to the other, either under water or at the surface. As the upper well area cooled (late October-November), all snakes were found at the water surface or below. Swimming snakes gulped air occasionally, but this was not observed in stationary animals. The frequency of surface activity declined during winter, as most snakes occupied sites well below the water surface. It is not known if these movements ceased completely because den visits were infrequent during winter. However, surface activity was high during early April and peaked during emergence.

Snakes usually emerged and departed from the den in early April. Emergence in spring was correlated qualitatively with the formation of a strong thermal gradient in the upper well region. For example, ground-level air temperatures were similar (about 9°C) on 31 March and 10 April, 1984. Emergence did not occur, however, until the latter date which coincided with the development of a stronger water surface-to-ground surface gradient (Fig. 2).

Cloacal temperatures of newly emerged *T. sirtalis* usually approximated substrate temperatures ($\bar{x} \pm SE = 4.8 \pm 1.1^\circ\text{C}$; $N = 23$). However, two garter snakes basking on snow drifts had body temperatures (3.3°C and 4.0°C) that were 1.3°C and 1.7°C higher than snow surface temperatures. The lowest cloacal temperature recorded for a newly emerged snake was 1.7°C. Garter snakes were active at these temperatures, and were capable of excreting cloacal substances and defensive behavior. When disturbed by an observer, newly emerged garter snakes became compressed dorso-ventrally and assumed a threatening posture with the mouth agape and oriented skywards. However, snakes displaying this behavior rarely struck.

Spring emergence occurred over a period of several days. Snakes usually dispersed in a southwesterly direction upon emergence and moved toward a large wetland area 0.6 km away. They presumably initiated courtship activities and spent the summer in this area. Courtship behavior in the vicinity of the hibernaculum was rarely observed.

DISCUSSION

The use of subterranean communal hibernacula by snakes at northern latitudes confers several advantages upon their inhabitants. Snakes are protected from damaging temperatures and predators, and mates are readily available in spring (Gregory 1974, 1982).

The extent to which communal hibernacula may influence the geographical and local distributions of species is apparently unknown. However, the artificial den in this study (and similar artificial structures in the area) seems critical to the existence of the garter snake population, since large expanses of sandy soil and a paucity of exposed bedrock probably preclude these forms from locating suitable natural hibernacula in this locale. This view is in accord with Gannon (1978) who suggested that the range of prairie rattlesnakes (*Crotalus viridis*) is limited by the low availability of hibernacula in southern Canada.

The den in this study, like others (Klauber 1972, Galligan and Dunson 1979), had a southern exposure, which may prevent damaging internal thermal conditions and facilitate rapid warming in spring (Gregory 1982). Because of its high thermal conductivity, the

TABLE 2

Lengths, weights, and sex ratios of garter snakes captured at a hibernaculum in Portage County, Wisconsin, 1981-1984. Lengths and weights are expressed as means $\pm 1 SE$.

Season	N	Snout-vent length (cm)	Weight (g)	Sex ratio (male:female)
Autumn, 1981	151	51.5 \pm 0.8	—	—
Autumn, 1982				0.3:1.0
Male	4	45.0 \pm 2.4	33.0 \pm 3.8	
Female	13	49.3 \pm 1.9	57.6 \pm 3.6	
Spring, 1983				3.5:1.0
Male	7	45.4 \pm 1.7	39.8 \pm 4.9	
Female	2	49.4 \pm 2.5	59.7 \pm 10.7	
Autumn, 1983				0.9:1.0
Male	30	45.7 \pm 1.1	41.7 \pm 2.6	
Female	34	54.0 \pm 1.7	81.2 \pm 9.9	
Spring, 1984				0.9:1.0
Male	6	45.1 \pm 1.6	38.6 \pm 3.8	
Female	7	56.7 \pm 3.2	86.8 \pm 16.7	

metal den cover may have also played a similar role. In addition to its effect upon gradient formation, the cover may have been functionally important in that most incident light was excluded from the den. Aleksuik (1976) suggested that constant darkness is required when *T. sirtalis* prepare physiologically for hibernation.

Garter snakes arrived at the den in early fall, when daily maximum temperatures were between 12 and 17°C; temperatures at night sometimes fell below 0°C. Precipitation markedly decreased arrival frequency, and probably hampered den location more than low temperature did. Parker and Brown (1980) reported a similar range of temperatures during arrival and the same influence of precipitation on arrival frequency of *Masticophis* and *Pituophis* in Utah.

In each year of the present study, *T. sirtalis* remained underwater for lengthy periods during winter. Although other snakes select dens with high humidity regimes or near ground-water level (Carpenter 1953, Klauber 1972), no such account of prolonged submergence during winter dormancy has been given. Consequently, the associated gas-exchange problems remain unstudied.

Despite markedly decreased metabolic demands, the average garter snake (55.8 g) required 6.70 ml oxygen per day, based upon rate-temperature data for *T. sirtalis parietalis* (Aleksuik 1971). Possible modes of oxygen acquisition include the infrequent gulping of air at the water surface and transintegumentary uptake. Even though these events would not necessarily be mutually exclusive, possible limitations (e.g. impenetrable ice cover, hypoxic well water) may confound simple explanations. Also, the possibility of anaerobic production of ATP cannot be excluded. Further investigation of this phenomenon is clearly needed.

Submerged hibernation by terrestrial snakes is adaptive for several reasons. Body temperatures of these snakes are relatively stable because water acts as a thermal buffer owing to its high specific heat. Also, the warmest den microsites available to snakes during winter are underwater. Some snakes (e.g. *Elaphe obsoleta*, *Coluber constrictor*, *Crotalus viridis*) are known to move toward and occupy the warmest microsites in hibernacula (Sexton and Hunt 1980, Sexton and Marion 1981). A tolerance for submerged conditions presumably allows *T. sirtalis* to do the same. Furthermore, free-choice submergence prevents dehydration in field and laboratory-hibernating garter snakes from the Wisconsin den (Costanzo 1985). In the present study, *T. sirtalis* (N = 13) overwintering in the laboratory (3 to 5°C, >70% relative humidity) contained up to 16% less moisture than submerged control individuals (\bar{x} = 74.4% of fresh body weight; N = 84; Costanzo 1985). The frequently observed dehydration response in terrestrial reptiles during winter may have a deleterious impact upon survival rates (Gilles-Baillien 1974). Submerged snakes may be free of these consequences.

The effect of depth-temperature gradient (D-TG) reversal on the timing of snake entrance and emergence at hibernacula has been reported by other investigators (Carpenter 1953, Sexton and Hunt 1980, Sexton and Marion 1981). In the present study, the establishment of an inverse D-TG also appeared to draw *T. sirtalis* toward the bottom of the den during late autumn. This effect may have enabled these individuals to locate preferred

thermal microsites, while also protecting them from potentially damaging surface temperatures.

Garter snakes emerged from the hibernaculum following the reversal of the D-TG in spring. This finding agrees with published experimental evidence for the role of D-TG reversal in the termination of dormancy in some snakes (Sexton and Marion 1981). Emergence occurred during the stronger of two recorded gradients, even though ground surface temperatures were similar. Therefore, external ambient temperatures probably do not play a direct role in the initiation of emergence behavior, but may be more important for the establishment of a suitable D-TG. Because observations were limited, however, carefully controlled experiments would be needed to determine the gradient-strength thresholds that elicit entrance and emergence behaviors.

Endogenous rhythms have also been implicated in the onset and termination of hibernation in snakes (Drda 1968) and lizards (Garrick 1972). However, no data were collected in support or dispute of this hypothesis during this investigation.

The mechanisms by which snakes relocate traditional dens in autumn are unknown (Gregory 1982). Solar cues (Landreth 1973, Newcomer et al. 1974) and topographical landmarks (Parker and Brown 1980) may be important in this regard; however, there are findings to the contrary (Brown and Parker 1976). Recently, Brown and MacLean (1983) and King et al. (1983) proposed that chemical cues from conspecifics might enable snakes to relocate hibernacula. Supporting evidence for chemical cues is provided by the observations of "trailing" behavior in the present study and the demonstration of increased "trailability" in *Thamnophis* during autumn (Ford 1981). The latter, however, attributed his findings to reproductive activities. Additionally, other studies (Brown and Parker 1976, Parker and Brown 1980) have documented late arrival dates for young snakes at hibernacula. Although Gregory (1982) suggested that young snakes may simply remain active for a longer period of time in autumn, it is conceivable that younger snakes require additional time to locate dens via chemotaxis (Brown and MacLean 1983). Although smaller *T. sirtalis* did arrive later in autumn at the Wisconsin den, this trend may have partly reflected sexual differences in arrival timing. Sex-ratio data for the period during which these observations were made are lacking; however, of the snakes collected from 1982 to 1984, males ($\bar{x} \pm \text{SE} = 45.5 \pm 0.8$ cm; N = 47) were significantly (Student's t-test, $t = 26.7$, $P < 0.05$) smaller than females ($\bar{x} \pm \text{SE} = 53.1 \pm 1.2$ cm; N = 56). Gregory (1982) reported that at several dens male snakes tended to arrive later than females. This may have also been the case with the den in the present study. Large (> 60 cm), early-arriving *T. sirtalis* were undoubtedly females. These observations were consistent nevertheless with the pheromone-use hypothesis, as only females are known to establish scent-trails (Ford 1981).

Although defense behavior at winter temperatures has been noted in several snake species (Carpenter 1953, Sexton and Hunt 1980, Marion and Sexton 1984), this phenomenon merits further investigation. Upon emergence in spring, cold ($\bar{x} = 4.8^\circ\text{C}$) *T. sirtalis* responded to perturbation with excretion of cloacal contents, dorso-ventral compression of the body, and

mouth-gaping (without striking) in a skyward orientation. This behavior is similar to the "high intensity defensive postures" demonstrated by a hibernating prairie rattlesnake (*Crotalus viridis*) at a substrate surface temperature of 5°C (Marion and Sexton 1984). In the same study, *C. viridis* struck only at surface temperatures of 8°C or greater; locomotion was possible, however, at temperatures as low as 1-2°C (1.7°C for *T. sirtalis* in the present study). At these low temperatures, escape from predators would be highly unlikely. Thus, the defensive behaviors of some snakes at very low temperatures appear to be impotent, yet useful, anti-predator mechanisms.

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