Herpetological Natural History, 7(1), 1999–2000, pages 59–66.

DEFENSIVE BEHAVIORS OF PINE SNAKES (*PITUOPHIS MELANOLEUCUS*) AND BLACK RACERS (*COLUBER CONSTRICTOR*) TO DISTURBANCE DURING HIBERNATION

Joanna Burger
Division of Life Sciences, Rutgers University, Piscataway, New Jersey 08854, USA
Email: burger@ biology.rutgers.edu

Robert T. Zappalorti
Herpetological Associates, Inc., 536 Seaman Avenue, Beachwood, New Jersey 08722, USA

and

Michael Gochfeld
Environmental and Community Medicine, UMDNJ,
Robert Wood Johnson Medical School, Piscataway, New Jersey 08854, USA

Abstract. In the wild, mammalian predators sometimes dig up hibernacula and prey upon overwintering snakes. We disturbed 198 northern pine snakes (*Pituophis melanoleucus*) and 41 northern black racers (*Coluber constrictor*) during hibernation in late winter when air temperatures were 7–10°C, and recorded their responses. We measured the snakes' ability to protect themselves and to escape from a simulated predator. Within 2 min of excavation, 41% of racers and 49% of pine snakes began to move, and about 25% struck defensively at a stimulus. Nearly 29% of pine snakes hissed, whereas only 5% of racers did so. There were few significant differences in behavioral responses between the two species. However, pine snakes had significantly lower interstrike intervals than did black racers and struck sooner at a stimulus than did black racers. For pine snakes, time to first hiss, height of the first strike, and distance moved decreased with increasing cloacal temperature (mean = 7.5°C, range = 4–12°C), but increased with body size (mean = 545 g, range = 24–1414 g). Because of low body temperatures, neither species had the ability to move very far when first taken from hibernation. The snakes' delayed reaction and low defensive behavior rates suggest that both species could not avoid predation under these circumstances.

Key Words. New Jersey Pine Barrens; Hibernation; Anti-predator behavior; Mammalian predators; Pine snake; Racer; *Pituophis melanoleucus*; *Coluber constrictor*.

Ambient temperatures markedly affect the behavior and physiology of ectotherms, and have important implications for their ecology and evolution (Huey 1982). In reptiles, amphibians, and fish, ambient temperature affects metabolic rates and activity (Andrews 1994), cold resistance (Vincent and Secoy 1978), hibernation (Gregory 1982), distribution (Gregory 1982), vocal performance (Navas 1996), habitat use (Zimmerman et al. 1994) and geographical range (Muth 1980). In reptiles, activity often decreases as ambient temperatures decrease, and growth rate can be slower (Autumn and DeNardo 1995).

Daily and seasonal trends in temperatures are gradual and moderately predictable in most geographic regions. Reptiles seek protection or shelter before temperatures become intolerable, and before they have limited mobility and are vulnerable to predators (Bogert 1949). Under some circumstances, cold, relatively immobile reptiles can be exposed to hazards, such as when a hibernating individual is disturbed by a predator. Hibernating reptiles that are discovered by predators presumably are extremely vulnerable, and are unable to defend themselves because of their torpid condition.

Snakes hibernate in a variety of situations including rock piles, stump holes, caves, rodent burrows, crevices in shale, talus slopes, hard-packed sand, old wells, and in artificial refugia (Brown and Parker 1976; Burger et al. 1988; Kauffeld 1957; Parker and Brown 1973; Sexton and Hunt 1980; Zappalorti and Reinert 1994). Such sites are relatively safe from predators, but occasionally a mammal such as a coyote (*Canis latrans*), fox (*Vulpes fulva*), skunk (*Mephitis mephitis*), or shrew (*Sorex* spp, *Blarina* spp) digs up or enters the hibernaculum, thereby exposing snakes to the cold and/or to predation (Burger et al. 1988).

We examined the behavior of northern pine snakes (*Pituophis melanoleucus*) and northern black racers (*Coluber constrictor*) that were purposefully disturbed while they were hibernating in the Pine Barrens of southern New Jersey. We have been studying natural hibernacula since 1986 to examine philopatry, growth rates, injuries, survival rates, and longevity of pine snakes (Burger et al. 1988, 1992) to understand how to improve artificial hibernation sites in the face of continued residential development. In excavating the hibernacula as part of a state-approved project, we had an opportunity to examine various anti-predator responses of the snakes. We were particularly interested in whether excavated snakes were sufficiently mobile to avoid predators, and whether they responded defensively. We were also interested in the effects of cloacal temperature and body size on response behavior of hibernating snakes. We predicted that snake size affects behavior becanse smaller snakes, with a larger surface to volume ratio, could heat and cool more rapidly. In the wild, hibernacula are sometimes invaded by predators such as foxes and raccoons (*Procyon lotor*), and snakes may face these predators when they emerge in early spring.

In the New Jersey Pine Barrens, pine snakes avoid winter conditions by moving to underground hibernacula (Burger et al. 1988, 1992). Pine snakes often hibernate in abandoned burrows of striped skunk, red fox, and woodchuck (*Marmota monax*), digging narrow side tunnels that can extend 3–6 m into adjoining hard-packed soil (Burger et al. 1988). We have documented subterranean predation on hibernating pine snakes by humans, fox, skunk, and short-tailed shrews (*Blarina brevicauda*), although only the former three will routinely dig up hibernacula (Burger et al. 1992). Although some pine snakes hibernate solitarily deep in decaying root systems, they may hibernate together in groups of as many as 33 individuals (J. Burger and R.T. Zappalorti, unpubl. obs.). These communal groups regularly include black racers that also make use of the extensive burrow system of the pine snakes.

METHODS

We have studied hibernacula of pine snakes and black racers in the New Jersey Pine Barrens for over 10 years (1986–98). When a hibernaculum was discovered, all snakes were temporarily removed, marked, and measured. All snakes encountered were marked by injecting a passive integrative transponder (PIT) tag which can be read at subsequent encounters using a radio frequency wand (Elbin and Burger 1994).

After all snakes were removed from their hibernaculum, we rebuilt it, reconstructing a main underground chamber using cement blocks for walls and plywood or sheet metal for the roof. Additionally, small cement blocks were used to form a permanent tubular entrance up to the ground surface. The entrance blocks were offset slightly, creating a sufficiently small opening so that a predator as large as a fox or skunk could not enter. The entrance was further obscured by logs and leaf litter to conceal its location from human poachers. In the 13 years we have studied these hibernacula, only three skunks and a short-tailed shrew entered the rebuilt hibernacula. In spite of our annual disturbances, and that of an occasional mammalian predator, the pine snakes and black racers have continued to use these overwintering sites, although the total number of snakes fluctuates from year to year. There is some natural shifting from den to den by some pine snakes and black racers

TABLE 1. Raw data and Kruskal-Wallis χ^2 and P values for physical characteristics and behavioral comparisons of pine snakes (*Pituophis melanoleucus*) and black racers (*Coluber constrictor*) in the New Jersey Pine Barrens following disturbance during hibernation. Data values are given as means ± standard error, NS indicates nonsignificant statistical differences.

Data	**Pine Snake** n = 198	**Racer** n = 41	χ^2	P
Depth (cm)	103±2.24	71.3±2.94	41.13	0.001
Horizontal distance of entrance to chamber (cm)	272±5.82	232±11.02	12.19	0.002
Cloacal temperature (°C)	7.45±0.10	6.91±0.21	4.11	NS
Soil temperature (°C)	7.10±0.12	6.65±0.25	3.71	NS
Air temperature (°C)	7.73±0.14	7.63±0.37	1.22	NS
Total weight (g)	545±26.57	232±19.11	20.03	0.001
Snout–vent Length (cm)	98.7±2.35	84.0±2.40	21.52	0.001
Removal time (after midnight)	12:04±0:08	10:57±0:16	14.02	0.001
Latency from removal time:				
First strike (min:sec)	7:14±0:50	5:33±1:38	3.29	NS
First hiss (min:sec)	4:28±0:39	10:00±5:00	4.12	NS
First move (min:sec)	1:57±0:21.3	1:24±32.9	1.30	NS
Strike (First)				
Height (cm)	9.64±2.25	8.75±2.43	0.85	NS
Length (cm)	13.6±1.58	12.1±2.37	1.76	NS
Distance moved				
first 10 s (cm)	21.0±2.11	11.3±1.87	1.27	NS
second 10 s (cm)	25.6±2.99	18.0±3.49	1.33	NS
Time to strike again on own (min:sec)	1:52±0:40	6:18±1:17	7.10	0.008
Strike behavior after 5 min				
Time (min:sec)	2:56±0:47	6:20±1:41	4.37	0.04
Distance (cm)	125±42.7	29.1±14.3	1.00	NS
Height (cm)	9.03±1.27	6.30±1.45	0.90	NS
Length (cm)	23.8±2.83	17.2±4.73	1.08	NS

(J. Burger and R.T. Zappalorti, unpubl. data).

In March and early April, we excavated from five to ten hibernacula each year from 1990–97. Each hibernaculum contained from 1–33 snakes. We examined the behavior of 198 pine snakes and 41 black racers disturbed in these hibernacula. We carefully excavated all burrow openings, following each tunnel by removing sand by hand or with a small trowel. Two to three hours were required to carefully excavate a hibernacnlum. When we first located any snake, we measured the distance between where the snake was hibernating and the hibernaculum entrance at the ground surface. When any portion of a snake was exposed, we uncovered its cloaca before the snake was exposed to the outside air. Before each snake was removed completely from the sand we took its cloacal temperature with a Schultheis thermometer, as well as ambient air and sand temperature in its burrow. Each snake was immediately placed on the flat sand surface above ground for observation. We recorded the following: time of day, substrate temperature at the surface, and air temperature; time to first strike, hiss and move; height and vertical distance of the first strike; distance moved by the snake in the first and second 10 s; and time to strike again. At 5 min, the observer presented a bare hand, palm open, moving the hand from 50–5 cm towards a snake's nose. We recorded whether the snake remained motionless, withdrew its head, or raised its head to threaten or strike.

Following the excavation of hibernacula each day, we brought all snakes to the laboratory where we recorded the following: sex, snout–vent length (SVL in mm), total length in mm, and mass in g. Any snake without a PIT tag was given one at this time. Snakes were maintained overnight at 4–10°C, and then returned to their original hibernaculum. Although a few specimens came out of the dens after release, most remained in the hibernacula for another 2–4 weeks before emerging normally in early April. Behavior was recorded for some of the same snakes in subsequent years; an individual's behavior was not consistent from year to year (correlation coefficient not significant, r = 0.06), in marked contrast to reports by Arnold and Bennet (1984). Similarly, there were no behavioral differences as a function of gender of the snake, and gender is not considered further in this paper.

We use Wilcoxon χ^2 test to compare the behaviors of the two species, and Kendall τ as a nonparametric measure of correlations. Probability levels < 0.05 were considered significant.

RESULTS

Hibernating Depth and Temperature

Once inside a main chamber of a hibernaculum, individual snakes dug side tunnels, and then coiled themselves into tight compartments in the firm, moist sand at a depth of 1 m or more below the surface. The average distance from a hibernaculum's entrance to a pine snake was 272 cm compared to 232 cm for black racers (Table 1), and this distance was weakly correlated with SVL for pine snakes ($r = 0.09$, $df = 195$, $P < 0.05$). Racers typically were encountered closer to the hibernaculum entrance. Pine snakes ranged in mass from 24 g hatchlings to full adults (mean = 545 g, range = 24–1414 g); no hatchling black racers were found. Pine snakes were found at an average depth of over 1 m, whereas black racers were only about 71 cm below the soil surface (Table 1). Cloacal temperature (mean = 7.5°C, range = 4–12°C) and soil temperature (mean = 7.1°C, range = 1–13°C) where a snake was found were positively correlated for pine snakes ($r = 0.44$, $df = 196$, $P < 0.001$) and for black racers ($r = 0.58$, $df = 41$, $P < 0.001$). Cloacal temperature was inversely related to SVL for pine snakes ($r = 0.21$, $df = 196$, $P < 0.0001$), but no significant relationship existed for black racers. While

TABLE 2. Correlations of pine snake (*Pituophis melanoleucus*) behavior with physical measurements (n = 198). No significant correlations were observed for racers. Numbers given are Kendall-τ correlation coefficients (probabilities) with P-values in parentheses. Nonsignificance (NS) was set at $P > 0.05$.

Behavior	Temperature			Weight	SVL
	Cloacal	Soil	Air		
Time to strike	NS	NS	NS	NS	NS
Time to hiss	–0.20 (0.04)	–0.32 (0.001)	NS	0.17 (0.07)	NS
Time to move	NS	0.15 (0.04)	0.24 (0.002)	NS	NS
Height of first strike	–0.27 (0.02)	NS	NS	NS	0.20 (0.07)
Length of first strike	NS	NS	NS	NS	NS
Distance moved in first 10 s	NS	–0.14 (0.01)	–0.16 (0.004)	0.12 (0.03)	0.16 (0.004)
Distance moved in second 10 s	–0.21 (0.003)	–0.23 (0.001)	–0.18 (0.01)	0.20 (0.004)	0.21 (0.003)
Time until second strike	NS	NS	0.33 (0.09)	NS	NS
Time to strike 5 min after removal	NS	NS	–0.46 (0.03)	0.40 (0.03)	0.40 (0.03)

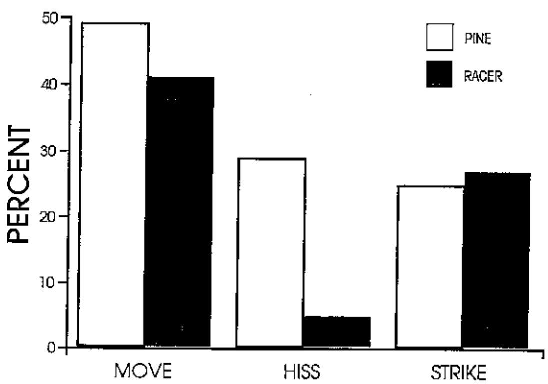

Figure 1. Behavior of pine snakes (n = 198) and black racers (n = 41) within 2 min of removal from a hibernaculum.

still partly in their tunnels, 38% of 198 pine snakes hissed and 39% gave off a small musk odor.

Snake Behavior After Removal

Somewhat less than 50% of the 198 pine snakes moved, and approximately 25% struck within the first 2 min of removal from their tunnel (Fig. 1). Once at the surface, pine snakes were more likely to hiss than were black racers (Fig. 1). There were few other significant differences in behavior between the two species (Table 2). Pine snakes had a lower interstrike interval than did black racers, and struck more quickly when exposed to a stimulus than did black racers.

In general, snakes performed defensive behaviors sooner at higher cloacal, soil and air temperatures (Table 3). Larger snakes took longer to move, hiss or strike than did smaller ones (Table 3). In part, this results from the fact that larger pine snakes had lower cloacal temperatures (see above).

Our data suggest that pine snakes either hiss and strike relatively soon, or they move away (Table 4). Similar correlations were not carried out for black racers because of the smaller sample sizes.

DISCUSSION

The best defense of a hibernating snake is to avoid detection in the first place (Endler 1986), particularly since the snake is relatively cold and immobile. Presence in an underground burrow reduces the probability of discovery. Firstly, a snake is often 2 m or more from the entrance, and the entrance is often too small for a mammalian predator to enter. Secondly, the hibernaculum must be discovered by a predator, and presumably this

TABLE 3. Correlations of defensive behaviors for pine snakes (*Pituophis melanolaucus*; n = 198). Kendall-τ and the sample size of snakes performing the behavior in parentheses are given above the diagonal, probability is given below the diagonal. Nonsignificance was set at $P > 0.05$.

Behavior	Time to Hiss	Time to Strike	Height of first Strike	Length of first Strike	Time to Move	Distance moved in 1st 10 s	Distance moved in 2nd 10 s
Time to hiss	–	0.70 (37)	NS	–0.43 (24)	NS	NS	NS
Time to strike	0.001	–	NS	NS	NS	NS	0.58
(10)							
Height of first strike	NS	NS	–	0.33 (33)	NS	NS	NS
Length of first strike	0.006	NS	0.01	–	NS	NS	NS
Time to move	NS	NS	NS	NS	–	–0.46 (92)	NS
Distance moved in 1st 10 s	NS	NS	NS	NS	0.0001	–	0.35 (96)
Distance moved in 2nd 10 s	NS	0.03	NS	NS	NS	0.0001	–

opportunity is strongest in the fall when many snakes have entered through one or two openings in the ground, leaving a strong odor or scent-trail. Such chemical cues would be strong again in the spring when some snakes have departed, leaving their odor on the entrance. Thirdly, with time, the tunnel is covered over with sand, leaves, and twigs which obscure the opening and possibly the scent-trail.

Except at the time of ingress or egress when snakes are moving to and from their hibernaculum chamber, pine snakes and black racers were usually a considerable distance (> 2 m) from the entrance. Furthermore, black racers were an average of 70 cm, pine snakes an average of 103 cm below the ground surface. Thus, a predator would have to dig deeply into the sand, while following the snakes' scent trails and wonld expend considerable energy in finding a sluggish snake. A potential predator has to deal with three-dimensional space, and not the usual two-dimensional space of some terrestrial predator-prey interactions (Webb 1986). The deeper a hibernaculum is excavated, the greater the chance of collapse, further burying the snakes and providing them with additional protection. Torpid snakes could be anywhere in the side chambers, and their odors may be distributed throughout the sand tunnels. We observed that hibernating snakes are usually distributed in groups of one to three in side chambers, rather than aggregated in a main chamber. Thus, if one or two individuals were discovered, the rest may not be. Following the small narrow tunnels to the hibernating snakes is difficult. We did so by placing thin marker rods in the tunnels, slowly excavating the sand around them. Even so, we sometimes lost the fragile tunnels due to collapsing sand. A coyote, fox, or skunk digging in the burrow system may similarly lose the tunnel.

Pine snakes and black racers are probably most vulnerable to predators when they first enter a hibernaculum in the fall due to their strong scent trail, and just before they depart in the spring when they are near the main chamber or the surface. Under these circumstances, a pine snake dug up by a predator can either remain still, move deeper into its tunnel, or try to escape over the opened hibernaculum sands toward the surface. Regardless of the sand temperature, most snakes moved deeper into the hibernaculum, although their movements were quite slow and may not be sufficient to deter a predator. However, if several snakes are excavated at the same time, an individual may escape predation if another individual is eaten first.

As with other aspects of behavior of reptiles, the escape and defensive behaviors of pine snakes were related to cloacal temperature and air temperature. Warmer snakes had lower latencies to respond. Larger snakes had lower body temperatures and responded more slowly than smaller ones. Low temperature hatchlings responded less quickly than hatchlings with high body temperatures, indicating that behavior was a function of temperature. All of our snakes, however, were tested at lower temperatures than those used by other researchers for such experiments. In laboratory studies, Hertz et al. (1982) showed that defensive responses of two agamid lizards changed as a function of body temperature. At lower body temperatures the lizards rarely ran but attacked aggressively. Schieffelin and Qneiroz (1991), however, reported the opposite pattern for garter snakes (*Thamnophis sirtalis*); the snakes were less aggressive at low temperatures. Goede and Duvall (1989) reported that pregnant prairie rattlesnakes (*Crotalus viridis*) exhibited a temperature dependent shift in defensive responses, although non-pregnant females and males did not.

A number of other factors affect anti-predator responses in snakes besides thermal differences, including body size, age, stimulus intensity, sex (Greene 1986, 1988), and whether a female is gravid or not (Bauwens and Thoen 1981). For garter snakes, both qualitative and quantitative aspects of anti-predator behavior occur as a function of increasing intensity of the threat (Bowers et al. 1993). In our observations, the stimulus intensity remained the same: all snakes were disturbed during hibernation in a uniform way, and were faced with a consistent human predatory stimulus. For the most part, both species responded similarly, although pine snakes often struck sooner than black racers and hissed more often than black racers. Both species responded slowly, both in terms of defense and moving away from the potential predator.

Only about a third of the snakes ever struck, and this was usually delayed for 5 min or more. Since striking was slow, and not very strong (low strike distances), it would be an ineffective defense. Moving immediately away from the disturbance would be more effective. Hissing also would be ineffective against the mammalian predators that dig up hibernacula.

Black racers may be taking advantage of the burrowing ability of pine snakes. Because black racers are last to enter the hibernacula (R.T. Zappalorti, unpubl. data), they are usually found closer to the entrance within the den, and are located in the well-excavated tunnels and chambers previously dug by pine snakes. They are not equipped to burrow as well as pine snakes (Carpenter 1982; Burger and Zappalorti 1986, 1991), and merely follow the pine snake tunnels into the hibernaculum. This appears to be a form of social parasitism not previously described for reptiles (see Burger and Gochfeld 1995 for avian references).

From the perspective of pine snakes, however, having racers closer to the entrance in the same hibernaculum may result in decreasing their predator threat. Predators normally would reach racers before they reached pine snakes, giving the pine snakes time to move deeper into the hibernacula.

ACKNOWLEDGMENTS

Over the last decade, many graduate students, friends, and colleagues have helped us with our annual "snake dig," and we thank them for their assistance and companionship: T. Benson, W.I. Boarman, W. Callaghan, J. Dowdell, S. Elbin, R. Farrell, R. Ford, S. Garber, J. Hill, B. Lauro, W. Mara, P. Mooney, B. Palustis, G.L. Rocco, C. Safina, J. Saliva, D. Shealer, C. Sutton, M. Torocco, and N. Tsipoura. The New Jersey Department of Environmental Protection, Division of Parks and Forestry allowed ns to conduct this research on state park land. The Division of Fish, Game, and Wildlife also allowed access onto Wildlife Management Areas and provided the necessary permits to conduct this long-term research project in New Jersey.

LITERATURE CITED

Andrews, R.M. 1994. Activity and thermal biology of the sand-swimming skink *Neoseps reynoldsi* diel and seasonal patterns. Copeia 1994:91–99.

Arnold, S.J. and A.F. Bennett. 1984. Behavioural variation in natural populations. III: antipredator displays in the garter snake, *Thamnophis radix*. Anim. Behav. 32:1108–1118.

Autumn, K. and D.F. DeNardo. 1995. Behavioral thermoregulation increases growth rate in a nocturnal lizard. J. Herpelol. 29 :157–162.

Bauwens, D. and C. Thoen. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. 50:733–743.

Bogert, C.M. 1949. Thermoregulation in reptiles, a factor in evolution. Evolution 3:195–211.

Bowers, B.B., A.E. Bledsoe, and G.M. Burghardt. 1993. Responses to escalating predatory threat in garter and ribbon snakes (*Thamnophis*). Comp. Psychol. 107:25–33.

Brown, W.S. and W.S. Parker. 1976. Movement ecology of *Coluber constrictor* near communal hibernacula. Copeia 1976:225–242.

Burger, J. and M. Gochfeld. 1995. Nest site selection by Eared Grebes in a Franklin's Gull colony: structural stability parasites. Condor 97:577–580.

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

Burger, J. and R.T. Zappalorti. 1991. Nesting behavior of pine snakes *(Pituophis melanoleucus)* in the New Jersey Pine Barrens. J. Herpetol. 25:152–160.

Burger, J., R.T. Zappalorti, M. Gochfeld, W.I. Boarman, M. Caffrey, V. Doig, S.D. Garber, B. Lauro, M. Mikovsky, C. Safina, and J. Saliva. 1988. Hibernacula and summer den sites of pine snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens. J. Herpetol. 22:425–433.

Burger, J., R.T. Zappalorti, J. Dowdell, T. Georgiadis, J. Hill, and M. Gochfeld. 1992. Subterranean predation on pine snakes (*Pituophis melanoleucus*). J. Herpetol. 26:259–263.

Carpenter, C.C. 1982. The bullsnake as an excavator. J. Herpetol. 16:394–401.

Elbin, S.B. and J. Burger. 1994. Implantable microchips for individual identification in wild and captive populations. Wildl. Soc. Bull. 22:677–683.

Endler, J.A. 1986. Defense against predators. In: M.E. Feder and G.V. Lauder (eds), *Predator-Prey Relationships: Perspectives from the Study of Lower Vertebrates*, pp. 109–133. Univ. of Chicago Press, Chicago, Illinois.

Goode, M.J. and D. Duvall. 1989. Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. 30:676–679.

Greene, H.W. 1986. Natural history and evolutionary biology. In: M.E. Feder and G.V. Lauder (eds), *Predator-Prey Relationships: Perspectives from the Study of Lower Vertebrates*, pp. 99–107. Univ. of Chicago Press, Chicago, Illinois.

Greene, H.W. 1988. Antipredator mechanisms in reptiles. In: C. Gans and R.B. Huey (eds.), *Biology of the Reptilia, Vol. 16*, pp. 1152–1263. Liss, New York.

Gregory, P.T. 1982. Reptilian hibernation. In: C. Gans and F.H. Pough (eds.), *Biology of the Reptilia, Vol. 13, Physiological Ecology*, pp. 53–154. Academic Press, New York.

Kauffeld, C.F. 1957. *Snakes and Snake Hunting*. Hanover House, Garden City, New York.

Hertz, P.E., R.B. Huey, and E. Nevo. 1982. Fight versus flight: body temperature influences defensive responses of lizards. Anim. Behav. 30:676–679.

Huey R.B. 1982. Temperature, physiology, and the ecology of reptiles. In: C. Gans and F.H. Pough (eds.), *Biology of the Reptilia, Vol. 12, Physiology*, pp. 25–92. Academic Press, New York.

Muth, A. 1980. Physiological ecology of desert iguana (*Dipsosaurus dorsalis*) eggs: temperature and water relations. Ecology 61:1335–1343.

Navas, C.A. 1996. Thermal dependency of field locomotor and vocal performance of high–elevation anurans in the tropical Andes. J. Herpetol. 30:478–487.

Parker, W.S. and W.S. Brown. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. Herpetologica 29:319–326.

Schieffelin, C.D. and A. de Queiroz. 1991. Temperature and defense in the common garter snake: warm snakes are more aggressive than cold snakes. Herpetologica 47:230–237.

Sexton, O.J. and S.R. Hunt. 1980. Temperature relationships and movements of snakes (*Elaphe obsoleta and Coluber constrictor*) in a cave hibernaculum. Herpetologica 36:20–26.

Vincent, T.K. and D.M. Secoy. 1978. The effects of annual variation in temperature on cold resistance in a Northern population of the red-sided garter snake, *Thamnophis sirtalis parietalis* (Reptilia, Serpentes, Colubridae). J. Herpetol. 12:291294.

Webb, P.W. 1986. Predator-prey relationships. In: M.E. Feder and G.V. Lauder (eds.), *Predator-Prey Relationships: Perspectives from the Study of Lower Vertebrates*, pp. 24–68. Univ. of Chicago Press, Chicago, Illinois.

Zappalorti, R.T. and H.K. Reinert. 1994. Artificial refugia as a habitat improvement strategy for snake conservation. In: J.B. Murphy, J.T. Collins, and K. Adler (eds.), *Captive Management and Conservation of Amphibians and Reptiles*, pp. 369–375. Contr. Herpetol., Vol. 11, Ithaca, New York.

Zimmerman, L.C., M.P. O'Connor, S.J. Bulova, J.R. Spotila, S.J. Kemp, and C.J. Salice. 1994. Thermal ecology of desert tortoises in the eastern Mojave Desert: seasonal patterns of operative and body temperatures, and micro habitat utilization. Herpetol. Monogr. 8:45–59.