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Hibernacula and Summer Den Sites of Pine Snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens

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ABSTRACT.—We examined eight summer dens (used only in summer) and seven hibernacula (occupied both in winter and summer) of the snake *Pituophis melanoleucus* in the New Jersey Pine Barrens, comparing above ground characteristics of hibernacula and summer dens with characteristics at nearby random points. Temperatures at the soil surface and at 10 cm depth were significantly warmer, and there was less leaf cover around the random points compared to the entrances of the hibernacula and summer dens. Hibernacula had significantly more vegetation cover within 5 m, more leaf cover over the burrow entrance, and were closer to trees than were summer dens. Most hibernacula and summer dens were beside old fallen logs (73%), the entrance tunnels following decaying roots into the soil. Excavation of the hibernacula and summer dens indicated that most hibernacula appeared to be dug by the snakes and had an average of eight side chambers and 642 cm of tunnels, compared to less than one side chamber and 122 cm of tunnels for summer dens. Except for hatchlings, most snakes in hibernacula were located in individual chambers off the main tunnel; all snakes were at depths of 50–111 cm ($\bar{X}$ = 79 cm). Pine snakes may select optimum hibernation sites which reduce winter mortality.

Snakes avoid the thermal stress of winter by hibernating in underground hibernacula. Snakes hibernate solitarily or aggregate in groups of up to several thousand individuals, and in monospecific or heterospecific groups (Parker and Brown, 1973; Gregory, 1977, 1984). Presumably snakes hibernate below the frost line, and the locations of snakes within hibernacula are related to thermal clines within the tunnels and chambers (Bailey, 1949; Sexton and Hunt, 1980). When hibernating, there is a depression in energy metabolism of heart tissue and in heart rate (Aleksiuk, 1976). However, snakes may shift locations within a hibernaculum during the winter (Sexton and Hunt, 1980), and may even come out and bask on warmer days (Jacob and Painter, 1980).

Snakes hibernate in a variety of habitats including rock piles (Parker and Brown, 1973), old wells filled with debris (Brown et al., 1974), old stumps and hummocks (Storm, 1955; Viitanen, 1967), caves (Drda, 1968; Sexton and Hunt, 1980), unused rodent burrows (Cohen, 1948; Viitanen, 1967), crevices in shale (Bothner, 1963), ant mounds (Criddle, 1937; Carpenter, 1953), prairie dog burrows, and limestone crevices (White and Lasiewski, 1971). Indeed, some species such as vipers (*Vipera berus*) occupy a variety of sites including most of the above mentioned sites during hibernation (Viitanen, 1967). Most species appear to depend upon finding suitable sites with natural crevices rather than making their own burrows (Woodbury, 1951; Viitanen, 1967).

General aspects of hibernation in snakes have been studied, including temperature relationships and tolerance (White and Lasiewski, 1971; Brown et al., 1974; Jacob and Painter, 1980; Sexton and Hunt, 1980), winter mortality (Hirth, 1966), species comparisons (Parker and Brown, 1973), and movement into and away from hibernacula (Brown and Parker, 1976). In general, most of the studies used one of three techniques: (1) snakes were monitored as they arrived or emerged from hibernacula, (2) hibernacula were excavated, or (3) experiments examined temperature relationships in the laboratory (Jacob and Painter, 1980) or in a constructed hibernaculum (Bailey, 1949; Gillingham and Carpenter, 1978). Nonetheless, there are few data on several aspects of hibernation ecology and behavior including selection of hibernacula, differences between winter hibernacula and summer dens, and snake positions in hibernacula. We have found no studies of summer dens.

In this paper we describe and compare characteristics of seven hibernacula (used summer and winter) and eight summer dens (used only in the summer) for pine snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens, and compare aboveground characteristics of hibernacula and summer dens with those at randomly-chosen sites within the same vicinity. We were particularly interested in attributes of sites used, how the snakes were distributed within hibernacula, and whether the snakes modified or dug their own hibernacula. Pine snake females dig long underground burrows and lay their eggs in these subterranean nests, suggesting the possibility of hibernaculum construction (Burger and Zappalorti, 1986, and unpublished data). If snakes do construct their own hibernacula, they may nonetheless prefer particular sites over others, and we examine this possibility in pine snakes.

METHODS

We studied pine snakes in Atlantic, Burlington, and Ocean counties in the New Jersey Pine Barrens. From 1981 to 1985 we marked all openings in the ground where pine snakes had been observed to emerge or enter. In early March 1986, well before ground temperatures had increased or any pine snakes had emerged (our earliest record for emergence in New Jersey is 8 April), we carefully excavated all such burrow openings. This exacting work required up to 10 people to trace the path of burrows and unearth their contents while protecting the snakes therein.

Before excavation we recorded the following data at each opening: distance between openings, slope of entrance, slope of tunnel, air temperature at 1 m, soil surface temperature, soil temperature at 10 cm, soil moisture (on a scale of 0–8), % ground vegetation cover within 1 m and 5 m, % cover over the entrance, leaf cover within 1 m of entrance, distance and height of nearest herb, distance and height of nearest tree, number of trees within 5 m and 10 m, distance and length of nearest fallen log (potential hiding and basking site), and length and width of soil pile by entrance. We recorded similar data from two randomly chosen points within 30 m of each entrance. Randomly chosen points were generated using a random number table to choose a compass direction and a distance. Data from those random points were used to determine if snakes selected particular sites for hibernacula or summer dens.

We defined those burrows with hibernating snakes as hibernacula (all of which also served as summer dens), and those without hibernating snakes as summer dens (since they had been used only in the summer). Following excavation each burrow was designated as a hibernaculum or summer den.

After recording site characteristics we carefully excavated the burrows by placing a meter stick in the tunnel and removing soil with a hand trowel or by hand to be sure that all side tunnels were located. The tunnels and chambers were hard-packed, making it possible to determine their extent. Whenever the tunnel changed direction we recorded the angle of the tunnel and its length, mapping the size (height and width) of tunnels and side chambers as we proceeded. Snakes were removed and their cloacal temperatures taken within 5 sec. with a Schultheis quick-reading mercury thermometer, while another person recorded soil temperature of the chamber (ca. 1.5 cm into soil), measured the depth of the snake's location, and measured the length, width and height of the chamber. The snake was sexed (by eversion of the

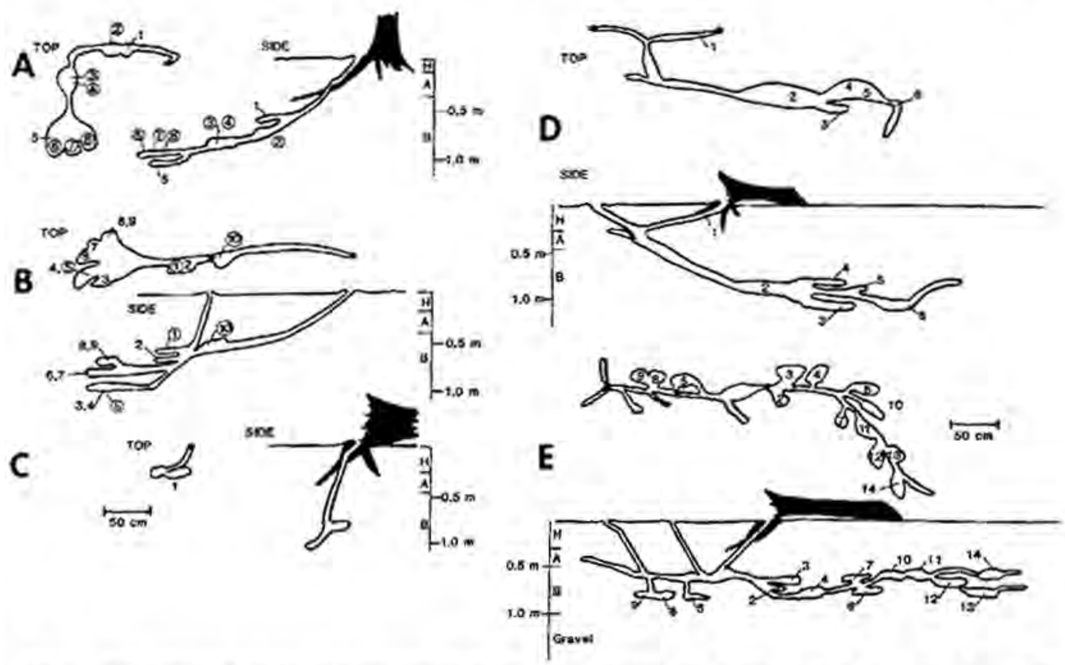

FIG. 1. Scale diagram of five hibernacula (A–E) showing top and side views. Shown are depth in meters, the location of the humus (H), and A and B soil horizons. Numbers indicate the locations of hatchlings (circled numbers) and adult (not circled) pine snakes.

hemipenes or by external morphology; Gregory, 1983), weighed, and measured (snout-vent and total length; Quinn and Jones, 1974). After excavation we recorded the depth of the humus layer, A and B horizon, and gravel layer.

Following excavation of the entire burrow system we re-constructed it using old logs, debris, soil, railroad ties, orangeburg pipe, and cement blocks to construct artificial tunnels, chambers and predator-proof entrances. We used procedures we had field-tested with artificial hibernacula over the preceeding four winters (Frier and Zappalorti, 1983). Snakes used and survived in these artificial hibernacula. All snakes were returned to their original hibernaculum. Unless otherwise noted we give means ± one standard deviation in the text.

RESULTS

Site Characteristics of Hibernacula and Summer Dens.—We excavated seven hibernacula and eight summer dens and found 42 pine snakes and three black racers (*Coluber constrictor*). All burrow systems were within 100 m of nesting areas used by females, and most were only 10–15 m from nest chambers. The burrow systems were located at six sites, separated by several km, and each site had at least one hibernaculum and summer den in the vicinity. Of the seven hibernacula, two were used for four years, three were used for at least three years, and two were used for two years. Of the eight summer dens, three were used for four years, two were used for three years, and three were used for two years. Once we found a burrow, we documented that it was used in the following years. Thus our estimates of usage are minima, and the same hibernacula and summer dens may be used for many years.

Eleven (73%) of the burrow systems were within 1 m of decaying logs (Fig. 1) with the tunnels going down into the decaying root system. The other four were on open sand. None of the random points fell within 1 m of logs. Over half of the hibernacula

TABLE 1. Comparison of characteristics of hibernacula and summer den openings of pine snakes with random points (means ± standard error).

	Hibernacula	Random points	Summer dens	Comparison of all three types χ^2 (P)[2]
Number of sites	7	24	8	
Number of entrances	13	—	11	
Aboveground characteristics:				
Temperature at soil surface	11.4 ± 2	19.9 ± 2	13.3 ± 2	10.73 (0.004)
Temperature of soil (10 cm)	7.6 ± 1	15.1 ± 1	10.1 ± 1.6	16.72 (0.0002)
% vegetation cover within 1 m	39 ± 7	38 ± 10	35 ± 10	NS
% vegetation cover within 5 m	45 ± 7	46 ± 10	27 ± 5	5.99 (0.05)
% cover over entrance	39 ± 7	29 ± 10	38 ± 10	5.64 (0.05)
% leaf cover around entrance	55 ± 8	13 ± 6	23 ± 7	15.47 (0.0004)
Distance to nearest vegetation (cm)[1]	27 ± 11	19 ± 7	43 ± 13	5.00 (0.08)
Height of nearest vegetation (cm)	87 ± 7	56 ± 14	45 ± 10	NS
Distance to nearest tree (cm)	130 ± 38	255 ± 48	276 ± 48	5.98 (0.06)
Height of nearest tree (cm)	333 ± 90	331 ± 64	262 ± 43	NS
Number of trees within 5 m	26 ± 10	15 ± 5	9 ± 2	NS
Number of trees within 10 m	138 ± 29	41 ± 12	24 ± 6	5.98 (0.05)
Distance to nearest log (cm)	620 ± 27	481 ± 11	541 ± 28	NS
Length of nearest log (cm)	426 ± 78	342 ± 91	537 ± 13	NS
Surface soiil moisture	1.5 ± 0.1	1.3 ± 0.03	1.3 ± 0.06	NS
Burrow characteristics:				
Width of opening (cm)	9 ± 2		12 ± 2	NS
Number of entrances	1.9 ± 0.2		1.2 ± 0.1	NS
Mean distance between entrances (cm)	150 ± 10		80 ± 0	—[3]
Slope of entrance	34 ± 3		37 ± 5	NS
Slope of burrow at entrance	39 ± 7		37 ± 5	NS
Mean number of side chambers	8 ± 2		0.3 ± 0.1	10.9 (0.001)
Mean length all tunnels (cm)	642 ± 100		122 ± 7	5.3 (0.02)
Depth of humus (cm)	21 ± 2		22 ± 2	NS
Depth of A horizon (cm)	43 ± 2		42 ± 2	NS
Depth of B horizon (cm)	82 ± 6		81 ± 6	NS

[1] Not trees or shrubs.
[2] Given are Kruskal-Wallis χ^2 values and (Probability): compares summer dens and hibernacula for burrow characteristics.
[3] Too few to compare.

had two entrances, but only 25% of the summer dens did. Nearly half of the burrow systems had visible piles of dirt at their entrance ($\bar{X}$ width = 43 ± 11 cm, $\bar{X}$ length = 67 ± 20 cm) similar to those at the entrance of nest burrows (Burger and Zappalorti, 1986). Only two of the hibernacula had large enough entrances to have been previously used by a fox (or other large mammal). These large burrows extended only 45 cm underground, and the narrow snake burrows extended at least another 58 cm below.

Analysis of variance (ANOVA) tests indicated significant differences among hibernacula, summer den openings, and random sites with respect to temperatures of the soil and soil surface, % vegetation cover within 5 m, % vegetation cover over the entrance, % leaf cover around the entrance, distance to nearest tree, and number of trees within 10 m (Table 1). In general, hibernacula and summer dens had more cover over the opening and more leaf cover around the opening than did the random points. Surface temperatures were lower at the hibernacula and summer den sites than at the random points. There were no differences with respect to vegetation cover within 1 m of the opening, height of nearest vegetation, height of nearest tree, number of trees within 5 m, or characteristics of nearest log.

Comparing hibernacula to summer dens we found differences in the distance to trees, tree cover, and % vegetation cover within 5 m. Summer dens had less cover within 5 m (Kruskal-Wallis $\chi^2 = 3.99$, $P <$

0.04), less leaf cover ($\chi^2 = 5.02$, $P < 0.02$), shorter nearest vegetation ($\chi^2 = 4.05$, $P < 0.04$), and greater distance to trees ($\chi^2 = 7.36$, $P < 0.006$) than hibernacula. All of these characteristics suggest summer dens are more in the open with less cover of all types than are hibernacula, and this difference is reflected in higher soil temperatures even in late winter.

Similarly, compared with random sites, hibernacula had lower surface temperatures ($\chi^2 = 8.63$, $P < 0.003$), soil temperature ($\chi^2 = 14.14$, $P < 0.0002$), higher surrounding leaf cover ($\chi^2 = 11.12$, $P < 0.0009$), higher % cover over the opening ($\chi^2 = 4.21$, $P < 0.05$), closer trees ($\chi^2 = 3.57$, $P < 0.05$), and more trees within 10 m ($\chi^2 = 3.89$, $P < 0.05$). These data confirm that hibernacula are in relatively more protected areas than random sites.

Burrow Characteristics of Hibernacula.—Diagrams, drawn to scale, for five of the seven hibernacula are shown in Fig. 1 (showing top and side views). The systems varied from simple, one-tunnel burrows leading to one or two chambers, to more complex burrows with several tunnels and up to 14 side chambers. Tunnels did not always go in a straight line but sometimes had 90° angles (Fig. 1A). Simple burrows usually went fairly straight to the chamber, and did not involve side tunnels or chambers. More complex burrows (Fig. 1) involved several entrances, several tunnels, and several chambers. These complex hibernacula had been used for at least four years.

Tunnels usually initially followed an old root into the ground (or in two cases a fox burrow). However, in all cases the hibernacula burrows narrowed and extended beyond and below the root or fox burrow. Tunnels were 5–7 cm high and 5–12 cm wide. They widened into chambers where snakes were located. These chambers were seldom higher than 10 cm. Tunnels of the same burrow system were often at different depths and the chambers were usually at still different depths (Fig. 1). Only careful excavation by hand indicated the complexities of the burrow system.

Mean characteristics of hibernacula are given in Table 1. Entrances were narrow,

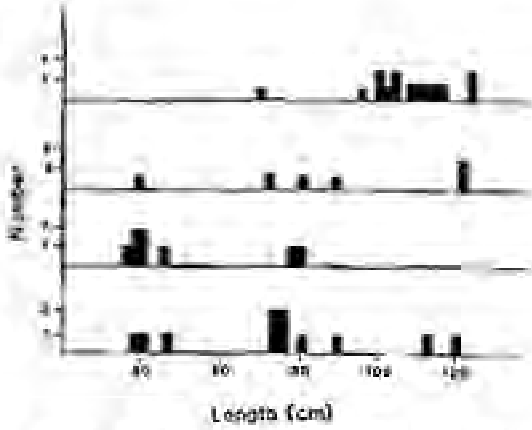

FIG. 2. Size distribution of snakes in pine snake hibernacula for five burrow systems.

with slopes about 30° leading into even narrower tunnels. The average hibernaculum system had 8 side chambers and a mean length of over 600 cm.

In all cases (except for one hatchling), snakes were located in the B soil horizon above the gravel layer, between 50–111 cm ($\bar{x} = 79 \pm 21$ cm) below the surface. Most snakes were coiled or partially coiled, and no snake was fully extended in the tunnels.

There were 15 hatchlings in the hibernacula and 27 older snakes. Most hatchlings were located in chambers with other snakes (usually other hatchlings). Yearling and older snakes, however, were usually located alone in a side chamber (almost 90%) or were located near a hatchling (refer to Figs. 1, 2). The mean length × width of side chambers was 214 ± 94 cm², and there was no relationship between snake SVL and chamber size (Kendall tau = 0.051).

Snakes in the seven hibernacula tended to segregate by size (Fig. 2). In hibernacula 1 and 3 (Fig. 1) there were snakes of different sizes, but in two hibernacula all the snakes were small, in four they were very large, and no hatchlings were found in the hibernacula with only one or two snakes. Of the 42 snakes located, 20 were males and 22 were females. There were no significant sexual differences in weight, total length, SVL or cloacal temperature. All snakes located were able to move immediately when removed from their cham-

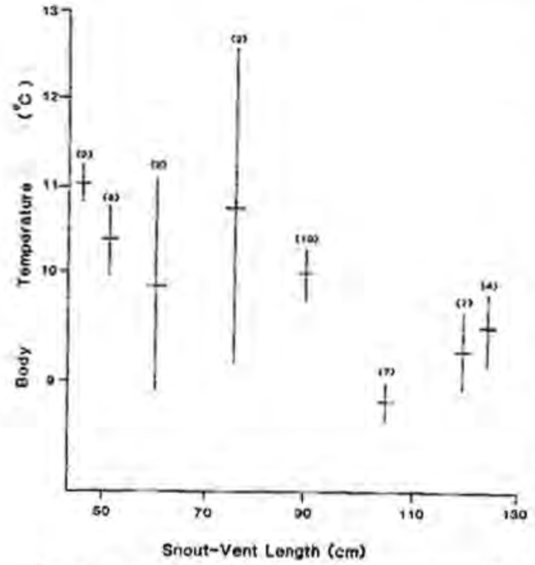

FIG. 3. Cloacal temperatures of pine snakes within 5 sec of removal from their hibernaculum as a function of snout-vent length.

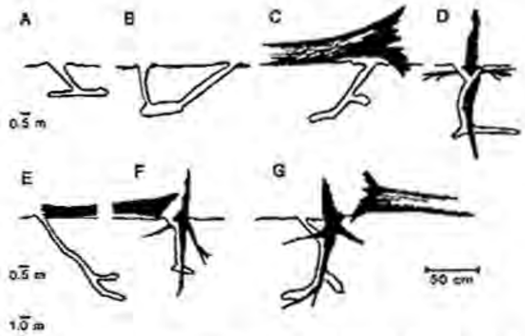

FIG. 4. Scale diagrams of side views of pine snake summer dens.

bers, half of the large snakes hissed, and six attempted to strike (although they were sluggish).

Mean temperature of the burrows where snakes were located ($\bar{x} = 8.8 \pm 1.1$, range 7–11°C) was less than cloacal temperatures of the snakes ($\bar{x} = 9.8 \pm 1.4$, range 8–14°C). Regression procedures indicated that SVL was the only variable that contributed significantly to explaining the variation in cloacal temperature ($F = 3.88$, $P < 0.05$; Fig. 3). Longer snakes had lower temperatures. As might be expected, soil temperature was inversely related to depth ($r = 0.46$, $P < 0.004$), but cloacal temperature was not related to depth or soil temperature where snakes were located.

Summer Dens.—Most summer dens (75%) were located near fallen, decaying logs, and the tunnels followed the roots directly down into the ground. Usually there was only one entrance, leading into a tunnel that sloped about 37°. Tunnels were short ($\bar{x} = 122$ cm), usually extending only into the lower part of the A horizon or the top of the B horizon (Table 1), and having only one or two chambers (Fig. 4).

Comparison of Hibernacula and Summer Dens.—Although hibernacula often had more entrances than summer dens, both burrow systems were usually located near decaying logs, had equivalent tunnel slopes, and were in similar soil profile areas (no significant difference in the location of A and B soil horizon, Table 1). In terms of internal characteristics only the temperature (see above) and complexity varied; hibernacula had significantly more chambers and longer tunnels than summer dens. There were no differences in soil moisture.

DISCUSSION

Hibernacula and Summer Den Location.—Pine snake hibernacula and summer dens were non-randomly distributed, usually near decaying logs, and had more cover over the opening, more leaf cover around the opening, and lower surface and soil temperatures than the random points. Further, hibernacula and summer dens differed significantly from each other, with hibernacula having lower March soil temperatures, more vegetation cover within 5 m, being closer to vegetation, and having more trees within 10 m than summer dens.

These data indicate that sites for hibernacula and dens have attributes not uniformly distributed in the Pine Barrens. The factors combine to show that hibernacula are in more protected sites (more herb cover, more vegetation, more and closer trees) than are either summer dens or random points. Presumably sites that are more protected by vegetation might be less vulnerable to daily temperature changes, and would be more conservative with respect to internal burrow temperatures in the spring. That is, sites exposed to the sun (low cover, few trees, distant trees) should warm up sooner and be more variable than those with more cover. Snakes in such dens might emerge too early in the spring before temperatures have warmed up sufficiently. In the early spring snakes often emerge on warm days to bask and return to the hibernaculum at night. We have also observed hatchlings basking at the entrance with only their heads in the sun.

Several studies have shown that spring emergence is temperature dependent (Vetas, 1951; Jacob and Painter, 1980), although Drda (1968) noted that a temperature increase did not signal the end of hibernation for four species of *Elaphe*, *Coluber* and *Agkistrodon*. Sexton and Hunt (1980) proposed that emergence is dependent on reversals in the thermal gradient between the surface and the subsurface. Nonetheless, it is clear that some form of temperature relationship signals emergence.

Hibernaculum and Summer Den Construction.—Previous studies have noted that snakes do not construct their burrow systems, but rely on naturally occurring formations (caves, rock piles, shale crevices or burrows of other animals; e.g., Woodbury, 1951; Viitanen, 1967). Clearly, snakes do not construct rock piles or caves. However, all the hibernacula and summer dens located in the Pine Barrens were in soft sand and not in naturally occurring formations, and we believe that the snakes dug most of these burrow systems.

The two possibilities for burrows, given their construction in the sand are: (1) that snakes modify abandoned burrows of other animals, or (2) that snakes dig their own burrow system. Several other animals in the Pine Barrens dig burrow systems, including red fox (*Vulpes fulva*), woodchuck (*Marmota monax*), striped skunk (*Mephitis mephitis*), red-backed vole (*Clethrionomys gapperi*), woodland (or pine) vole (*Pitymys pinetorum*) and chipmunk (*Tamias striatus*; Van Gelder, 1984).

Except for two hibernacula we believe it unlikely that snakes were using the abandoned burrow systems of large animals such as foxes or skunks, because the tunnel systems had sections that were only 5–8 cm wide near the burrow entrance, and were thus too narrow to admit these larger species. Further, if the tunnels were large enough for these species, the snakes would be vulnerable to predation by them. One artificial hibernaculum constructed with tunnel openings of 10 cm was opened in the spring, and found to be used by a skunk with no sign of the several pine snakes and corn snakes (*Elaphe guttata*) that had entered it the previous fall. Either the snakes left before or when the skunk arrived, or they were eaten.

Small mammals such as voles could have initially dug the snake burrows. At the very least the pine snakes modified them extensively since there were numerous side chambers the size of snakes. Chambers were the same height as the tunnels, and were wide and long, just accommodating the snakes that lay coiled within them. It is unlikely that the pine snakes would find a rodent burrow with so many side chambers. In all cases pine snake hibernacula and summer den tunnels extended beyond and below roots (or the fox dens in two cases). Thus, although they followed roots to initially start the tunnel system, they quickly abandoned the roots. At the depth where the snakes hibernated, the tunnels and side chambers were narrow and of the same size as the coiled snakes. The ability to dig extensive tunnels and chambers may be an effective antipredator strategy against large mammals.

For several reasons, we believe it more likely that the snakes constructed some of the burrows because: (1) pine snakes are known to dig similar long burrows for nesting (Zappalorti et al., 1983; Burger and Zappalorti, 1986); (2) the piles of sand at the entrances resembled those deposited by female pine snakes when constructing nesting burrows; (3) the tunnels in the burrows were uniformly narrow; (4) there was no evidence of stored food or nesting material typical of small rodents; (5) the tunnels had numerous side tunnels sufficient to hold the coiled pine snakes; and (6) the number of side chambers was usually equal to the number of snakes in the hibernaculum. Given that pine snakes are capable of digging such burrow systems, and that burrows are tailored to the number and size of pine snakes hibernating within them, it seems parsimonious to conclude that they do in fact dig them. The tunnel systems are remarkably like some nest burrow systems dug by iguanas (*Iguana iguana*; Rand and Dugan 1983, Fig. 2). No other snakes are known to dig hibernacula or summer dens, but also no other snakes dig subterranean nests with 2–3 m long tunnels (Burger and Zappalorti, 1986). That their hibernacula are successful is attested by the lack of any winter mortality in the hibernacula we excavated. Other studies have always reported winter mortality (see below).

Temperature Relationships.—Hibernacula were excavated at the end of the winter prior to emergence, and most non-hatching year snakes were in chambers by themselves, in contrast to some other snakes that hibernate in tightly coiled groups of several to hundreds (Brown et al., 1974; Aleksiuk, 1976). Thus it is unlikely that the pine snakes, except for the hatchlings, were deriving any thermal benefit from conspecifics. Brown et al. (1974) reported no difference in temperature of solitary versus individual snakes in groups of 2–6.

At wintering depths, minimum temperatures are not reached until early April (Viitanen, 1967). In the New Jersey Pine Barrens mean air temperatures vary from a low of 2.5°C in December to 1.4°C in February, and soil surface temperatures vary from 4.7°C in December to 1.0°C in February (Zappalorti and Reinert, 1986). Temperatures in hibernacula vary with the species and geographic location. Average body temperature of overwintering snakes range from 0–13°C (Jacob and Painter, 1980), but the seven studies surveyed reported temperatures for only 1–11 individual snakes (except for *Thamnophis*). *Thamnophis radix* can withstand temperatures as low as −2°C for as long as 28 days, but these snakes are known to hibernate near the surface (Bailey, 1949). Schroder (1950) noted that the overwinter temperature of 2 pine snakes was 6.7°C, close to that reported in this study. Thus the temperatures we found for pine snakes are within the typical range for hibernating snakes.

Winter Mortality.—In the present study we found no winter mortality; all snakes in the hibernacula were alive and well. This is in marked contrast to other studies that report mortality rates of 5–20% for *Coluber constrictor* (Brown and Parker, 1984), 11–35% for *Elaphe vulpina* (Gillingham and Carpenter, 1978), 15% for *Vipera berus* (Viitanen, 1967), and 34–50% for *Masticophis*, *Crotalus*, and *Coluber* (Hirth, 1966). Some of these studies may have overestimated mortality because some live snakes may have emerged undetected; however Gillingham and Carpenter (1978) followed snakes within the hibernaculum.

The low mortality found in this study may indicate that hibernaculum sites of pine snakes are optimal because the snakes can completely dig or modify existing burrows to appropriate depths to avoid thermal stress or drowning (Viitanen, 1967). Indeed, no burrow contained water despite frequent rains in the days before we dug them up. The ability to dig extensive burrows would free pine snakes from excessive inter- and intraspecific competition for hibernation space, and allow for optimum site selection to avoid winter mortality.

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