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Long-Term Use of Hibernacula by Northern Pine Snakes (*Pituophis melanoleucus*)

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Abstract.—Understanding the specific habitat requirements of reptiles during different life stages or seasons are critical to conserving viable populations. Northern Pine Snakes (*Pituophis melanoleucus*) are one of the few species that spend the winter in underground hibernacula, which they excavate themselves. We report on 26 years (1986–2011) of monitoring Pine Snake use at seven hibernacula in the New Jersey Pine Barrens. Our goal was to determine the frequency of repeated use, number of snakes present by year, disruptions of hibernacula, and the relationship between number of snakes present and the probability of occupancy of each hibernaculum in successive years. The overall goal was to determine the importance of protecting known hibernation sites regardless of whether they appear occupied in a given season. These data suggest that, if no snakes are observed entering a particular hibernaculum over a limited time period, it does not mean none are there or that none will use it in successive years. The variability in use suggests not only that predation and human disturbance can result in nonoccupancy the following year but that environmental and temperature-related conditions force snakes to have alternative hibernacula to reduce risk and ensure survival. Pine Snakes are listed as threatened by the New Jersey Department of Environmental Protection for many reasons, including habitat loss. There is continued pressure from developers to destroy habitat during development, including critical hibernation sites. The long-term use of specific hibernacula, even with periods of low or no use, suggests that these resources should be protected to provide a matrix of available overwintering sites.

For ectotherms such as snakes, hibernation is crucial to survival in temperate zone winters because they are unable to generate metabolic heat (Gregory, 1982; Brown, 1993; Brown and Weatherhead, 2000). To protect themselves from freezing, snakes living in colder climates must spend more time in hibernacula. There may be fewer suitable hibernacula locations (Harvey and Weatherhead, 2006); therefore, these hibernation sites are used repeatedly and by groups of snakes (Fitch, 1960; Johnson, 1995; Shine and Mason, 2004; Gerald et al., 2006). Thus, the importance of hibernation sites to snakes at the northern limit of their range is an important question for conservation and management of these species.

Between 1986 and 2011, we studied the hibernation behavior and hibernaculum use by Pine Snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens, which is at the northern limit of their range both historically and currently. This research is important for conservation biologists and wildlife managers, not only because understanding the importance of hibernacula to rare snakes has implications for population density and survival but also because hibernation sites are threatened by habitat loss, fragmentation, and development interests.

New Jersey is the most densely populated state in the nation and has experienced habitat loss of roughly 0.27% per year for decades (Hasse and Lathrop, 2008); the rate of loss has been similar for Pine Snake habitat (0.29%/year, Golden et al., 2009). New Jersey Pine Snakes live in the Pine Barrens, which are partly protected within the Pinelands National Preserve. However, protection is incomplete. There are extensive housing and commercial developments within the preserve, and certain areas, including those occupied by Pine Snakes, are designated as limited development zones. The increasingly fragmented habitat is surrounded by suburban and urban areas. Only recently have conservation biologists begun to focus on habitat loss, connectivity, and biodiversity in urban and suburban landscapes (Rees, 1997; Fernandez-Juricic, 2000; Haxon, 2000; Burger et al., 2007).

Pine Snakes are listed as threatened in New Jersey. Although recently challenged by the New Jersey Builders Association, the threatened status was upheld. Even so, habitats and specific features of Pine Snake habitat (such as hibernacula) are continually threatened by developer's applications, poor or unproven mitigation, and political pressure to allow development.

We address five questions. (1) Are there differences in use of hibernation sites in open patches (nearly complete sun penetration) within pine forests compared to other habitats? (2) How many snakes use individual hibernacula over a long period of time? (3) How often are specific hibernacula used? (4) What is the probability that a given hibernaculum used one year will be used the next year or in successive years? (5) Is there a relationship between the number of snakes in a hibernaculum and its use in successive years?

These questions are important to understand the conservation needs of Pine Snake populations, for developing paradigms to apply to other snakes living in temperate climates, and for providing evidence of the importance of protecting known hibernacula from development. This paper provides data for one species but suggests questions to examine with other species using communal, traditional dens and addresses the critical need for long-term data on snake behavior and ecology (Brown, 2008).

Materials and Methods

Study Species.—Northern Pine Snakes are cryptic, long-lived vertebrate predators that are at the top of the food chain in the New Jersey Pine Barrens (Golden et al., 2009; Burger and Zappalorti, 2011). They forage in a range of habitats in the Pine Barrens, including open sandy areas, Pitch Pine (*Pinus rigida*) uplands, Pitch Pine–Oak uplands and lowlands, and on the edges of Atlantic White Cedar (*Thuja occidentalis*) swamps

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(Burger and Zappalorti, 1988a, 1989). When not foraging, seeking mates, or nesting, they often seek shelter under debris, logs or low-hanging branches, or in shallow summer dens (Burger et al., 1988). In October, snakes begin to seek hibernation sites and often remain near them until they finally enter in late October to early November, depending on temperatures. Hibernation sites can also be used during the summer, and dens previously used only in the summer can be excavated deeper to become hibernacula (Burger et al., 1988).

Overall Protocol.—Our overall protocol was to identify possible hibernacula, select some for study, and follow the use of these hibernacula by annually excavating, finding the snakes, reconstructing the hibernacula the same day, and releasing the snakes back into the tunnels. Pine snakes dig their own hibernacula (or modify abandoned burrows or tree root channels), and tunnels normally extend less than 5 m from the hibernacula entrance. We defined a hibernaculum as a set of tunnels with one or more entrances, used by Pine Snakes over the winter but that do not connect with any other hibernaculum. Pine snakes resided in the tunnels, or in side chambers, and more than one snake can be in a side chamber (Burger et al. 1988).

All snakes were branded (1986–91) and pit tagged (1989 to the present), weighed, and measured. We studied Pine Snakes in Atlantic, Burlington, and Ocean Counties in the New Jersey Pine Barrens. Exact locations are not given because of the potential for illegal collection of snakes. Poaching of eggs and associated females can be as high as 40%/year (but averaged 28%, Burger et al., 1992), and in two instances hibernacula were dug up by poachers. Hibernacula are often adjacent to or within nesting habitats. Over the 26 years of the study, we handled and marked over 500 Pine Snakes in the seven main hibernacula studied.

Identification of Hibernacula.—From 1981 to 1985 we searched areas known to contain Pine Snake populations in October and November looking for basking snakes and observing all openings in the ground where Pine Snakes were observed to enter or leave. Methods for the initial excavation of hibernacula are described in Burger et al. (1988). Once a hibernaculum was excavated, we reconstructed it by building a chamber 1–1.5 m below ground with cement block sides and a wood or metal roof, with a cement block tunnel leading to the surface. Cement blocks with three holes were used because the openings are small enough to prevent entry by skunk or fox (when fox or skunk dug up hibernacula, they entered by digging their own hole down to the chamber).

In 1986, we examined hibernacula characteristics (Burger et al., 1988), identified the hibernacula for long-term study, and selected two types of hibernacula for study: (1) those located relatively in the open (open-canopy) that were created by farming and hunting in the early to mid-1900s, and (2) those in less optimal conditions (in woods, in debris piles, in old foundations, or in habitat currently managed for deer). We believed the latter category was suboptimal because foundations and debris piles did not provide sand for digging but, instead, allowed air movement down to the chambers, and closed canopies provided less sun penetration to the ground.

One hibernaculum initially considered in the open-canopy category was placed in the second category because it was destroyed inadvertently by managers. All hibernacula in the second category were separated by more than 10 km. In the first category, one hibernaculum was separated from another by 35 km; the second hibernaculum was separated from the third group by 3.5 km, and within the third hibernacula area, there were 5 hibernacula (separated by 39 m, 21.8 m, 8.5 m, and 64 m). Other hibernacula were added to the study when discovered (i.e., the first year there was obvious use by snakes).

Category 1 hibernacula were located on protected land or privately owned land with owner protection of snakes, whereas category 2 hibernacula were located in right-of-ways accessible to the public or private lands with either benign or antisnake owners, in addition to the one located on a wildlife management area where the hibernaculum was plowed up for deer management. Category 1 hibernacula were monitored for 26 years. Category 2 hibernacula were monitored for 10 years, and each hibernaculum was excavated only for two years following abandonment (hibernacula were usually destroyed by removal of debris, harassment by property owners, predators or disking, or the location had been used only by one or two snakes. Predators that dig up hibernacula (or use the burrow system) are Red Fox (*Vulpes fulva*) and Skunk (*Mephitis mephitis*).

Protocol for Assessing Hibernacula Occupancy.—All hibernacula in category 1 (open-canopy) were excavated each year regardless of prior occupancy. Hibernacula in category 2 (all others) were excavated for only two years after no snakes were found in them. All hibernacula were excavated between February 28 and April 13. The following criteria were used in determining the dates for excavation: lack of snow cover, ground that was not frozen, ambient temperature (above 10°C), temperatures the last two-three weeks, and absence of rain or snow.

Excavation involved digging directly down about 0.6 m with shovels and then carefully digging the rest of the way to the wooden or metal roof of the chamber. The chamber lid was lifted off, and any snakes located in the chamber were removed; in very warm years, some snakes were located in the chamber or entrance tunnel. We then removed the blocks and carefully scraped around the edges to find the small tunnels that led to side chambers dug by the snakes. Snakes were typically found in these side chambers. Because snakes prefer to dig in the red sand of the B horizon, we often created cinder block tunnels that directed snakes to the undisturbed sand. Tunnels were relatively easy to follow, and all tunnels were excavated by hand with small trowels by experienced biologists.

Once a snake was located, it was removed, weighed, and measured. All snakes were injected with a passive integrated transponder (PIT tag, Elbin and Burger, 1994), or their previous PIT number was recorded. Following complete excavation, the hibernaculum was rebuilt, and snakes were returned the same day into the entrance of the hibernaculum. Some snakes selected and re-used the same hibernaculum for up to 15 years, indicating that these research procedures did not unduly disturb some of the snakes (Burger and Zappalorti, in press).

Although we found dead hatchlings on several occasions (usually from dehydration, freezing, or being squashed by larger snakes) and two dead adults (frozen from being too close to the surface), these snakes were in good condition and appeared to have died recently. Thus, no partly decayed snakes or skeletons were found from previous years.

Hibernation Years.—We calculated hibernation years as a method to examine hibernaculum use over time. Hibernation years = the number of hibernacula × the number of study years. Ideally, this would be 7 × 26 (= 182) for the main hibernacula studied for 26 years. However, it was only 174 because of delayed starts at three hibernacula: (1) one was discovered in 1987 in the same areas as others and was added to our study; (2) one was not excavated the first two years before we added it; and (3) another was created in 1991 by snakes from a summer den (which had originally been a nest site). The creation of this hibernaculm followed the excavation of two nearby hibernacula by skunks in the same or the previous year.

Results

Hibernacula in debris piles, foundations, and in managed deer fields were not used consistently by snakes (occupied 26% vs. 58% of hibernacula years), had fewer snakes (5.1 ± 1.1 vs. 11.3 ± 1.1), and were subject to more predation (20% vs. 8%) than were those in open habitats. During the first 10 years of the study, hibernacula in open fields were more stable, had more snakes, and fewer were excavated by predators.

After the first 10 years, we studied the hibernacula in open fields (or at the edge of forests) for an additional 16 years, digging them up regardless of whether or not they had snakes in them for two consecutive years. All data presented in the rest of this paper are based on the 26-year dataset because the other hibernacula (type 2) were not followed thereafter. The number of snakes in these seven hibernacula ranged from one to 32 (mean = 11.3, SE = 1.1 when occupied, Fig.. 1).

In every case, there were years when hibernacula were not used by snakes, and these periods were sometimes as long as 10 years (Table 1). Often, periods of apparent abandonment followed the entrance of a predator such as a fox, skunk, or shrew into the hibernaculum. However, in some cases, snakes remained in unexcavated tunnels 30–70 cm away from the chamber, alive, even when the hibernaculum was invaded by a predator. There was no apparent connection between the hibernaculum entrance tunnel and the cavity dug by the predators. It is possible that the predator took one or more snakes and then abandoned the hibernaculum. Predation often led to lack of occupancy the following year (N = 5 of 9 predation events); some snakes survived predation events by remaining deeper in the hibernaculum. Human poachers dug up one hibernacula and did not put it back together (we later did so). This hibernaculum was not used by snakes for four years.

One of our objectives was to determine the probability of a hibernaculum being used in successive years if there were only a few or no snakes observed using the den. We treated each "hibernaculum and year studied" as a variable (although they are clearly not independent) and asked the question, if a hibernaculum was observed only during one year, what was the probability that the hibernaculum would be used the next year or in successive years as a function of the number of snakes found in them? A hibernaculum that was not used in one year had a 37% probability of being used in the following year, and a hibernaculum that was not used for two years had a 16% probability of being used the following year (Table 2). There was variation in the number of years a hibernaculum was not used, and the periods were often longer if it had been invaded by predators. Hibernacula with six or more snakes were almost always used the following year, and all were used two years later.

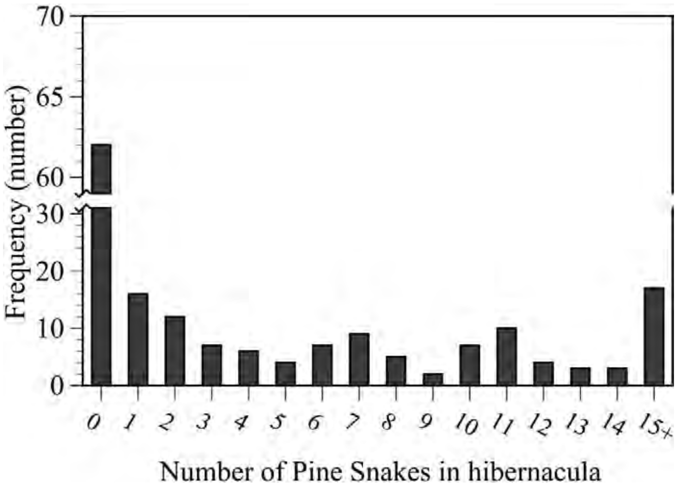

Fig. 1 Number of Pine Snakes in seven dens over a 26-year period in the Pine Barrens of New Jersey (total occupancies = 174).

Discussion

Methodological Issues.—Any long-term study has a number of difficulties that relate to inclement weather, seasonal differences among years (which affect phenology of organisms), and personnel changes. The date of our annual snake hibernation work ranged from 28 February to 13 April, depending on temperature (must be over 10°C), soil condition (ground not frozen), no snow cover, and suitable weather conditions (no snow, rain, or excessive wind). Although we had some personnel changes, the senior author was always present for the excavation of every hibernaculum, and the other authors were present for many years of excavations. We never injured a snake while digging, and in the next year, we never found any bones of dead snakes (indicating none were left or entombed and unable to leave). Our major concern was that snakes would abandon the use of a given hibernaculum because of our disturbance. However, this did not seem to be the case, because many snakes located as hatchlings used the same hibernaculum every year for several years. Some snakes were found in hibernacula in 15, 16, 17, and 18 different years (Burger and Zappalorti, 2011).

Philopatry and Communal Hibernacula.—The data provided in this paper demonstrate clearly that northern Pine Snakes in the Pine Barrens exhibit continued use of hibernacula and that many of these sites are communal. This is in contrast to the northern Pine Snakes living in Tennessee, where they hibernated singly (Gerald et al., 2006). Closely related species (*Pituophis ruthveni*) and sub-species (*Pituophis melanoleucus lodingi*) also hibernated singly at shallow depths (Rudolph et al., 2007; Baxley and Qualls, 2009). Thus, northern Pine Snakes in New Jersey may be the only members of the species that hibernate communally. Hibernating at deeper sites relates to their living in colder climates at the northern limit of the range as opposed to Pine Snakes from Tennessee, Mississippi, and Texas; and hibernating communally may be related to a limited number of available sites. Furthermore the selection of communal hibernation sites by Pine Snakes may indicate that stump holes are too small to accommodate several adult snakes. Large suitable hibernation sites, which provide sufficient protection from cold temperatures, may not be widely available.

Whether snakes hibernate singly or in groups may vary both within and among species. In this study, Pine Snakes hibernated alone and in groups, but a hibernaculum with only one snake in one year might be used by many (up to 14) the following year or by none. Other snakes can hibernate singly (Massassauga Rattlesnake, *Sistrurus catenatus catenatus*, Harvey and Weatherhead, 2006), in small groups (Black Rat Snake *Elaphe obsoleta obsoleta*, Prior and Weatherhead, 1996), or in large groups (Timber Rattlesnake, *Crotalus horridus*, Anderson, 2010).

TABLE 1. Total Pine Snakes in hibernacula (live and dead snakes are combined). The following symbols indicate: – the hibernaculum was not dug up that year, (S) disruption by skunks, (F) disruption by fox, (P) dug up by poachers.

		Ed's Place						
Year	Buck Run Sportsman Club	Site 1 (Big Tree)	Site 2 (right side)	Site 3 (lower)	Site 4 (center)	Site 5 (left of 4)	Davenport	Total snakes
1986	13	10	8	–	6	–	–	37
1987	1[a]	13	13	3 (S)	1	–	–	31
1988	12	16	6	0	0	–	0[a]	34
1989	10	15	17	0	0	–	21	63
1990	23	21	6	2 (S)	9		32	93
1991	14	7 (S)	10	0	5	11	30	77
1992	12	2	0	0	0	7	11	32
1993	12	0	3	0	0	0	19	34
1994	11	1	0 (P)	0	0	11	17 (F)	40
1995	11	0	0	0	0	6	10 (F)	27
1996	7	10	0	1	0	9	6	33
1997	7	11	0	0	0	2	11	31
1998	0 (S)	13	0	1	0	1	16	31
1999	2	16	1	0	0	0	15	34
2000	3	11	0	0	1	0	19	34
2001	4	6	2	0	3	0	17	32
2002	0 (S)	10	0	0	4	0	11	25
2003	0 (S)	5	1	1	0	0	4	11
2004	0	14	4	0	5	0	8	31
2005	2	25	11	2	0	0	2	42
2006	1	27	8	1	1	0	6	44
2007	0	7	3	0	4	0	7	21
2008	2	7	0	1	0	0	5	15
2009	1	7	0	0	0	3	2	13
2010	14	10	12	0	3	0	2	41
2011	2	8	4	0	8	7	1	30

Hibernating communally may expose snakes to predators and poachers, and such activities could provide a greater risk for small, local populations at the northern extent of their range (Prior and Weatherhead, 1996). However, communal dens that are used for many years may indicate safety from predators, as well as suitable overwintering conditions. In the present study, although skunk and fox dug into hibernacula (Burger et al., 1992), it is not clear how many snakes were actually eaten, because some snakes were found subsequent to the predation event further in the hibernaculum in side tunnels and chambers.

Open-Canopy Hibernation Sites Compared to Others.—In this study, we examined 16 hibernation sites initially, some in open-canopy habitats and others in closed-canopy or human-created habitats (debris piles, foundations, currently managed deer habitat). After 10–11 years, the hibernacula in the last category were abandoned or destroyed by predators and were unoccupied for at least two years. At that point, we discontinued studying them. This may have been a mistake and indicates the importance in conservation biology of having long-term datasets. We continued to monitor all the hibernacula in the former category, even if they had been abandoned for two years. Our 26-year dataset on seven hibernacula indicated clearly that all hibernacula were eventually used, even after an absence of use for 10 years. Based on this dataset, we suggest that there is a need for a long-term study of hibernacula in closed-canopy habitats to determine whether such sites generally have fewer snakes and

TABLE 2. Probability of finding snakes in hibernacula as a function of occupancy. Given is the percent of hibernacula used in successive years as a function of the number of live snakes found in the hibernaculum (i.e., numbers of times a hibernaculum with a given number of snakes was occupied in the following years and the percents of total occupancies of hibernacula with each number of snakes).

	Number of snakes in hibernaculum						
Successive years unoccupied	0	1	2	3	4	5	6 and over
0 (next year)	22 (37%)	5 (36%)	8 (73%)	3 (43%)	2 (40%)	2 (50%)	61 (95%)
1 (one year without snakes)	9 (16%)	6 (43%)	2 (18%)	1 (14%)	1 (20%)	1 (25%)	3 (5%)
2	5 (9%)	1 (7%)		2 (29%)	1 (20%)		
3	10 (18%)				1 (20%)		
4	4 (7%)	1 (7%)	1 (9%)				
5	2 (3%)			1 (14%)			
6	2 (3%)						
7	2 (3%)						
8	1 (2%)					1 (25%)	
9	1 (2%)						
10		1 (7%)					
Total	58	14	11	7	5	4	64
Percent of hibernacula/years	36%	9%	9%	4%	3%	2%	39%

[a]For example; of the hibernacula that were not occupied, they were reoccupied the next year 22/58 times, and reoccupied nine years later only once.
[b]The greatest number of snakes in one hibernaculum was 32.

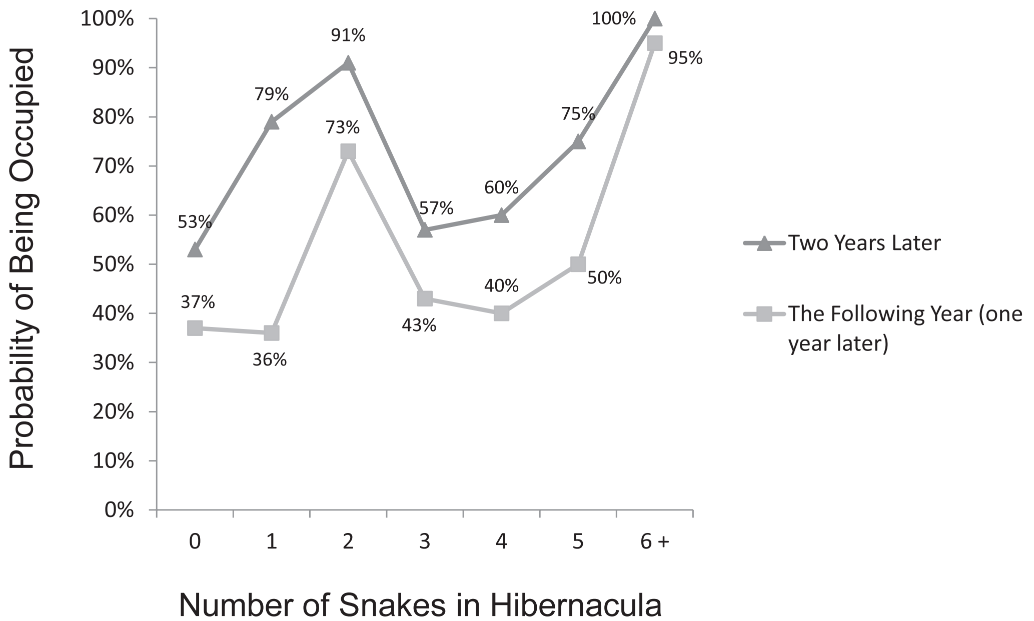

FIG. 2. Probability of a hibernation site being used by Pine Snakes in successive years as a function the number of snakes in the hibernacula. Shown is the probability for the following year and the cumulative probability for the next year.

are used less consistently. It may be that such sites are less optimal because they do not receive complete sun penetration. Another possibility is that open patches with complete sun penetration are optimal sites for females to dig nests and lay eggs (Burger and Zappalorti, 1986, 1992); therefore, hibernation sites in nesting areas are used as both summer den retreats and winter hibernacula. The strong chemical scent trails provided by adult snakes allow hatchlings to locate winter hibernacula (Reinert and Zappalorti, 1988; Burger, 1989). The open-canopy hibernacula were occupied more frequently by snakes, had a higher mean number of snakes using them (in winters they were used), fewer instances of predation, and were destroyed fewer times by people than were the other hibernacula.

Finally, hibernacula located in open canopy sites may simply be more suitable because there is full, or nearly full, sun penetration to the sand. If snakes at the northern limit of their range are indeed stressed during the winter, then small differences in habitat selection for hibernacula might provide the difference between survival and mortality. Over the 26 years, we have found seven frozen Pine Snakes (two adults, five hatchlings) that did not move deep enough in the hibernacula, indicating that this can happen; the frozen snakes were 40–60 cm from the surface.

Predictability of Continued Use.—Many snakes return to the same hibernation sites year after year (Woodbury et al., 1951; Fitch, 1960; Brown, 1992; Johnson, 1995; Prior and Weatherhead, 1996; Shine and Mason, 2004). Fidelity to the same site may indicate suitable and safe (from frost and predators) hibernation sites. Ideally, a strategy of using traditional hibernation sites, combined with the ability to move when necessary, could be optimal for species living at the northern edges of their range where they are more at risk.

One important aspect of a 26-year study of hibernacula is the ability to examine the probability of continued use as a function of occupancy, the number of snakes present, and the occurrence of predation or poaching. The long interval between occupancy of some hibernacula indicates that these sites are traditional, highly successful, and will continue to be used if they are not destroyed by people, as many of the ones in our 10-year study of other hibernacula were. Pine Snakes have evolved with fox and skunk, and after several years' absence (without the continued presence of predators), they return to use these sites again. Indeed, some of our marked snakes returned to these sites after several years' absence (unpubl. data). Pine Snakes are long lived and have the choice to return to the same hibernaculum or to choose a different hibernaculum, perhaps using a matrix of available ones, depending on environmental conditions.

One anomaly of the study is the variation in predictability of a hibernaculum being used in successive years. The probability of being used increased with the number of snakes (up to 2), and then declined, and finally increased again. Aside from hibernacula being close to nesting areas, we have no clear explanation of this pattern. It may well be a product of having a number of hibernation sites within a small area (e.g., the five dens at a field in Bass River State Forest) or the relative attractiveness of a hibernaculum, which had recent adult pheromone scent trails leading to it (Ford, 1978, 1986; Reinert and Zappalorti, 1988; Burger, 1989).

Conservation Implications.—The long-term den occupancy pattern by rare snakes illustrates that, once a natural hibernation site is located and documented, it should be protected regardless of the number of snakes found in it in any given year. Even a known hibernacula with no snakes in one year has a 37% probability of being occupied the next year and a 53% chance of being occupied two years later. Thus, the assumption that an abandoned hibernaculum will not be used, or that one with only one snake is unimportant, has a high risk of being wrong and, thus, could impact the snake population if these hibernacula are destroyed. These data have several implications for habitat protection, including the importance of observation and study for more than one year. The data suggest that unique habitat features or requirements, such as hibernacula, are used in a dynamic fashion and are part of a matrix of such features that provide the necessary protection for withstanding low winter temperatures in temperate climes and that some of these same features are used at other times as summer dens or nesting sites to avoid predators.

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