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Hibernation Site Philopatry in Northern Pine Snakes (*Pituophis melanoleucus*) in New Jersey

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ABSTRACT.—**Northern Pine Snakes (*Pituophis melanoleucus*) are one of the few snakes that spend the winter in underground hibernacula that they excavate. We report the use of hibernacula by Pine Snakes from 1986 to 2012 in the New Jersey Pine Barrens. We determined whether philopatry to a specific hibernaculum varied as a function of age, sex, and location of the hibernaculum. Three hibernacula were occupied nearly continuously for 27 yr by 1 to 27 snakes each year. With known-age snakes ($N = 120$), captured mainly as hatchlings and 2-yr-olds, we found that 23% were always philopatric. Philopatry was related to age of last capture, sex, and capture location. Philopatry was higher for 1) females compared with males, 2) snakes at two solitary hibernacula compared with a hibernaculum complex, and 3) snakes 6 yr old or younger, compared with older snakes. Of hatchlings found hibernating, 24% used the same hibernation site the next year, and 38% were located at year 4 or later. The number of snakes that always used the same hibernation site declined with the age of last capture. Snakes that entered hibernacula as hatchlings were found more often than those that entered as 2-yr-olds. For the seven snakes that were 14 yr or older, females were found 64–86 % of the time, whereas males were found 15 to 50% of the time. Understanding the behavior and habitat requirements of snakes during different seasons is central to life-history analysis and for conserving viable populations.**

Survival during cold winters presents different problems for ectotherms than for endotherms. Hibernation is crucial to survival for ectotherms in temperate-zone winters because they are unable to generate metabolic heat (Gregory, 1982; Brown, 1992; Brown and Weatherhead, 2000). In habitats where there are few suitable winter den locations (e.g., Harvey and Weatherhead, 2006), hibernacula are sometimes used repeatedly, often by groups of snakes (Burger et al., 1988; Johnson, 1995; Shine and Mason, 2004). The value of determining the location and use of snake hibernation sites at the northern limits of their range is important for conservation and management. Snake hibernacula in northern climates are located in rocky screes, limestone crevices, rocky talus slopes, and a variety of other places (Parker and Brown, 1973; Clark et al., 2008; Reed et al., 2012).

Seven underground hibernacula of Northern Pine Snakes (*Pituophis melanoleucus*) in New Jersey were occupied over a 26-yr period, some continuously (Burger et al., 2012). The probability of use from one year to the next was related to the number of snakes in the hibernaculum. If one was not used in one year, the probability that it would be used the following year was 37%, whereas the probability that an unused site would be used 2 yr later was 53%. Known hibernation sites should be protected because all hibernacula were used again during the study period, and if unused for one or more years, Pine Snakes eventually returned to use these dens (Burger et al., 2012).

Equally important as describing use of a given hibernaculum is determining how individual snakes use them, their fidelity to specific ones, and whether fidelity varies with sex and age of the snakes. Philopatry (fidelity to a given den site) is often associated with key habitat features that are patchily distributed and difficult to locate (Clark et al., 2008). In the New Jersey Pine Barrens, preferred hibernation sites are in abandoned mammal burrows or stump holes, and have partial or full canopy openings, with some sun penetration to the ground. These habitat features are limited (Burger et al., 1988, 2012).

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We studied the use of hibernation sites in Northern Pine Snakes between 1986 and 2012 in the New Jersey Pine Barrens, which is at the northern limit of their range (Burger and Zappalorti, 2011a). We were particularly interested in whether philopatry varied by sex, age, and location of hibernacula. Since males and females hibernate together, shifting sites may be a method of increasing gene flow the following breeding season, essential to maintaining population viability (Shetty and Shine, 2002; Allendorf and Luikart, 2006; Clark et al., 2008). This suggests that philopatry might be much higher in one sex or the other, or that it might be equal if both sexes move among hibernacula. If moving between hibernacula increases outbreeding, philopatry might be lower in adult snakes than in juveniles that are not yet breeding. Because male Northern Pine Snakes move greater distances than females (Gerald et al., 2006a), we predicted that philopatry might be lower in males than in females.

Here we address three questions: 1) What happens to hatchlings from monitored hibernacula? 2) Do Pine Snakes show philopatry, and does it vary by sex, age, and location of the hibernaculum? and 3) Do several hibernacula located in a very small geographical area act as one hibernaculum (hibernation complex) or several hibernacula with respect to philopatry? If they act as one, then philopatry for the snakes in the complex should be similar to philopatry in solitary hibernacula. If gene flow was an issue in these populations, due partly to isolation of suitable habitat patches, then one might predict that one sex would have significantly higher fidelity, and that fidelity would decrease when snakes reached sexual maturity. On the other hand, if suitable safe hibernation sites were very limited, then fidelity might be high. These questions are important for understanding the behavior and conservation needs of Pine Snake populations, for developing hypotheses to examine in other snakes living in temperate climates, and for providing evidence of the importance of protecting known hibernacula from succession and development. Indeed, development pressures in New Jersey have increased in recent years (see Discussion). As pointed out for other long-lived, hibernating snake species, only long-term data sets can address these questions (Brown, 2008).

Materials and Methods

Study Species.—Northern Pine Snakes are cryptic, long-lived vertebrates that are top predators (Golden et al., 2009; Burger and Zappalorti, 2011a). They live in open sandy areas, pitch pine (*Pinus rigida*) uplands, pitch pine–oak uplands, grassland fields, and on the edges of Atlantic white cedar (*Thuja occidentalis*) swamps (Burger and Zappalorti, 1988, 1989). The snakes often hide under debris, logs, or low-hanging branches, or take refuge in shallow summer burrows (Burger et al., 1988). They begin to move to hibernation sites in late September to October, and remain nearby until they finally enter dens in late October to early November. We define a hibernaculum as including a surface entrance (or series of openings), with a tunnel (or tunnels) leading to underground chambers where the snakes aggregate (Burger et al., 1988). A hibernaculum complex includes several hibernacula in proximity (Parker and Brown, 1973), and in our case, the hibernacula were separated by 8.5 m, 21.8 m, 39 m, and 64 m.

Study Protocol.—We studied Pine Snakes in Burlington, Cumberland, and Ocean counties in the Jersey Pine Barrens, but exact locations are not given because of the high pressure from poachers (Burger et al., 1992). Our overall method was to follow the use of hibernacula by annually excavating them, finding the snakes, reconstructing each hibernaculum the same day, and releasing the snakes back into their entrance tunnel. Hibernacula were excavated from 28 February to 30 March, depending upon temperature. In only one year did we excavate them later (6 April 1994). We used mark–recapture methods (Brown et al., 2007) over a 27-yr period (1986–2012).

All snakes were branded with a wood-burning tool (1986–1991) or tagged with passive integrated transponders (PIT) (1989 to the present), their mass was determined, and they were measured. Sex was determined by evertion of the hemipenes; snake age was defined as hatchling (end of first winter = 1-yr old); the following year it was defined as 2-yr old. We handled and marked over 500 individuals in our study. We present results from two data sets: 1) 152 hatchlings located during their first winter at three sites, and 2) 120 known-age snakes captured at least twice. Our handling of the snakes has not harmed them or influenced their natural behavior negatively (Burger and Zappalorti, 2011b).

Analysis and Measurement End Points.—In this paper we first examine the fate of 152 snakes found as hatchlings in hibernacula, and then we examine philopatry. We present a model for the fate of Pine Snakes from egg to age 4 yr and beyond, using literature values for clutch size and hatching rate, and our data for their fate thereafter.

We examined philopatry using two methods: 1) comparing philopatry with hibernacula in three sites (A, B, C), and 2) examining philopatry of a hibernaculum complex (site A), where five hibernacula were located within a 0.5-ha area, separated by 8.5 m, 21.8 m, 39 m, and 64 m. Since the hibernacula were all in proximity, we hypothesized that they may act as a hibernaculum complex. If this were the case, then we expected that the relative rate of philopatry would be the same for the three sites; if it were not the case, then each of the five hibernacula may be acting as single hibernaculum, and not as a complex.

For this analysis we used only known-age snakes, which consisted of snakes marked as hatchlings; 2-yr-old snakes (determined by snout–vent length [SVL], or marked at other times), and a few 3-yr-old individuals, PIT-tagged elsewhere as hatchlings, 2-yr-olds, or as determined by SVL. Although we marked and followed many other snakes of unknown ages, we did not use any of these in the analysis. Data were analyzed as a function of longevity as defined by last capture event for each snake.

We computed two measures of philopatry for the two hibernacula and hibernaculum complex: 1) number of times snakes were captured in the same hibernacula, and 2) mean philopatry, defined as the percentage of years snakes were found in the same hibernaculum. In the latter case, a 6-yr-old snake could have used the same hibernaculum anywhere from two to six times. If it used it six times, mean philopatry was 100%; if it used it three times, it was 50%. For hibernaculum complex A, we also examined the mean number of hibernacula within the hibernaculum complex that were used by each snake.

We used PROC general linear model (GLM) (SAS, 2005) procedures to examine the factors that contributed to explaining the variation in the dependent measures (number of times, mean philopatry, number of dens used in hibernaculum complex A). The procedure adds variables that contribute to explaining variation in the dependent variable, and computes the F-value, statistical significance, and the R^2. Variables entered in the models were age at last capture, sex (male or female), hatchling status (whether captured as a hatchling or the following year), and location (A, B, C). We also used chi-square tests for independence to examine differences in the number of dens used, percentage of snakes not found, and the age of last capture (for sex differences). $P < 0.05$ was considered significant.

Results

Fate of Hatchlings.—We illustrate the known information (clutch size, hatching rates) and fate of hatchlings and provide a schematic for the potential use of hibernation sites (Fig. 1). Female Pine Snakes have a mean clutch of 8.8 eggs (Burger et al., 1987), with 62 to 72% of nests hatching some young (Burger and Zappalorti, 2011b), and an overall hatching rate of 53% (Burger and Zappalorti, 2011b). The percentage of young that hatched in the three study sites is unknown, as is the percentage that reached one of the monitored hibernacula the fall of their first year. Burger and Zappalorti (1986, 1992) found up to 10 nests in the field where hibernaculum A was located, suggesting that up to 90 hatchlings per year might have entered some of the dens, but illegal poachers may have removed some gravid females and egg clutches.

From 1986 until 2012, 152 hatchlings were found in the three hibernacula, and, of these, only 37 (24%) were found the following year (year 2). In year 3, 24 of the 37 (16%) returned to the same hibernacula, and another 12 of the original hatchlings returned to the same hibernacula (they went to an unknown location in their second year, Fig. 1). Thus, in the third year, 36 of the original 152 (24%) hatchlings were back in their natal hibernaculum. In year 4 or later, 57 hatchlings (38%) were located. The sex ratio of hatchlings in hibernacula was 57 males and 95 females, and the sex ratio of surviving hatchlings at age 4 yr was 19 males (33%) and 38 females (40%). Thus, females returned more often to their natal hibernaculum than did males, there was differential survival, or both. These data were based on the total hatchlings found in all hibernacula. However, the data on philopatry in the rest of the paper are based on known-age snakes only, including hatchlings encountered two or more times, and 2-yr-olds easily identified by measurements, for a total of 120 snakes.

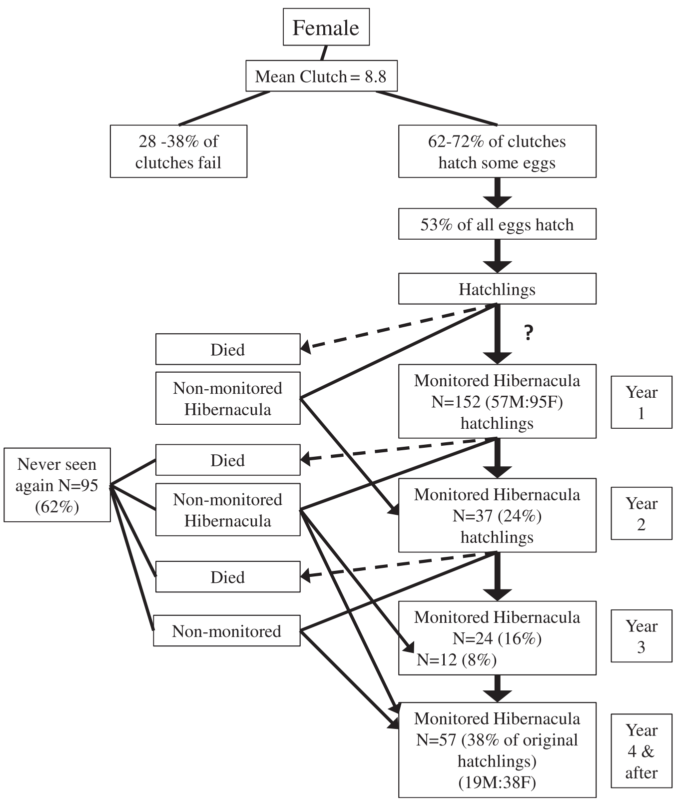

FIG. 1. Schematic of use of hibernacula by Pine Snakes in New Jersey. Shown is information known for the species, including clutch size (Burger et al., 1987) and hatching success (Burger and Zappalorti, 2011b), and new information on how hatchlings move among hibernacula, on the basis of 152 hatchlings found in the three hibernacula from 1985 to 2012. For ease of reading, snakes that die during each year are connected by a dashed line. The number that no longer return to a hibernaculum could either have moved to an unknown one, or died.

Philopatry as a Function of Age, Sex, and Location.—In this analysis we examined philopatry in all three major hibernacula, treating A as one hibernaculum complex. Models for the number of times snakes used the same hibernaculum, and the percent philopatry, were explained by age at last capture, hatchling status, and location (all $P < 0.0003$, Table 1). Sex, and an interaction between age at last capture and sex, also explained some of the variation in number of times snakes used the same hibernaculum (Table 1). That is, examining all factors under a GLM that affected the measures of philopatry, the data strongly suggest that age, site, sex, hatching status, and location play a major role.

TABLE 1. Models for the effect of independent variables on the number of times Pine Snakes used the home hibernaculum, and the percentage of philopatry. These models apply to the Pine Snakes in the three major hibernacula. NS = not significant in the PROC GLM model.

	Number of Times	% Philopatry
Model		
F	82.9	16.0
df	6	6
P	<0.0001	<0.0001
r^2	0.81	0.46
Factors entering $F(p)$		
Age at last capture	483 (<0.0001)	13.5 (0.0004)
Age at last capture × sex	36 (<0.0001)	1.3 (NS)
Sex	9.2 (0.003)	0.01 (NS)
Hatchling status	14 (0.0003)	42.3 (<0.0001)
Location	9.8 (0.0001)	7.5 (0.0009)

TABLE 2. Number of times Pine Snakes used the same hibernaculum as a function of longevity (age last encountered) (1985 to 2012). Number of times snakes that used the same hibernaculum is shown across the top. Sex for the older snakes is given as F = female and M = male. Note: Because this is an ongoing study, some snakes could live longer.

Age	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	Total
2	12																		12
3	16	9																	25
4	6	6	3																15
5	3	3	5	1															12
6	2	2	6	2	2														14
7	2	2	2	1															7
8		1	1	2	1														5
9		1	1			2													4
10		1		1	2	1													5
11						2		1											3
12				3															3
13																			0
14								F			F								2
15												M							1
16								M											1
17											M					F			2
18								M											1
19																			
20		M					M												2
21																			
22																			
23						M												F	2

Overall, only 27 snakes (23%) always returned to the same hibernaculum, and all of these were 6 yr old or younger (Table 2). The number of snakes that always used the same hibernaculum declined with the age of last recovery (Fig. 2, $\chi^2 = 714$, $P < 0.0001$). Snakes continued to use their natal site, although they also used other hibernacula. In this study, all snakes were located within their original hibernacula the last time they were found. The mean percentage of years snakes were found was lower at hibernaculum complex A than at the other locations (62% compared with over 75%; $P < 0.05$), was lower for snakes found as 2-yr-olds than for hatchlings (58% vs. 82%; $P < 0.01$), and was lower for males than for females (68% vs. 75%; $P < 0.01$).

Philopatry in a Hibernaculum Complex.—We examined the behavior of snakes using the five nearby hibernacula in the small area at site A. Since snakes had a choice, they could use any of the five, or others unknown to us. Only 45% of the variability in the number of dens snakes used was explained by age at last capture ($P > 0.0001$) and an interaction between age at last capture and sex ($P < 0,003$, Table 3). Variability (49%) in the percentage of philopatry was explained by hatchling status ($P < 0.0001$) and age at last capture ($P < 0.01$, Table 3). The number of dens used did not differ as a function of either sex or hatchling status. However, the percentage of years a snake was not found in any of the five hibernacula differed by sex; females were missed less often than males and thus had higher philopatry (Table 4). For both sexes, hatchlings were missed less often than those found as 2-yr-olds in our nonnatal hibernacula. That is, hatchlings showed greater philopatry to their natal dens than did older individuals that were not initially found as hatchlings.

For the seven snakes that were 14 yr or older, females were found 64–86% of the time, whereas males were found 15–50% of the time (Table 5). Thus, males moved away from the five dens more often than did females.

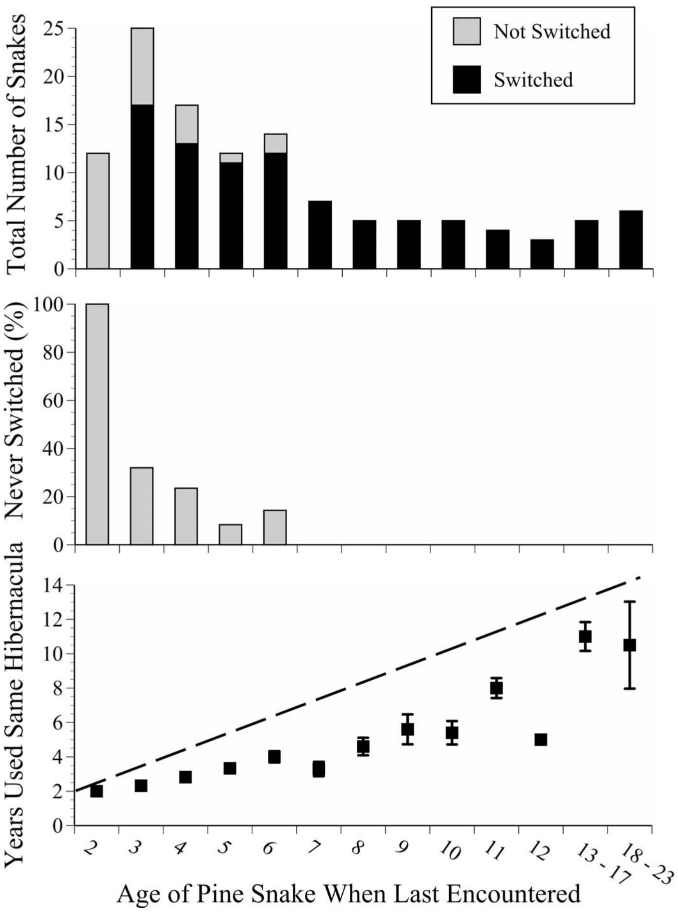

FIG. 2. Number of known-age Pine Snakes that switched hibernacula during the period until they were last encountered. Shown is the total number of snakes by the age when last encountered as a function of whether they switched or did not, the percentage of snakes that never switched sites, and the mean number of years that snakes used the same hibernacula as a function of age of last encounter. The dashed line indicates 100% philopatry at each age of last encounter. Snakes are represented only once (at the last age they were encountered). Snakes at any age could have lived longer, but not been captured, or could still be captured.

DISCUSSION

Methodological Issues.—Most large snakes are hard to see because they are cryptically colored, spend a good deal of time below ground or under debris, are differentially active during various seasons, have large home ranges, and secretly move about, making capture difficult (Webb and Shine, 1997; Gerald et al., 2006a; Burger and Zappalorti, 2011a). Although these factors apply to Northern Pine Snakes in New Jersey, they did not apply to our study because we conducted it during one time period (mainly in March) when snakes were still in their hibernacula, and we excavated the same dens for 27 yr (Burger and Zappalorti, 2011b). Since all had PIT tags (Elbin and Burger 1994), correct identification was not a problem. Although we captured over 500 snakes, in this study we used only hatchlings or 2-yr-olds easily identified on the basis of nonoverlapping SVL determined by a hatchling data set from the wild (3-yr-olds that were clearly identified were also used). Thus, the actual ages were known.

Fate of Hatchlings.—Determining the fate of hatchlings is complicated, even when using only snakes captured as hatchlings because the disappearance of a snake can be due to death,

TABLE 3. Models for the effect of independent variables on the number of dens used in the hibernaculum complex, and in the percentage of philopatry to specific dens within the hibernation complex. NS = not significant.

	Number of dens used	% philopatry
Model		
F	9.3	11.0
df	5	5
P	0.001	0.001
r^2	45	49
Factors entering $F(p)$		
Age at last capture	25.7 (0.001)	6.3 (0.03)
Age at last capture × sex	9.8 (0.003)	3.4 (NS)
Hatchling status	0.05 (NS)	16.7 (0.001)

collection by poachers, or movement to another hibernaculum. In our study, only 24% of hatchlings used the same hibernaculum the following year. In year 3, 24% were found in the natal hibernaculum, and a third of these had used a different one in the intervening year. At year 4, only 38% of the snakes were found again. This indicates that survival to age 4 yr in these hatchlings was at least 38%, and may have been higher because some snakes undoubtedly switched to other hibernacula

Philopatry.—Philopatry in snakes has been shown for home range or natal population areas (Shetty and Shine, 2002; Clark et al., 2008), basking sites (Webb and Shine, 1997), nesting sites (Burger and Zappalorti, 1992; Filippi et al., 2007), and hibernacula (Gerald et al., 2006b; Anderson, 2010). Many of these studies were conducted to examine gene flow among populations, were of short duration, and followed individual snakes for a short period of time. For example, Anderson (2010) tracked males for an average of 2.1 seasons, and females for 2.6 seasons. On average, a snake would have an opportunity to switch hibernacula only once or twice. Anderson (2010) reported that 3 of 82 snakes switched hibernacula over the study period. Gerald et al. (2006b) found that 2 of 6 (33%) Northern Pine Snakes in Tennessee used the same hibernation site the following year, indicating that undisturbed Pine Snakes will switch hibernation sites, which is similar to our previous findings with snakes of unknown ages (Zappalorti et al., 1983). Other species show low fidelity to hibernacula, and rarely use the same site from year to year (Harvey and Weatherhead, 2006). Had our study been only 2–3 yr long, philopatry might have been much higher because over such a short period, hibernation site suitability remains the same.

Snakes hibernate in a variety of situations, including 1) solitarily in old stump root systems, rodent burrows, crayfish holes, and rock crevices (e.g., Massasauga Rattlesnake, *Sistrurus catenatus*, Harvey and Weatherhead, 2006); 2) multispecies groups in relatively small rock piles ("den complexes," Parker and Brown, 1973); 3) small communal groups in hibernacula that are relatively small with one entrance (Northern Pine Snakes, Burger et al., 1988); 4) groups of hundreds in extensive rocky screes (Timber Rattlesnakes, *Crotalus horridus*, Brown, 2008); or in dense aggregations of several thousand (Garter Snake, *Thamnophis sirtalis parietalis*, Aleksiuk, 1976). There is also variation within a species. Northern Pine Snakes in New Jersey hibernate in extensive sand burrows with both conspecifics and other species of snakes, whereas those in Tennessee use concrete foundations and old stumps and do not hibernate with other conspecifics (Gerald et al., 2006b). Black Pine Snakes (*Pituophis melanoleucus lodingi)* in Mississippi hibernate singly as well (Rudolph et al., 2007). The variations within and among species

TABLE 4. Effect of sex and hatchling status on the number of dens used by Pine Snakes, the percentage of times snakes did not use any of the known hibernacula, and age of last capture at hibernaculum complex site A. NS = not significant; given are means ± SE.

	Overall $n = 62$	Males $n = 26$	Females $n = 36$	$\chi^2(p)$
# Dens used				
Overall	2.87 ± 0.14	2.85 ± 0.21	2.89 ± 0.19	0.03 (NS)
Hatchling	2.69 ± 0.23	2.44 ± 0.34	2.80 ± 0.30	0.3 (NS)
Nonhatchling	3.03 ± 0.16	3.06 ± 0.25	3.00 ± 0.20	0.0 (NS)
$\chi^2(p)$	1.6 (NS)	1.4 (NS)	0.5 (NS)	
% Not found				
Overall	35% ± 3%	41% ± 4%	30% ± 4%	3.8 (0.05)
Hatchling	22% ± 4%	28% ± 8%	19% ± 4%	0.9 (NS)
Nonhatchling	46% ± 3%	48% ± 4%	43% ± 3%	0.4 (NS)
$\chi^2(p)$	17.4 (<0.0001)	3.9 (0.05)	11.8 (0.0006)	
Age at last capture				
Overall	7.27 ± 0.67	8.12 ± 1.21	6.67 ± 0.76	0.4 (NS)
Hatchling	6.00 ± 0.87	5.33 ± 1.21	6.30 ± 1.15	0.2 (NS)
Nonhatchling	8.39 ± 0.98	9.59 ± 1.64	7.13 ± 0.98	0.7 (NS)
$\chi^2(p)$	4.3 (0.04)	3.2 (0.07)	1.4 (NS)	

means that the definition of philopatry also varies. Finding one hibernaculum with one or two openings (e.g., Pine Snakes) poses a different task from that of finding a large talus slope with several potential "entrances," or an even larger rock scree with dozens of potential entrances (e.g., Timber Rattlesnake).

Our data indicate that: 1) of 152 hatchlings found, 38% were located again; 2) of 120 known-age snakes, only 23% were always philopatric; 3) philopatry decreased with age, although some snakes were found in the same hibernaculum up to 22 yr later; 4) philopatry was lower for males than for females, for snakes that were found as 2-yr-olds rather than as hatchlings, and for snakes in hibernaculum complex A relative to the other two hibernacula. Although we had predicted the age and sex differences, we had expected philopatry to be higher in the hibernaculum complex. These differences are mainly due to snake age. As snakes age, the probability of switching hibernacula increases.

We suggest that these differences in philopatry are partly due to predators; over the study, hibernacula were opened by predators nine times, making them unsuitable because of residual predator scent and the possibility of predation. Predators identified were Red Fox (*Vulpes vulpes*) and Striped Skunk (*Mephitis mephitis*) (Burger et al., 1992; Burger and Zappalorti, 2011b). Hibernation sites were also used during the summer (Burger et al., 1988, 1992), and snake odors may attract mammalian predators. Hatchling Pine Snakes are able to discern and avoid the odor of predators (Burger, 1989).

Age-related differences in philopatry may be due to the wandering of adult snakes in search of food or mates. If a snake is far from its natal hibernaculum when cold weather sets in, it may seek the nearest suitable hibernaculum it recognizes from previous years. Snakes are vulnerable to freezing temperatures, and we have found a frozen female on the surface (after a rapid decline in surface temperature), and frozen adults and hatchlings in hibernacula entrances, a few inches below the surface.

TABLE 5. Example of hibernaculum use by Pine Snakes at site A where there were five hibernacula in a small area. M = male, F = female, * = location of initial capture.

Age at last capture	Sex	Use of hibernacula H1	H2	H3	H4	H5	% of times found
23	M	6*	1				30
23	F	12*	1	1	3	2	82
20	M	5*	1		1	1	40
20	M	3*					15
18	M	6	1			2*	50
14	F	4	1		1	6*	86
14	F	6*		1		2	64

Sex differences relate partly to age, as adult male snakes (3–4 yr or older) wander in search of females. In the present study, males showed less philopatry than females. The higher rate of philopatry in females may be a constraint of their nesting as they require open patches with complete sun penetration to allow incubation of eggs (Burger and Zappalorti, 1986; Burger et al., 1987). Since the hibernacula were near open patches, females may remain in the hibernating vicinity to nest, and if suitable prey animals are present, they may stay during the summer.

The snakes at hibernaculum complex A showed lower philopatry than did the snakes at the other sites. The reasons for the differences are less obvious, but may also relate to age. At least three hibernacula at complex A were always available as predators opened only one at a time. Snakes did not have to search elsewhere for a hibernaculum, because there were several old cement foundations at the complex that could serve as hibernation sites. In contrast, when the other two hibernacula were breached by predators, there may not have been other suitable hibernacula nearby. Further, since philopatry decreases with age, the possibility of having a higher proportion of older snakes at complex A reduces philopatry there. Pine Snakes at hibernaculum complex A averaged 6.97 yr old at last capture, compared with 5.92 yr old and 5.76 yr old for B and C respectively.

Conservation Implications.—In New Jersey, Northern Pine Snakes live only in the Pine Barrens, which are protected by the Pinelands National Preserve. However, there are extensive housing and commercial developments within the preserve, called regional growth areas. Continued development leads to fragmented habitat and loss of connectivity. Only recently have conservation biologists begun to focus on habitat loss, connectivity, and biodiversity in urban and suburban landscapes (Rees, 1997; Fernandez-Juricic, 2000; Burger et al., 2007). New Jersey is the most densely populated state in the United States, and Pine Snakes have lost habitat at the rate of 0.29%/yr for decades; therefore, over 50 yr, 18% of their habitat has been lost (Hasse and Lathrop, 2008; Golden et al. 2009). Pine Snakes are listed as threatened in New Jersey, and although their status was challenged by the New Jersey Builders Association, it has not changed. Upland habitat with hibernation sites are continually threatened by developers and political pressure because dens are less obvious than other critical habitats, such as nesting areas (Burger et al., 2012).

On the basis of our 27-yr data set from 120 known-age Pine Snakes, we report that philopatry for hibernation sites is relatively high in the early years of a snake's life, but decreases as snakes age. Older snakes will use the same sites, but not always in consecutive years. One female used the same hibernaculum complex for 19 of 23 yr. Conservation implications are clear; known hibernacula should be protected because there is a significant degree of philopatry in Pine Snakes. Our data indicate that specific hibernacula are important, and perhaps critical, to the survival of Northern Pine Snakes.

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