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Philopatry and nesting phenology of pine snakes *Pituophis melanoleucus* in the New Jersey Pine Barrens

J. Burger[1] **and R.T. Zappalorti**[2]

[1] Department of Biological Sciences, Rutgers University, Piscataway, NJ 08855, USA
[2] Herpetological Associates, Inc. 108 Berkeley Avenue, Beachwood, NJ 08722, USA

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Summary. We studied nesting behavior of pine snakes *Pituophis melanoleucus* from 1977 to 1989. Female pine snakes in the New Jersey Pine Barrens excavate tunnels and a nest chamber for egg deposition. Over 70% of all nests had old, hatched shells remaining in the nests from previous years. The presence of hatched shells and the incidence of recaptured females in the same nest indicates nest site tenacity for some females. From 1977 to 1988 we branded 98 females and 45 were recaptured in the same general nesting area. All 45 recaptured females were recaptured one to four times at the same nest site; two of these snakes were captured in three years at the same site and in one year at a different site. We conclude that females show a high degree of nest site philopatry. We suggest that high nest site philopatry is selected for because it promotes location of sites that are safe from predators (buried, hatched shells) and contain suitable temperature conditions.

Introduction

Preferences for particular habitats for breeding, migrating, or wintering are documented for a variety of vertebrates, and many animals return to particular places for breeding or overwintering (see references in Heatwole 1977; Cody 1985; Lemnell 1978; Holmes and Sherry 1989). Some vertebrates exhibit a high degree of philopatry to general sites for colonies or nests (Southern 1977; Congdon et al. 1983; Lutz and Dunbar-Cooper 1984; L'Arrivee and Blokpoel 1988), hibernacula (Brown and Parker 1976), or display sites (Buechner and Roth 1974), and often tenacity is to a particular site (i.e. birds, Southern 1977; lizards, Wiewandt 1983).

In birds philopatry may reduce the costs of territorial defense against recognized neighbors, reduce the threat of predators because predators and suitable hiding places are known, and reduce the potential risks of environmental insults. For reptiles, the above advantages apply because females may be vulnerable to predators while they are excavating nests and laying eggs. Reptiles are also constrained by thermal considerations. A female's choice of nest site can determine development times, sex of the offspring, and the subsequent behavior of her hatchlings through the thermal and hydric environment of her nest (Vinegar 1973; Bull 1980, 1985; Gutzke and Packard 1987; Packard and Packard 1988; Deeming and Ferguson 1988; Burger 1989, 1991). Thus, selection for nest site philopatry may be strong in reptiles, regardless of the females' ability to ascertain hatching. Yet this aspect of reptilian biology is difficult to study because a sufficient sample of reptile nests is difficult to locate under natural conditions over a series of years. Although turtles often return to the same general nesting area each year (Congdon et al. 1983), and lizards may exhibit nest site tenacity (Wiewandt 1983), few studies have examined nest site philopatry in reptiles over several years. Even descriptions of nest sites of snakes are usually limited to only one or a few nests (see review in Burger and Zappalorti 1986). Without locating nests, it is impossible to examine nest site philopatry. In this paper we describe nesting phenology and nest site philopatry of colubrid pine snakes, *Pituophis melanoleucus*. We address the following questions: (1) What is the nesting phenology of pine snakes; (2) does ambient temperature (from January to June) affect the timing of egg-laying; (3) are specific nest sites re-used in subsequent years; and (4) do females use the same nest site from year to year.

Pine snakes in the New Jersey Pine Barrens select nest sites in open clearings with sparse trees, shrubs or herbs that allow sun penetration for much of the day (Burger and Zappalorti 1986). They select both natural and disturbed sites with soft, moist sand where there are few roots to impede digging (Zappalorti and Burger 1985, 1991).

Offprint requests to: J. Burger

Methods

Known pine snake nesting areas in the Pine Barrens of New Jersey (Atlantic, Ocean and Burlington counties) were searched from mid-May through July 1977–1989 for gravid females, digging females, and nesting burrows. All known nesting areas were searched each year. However, these areas are separated by several kilometers and all of them could not be checked every day or every other day (due to time constraints). Some areas could not be visited for several days in some years due to heavy rains making the roads impassable to four-wheel-drive vehicles. However, the holes and dump piles remain for up to two weeks before the sand drifts back in, females do not cover their nests (Burger and Zappalorti 1991). Further, some nesting areas were destroyed by developers during the study, and we found new ones in other locations. Thus we could ascertain when a nest site was used, but could not always locate the specific female. Each known nesting area had 3–18 marked females living there (as determined by observations and radiotelemetry, Burger and Zappalorti, unpub.). The habitat in the study areas was primarily pitch pine, *Pinus rigida*, and black-jack oak, *Quercus marylandica*, in upland areas. General nesting habitats were railroad beds, sandy shoulders of paved or dirt roads, natural openings in the forest, clearings created by forest fires, and man-made clearings. These clearings, known as nesting areas, are surrounded by pine barrens forest.

Although there are no suitable nest sites within the forest, there are suitable sites within the clearings that are not used by pine snakes for nests (Burger and Zappalorti 1986). Using the raw data from Burger and Zappalorti (1986) we can show that there are some suitable sites near nest sites that have not been used (Table 1). The clearings with these unused but suitable sites are small areas up to 250 m long. Thus they are within the home range of the females, and the females move over these places as they return to their own site. These data were generated by using a table of random numbers to generate 31 points (not used by snakes for nesting) within clearings, and to generate 31 points in the surrounding forest.

Snake holes can be recognized because of their small size and pile of sand (dump pile) on one side of the opening. Snake holes lead to nests or are "test holes". Whenever snake holes were located they were excavated carefully by following the main tunnel, removing the sand by hand, feeling for side tunnels, side nest chambers, and old clutches (hatched egg shells from previous years). The following information was recorded at each snake hole: date, time, location, location of all clutches, hatched eggs, and presence of females within the nest, number of clutches, and clutch size. Nests were re-covered, and plexiglass was used over the top of clutches to ensure adequate air space above the eggs. No differences in nest temperatures were recorded, and no hatching differences were noted as a result of the use of plexiglass (Burger and Zappalorti, unpub. data). Branded females and those that had not laid eggs were released immediately after we covered the nest. Other unmarked females were branded (Clark 1971) and released a few hours later. These females were released back into their nest tunnels, and those that we observed ($n=50$) remained in or near the nest. The nest site was checked periodically over the next week. Females that had been interrupted returned to lay in the same nest where they were caught. Over the 13 years of the study we branded 5–9 new females each year. By following females equipped with radios we learned that females stay within an area with a diameter of less than 2 km (Burger and Zappalorti, unpub. data).

We used Kendall τ correlation coefficients to determine significant relationships among the distribution of temporal egg-laying variables and mean monthly temperatures. To calculate mean date we used the julian system, where the days of the year are numbered 1–365. This allowed us to calculate a mean $+$SD, and to correlate laying data with temperature data.

Results

Breeding chronology

Pine snakes emerge from their hiberacula in April, dispersing to nearby pine-oak forest areas. We have observed copulation in mid-May in the vicinity of nesting areas. From 1977 to 1989 the first gravid females appeared in early June. Test holes appeared from 14 to 23 June, and the first eggs were laid from 17 June to 29 June (Table 2). In most years the egg-laying period was only about 2 weeks and did not extend beyond 14 July. The longest egg-laying period was 18 days (1979).

Temporal measures of egg-laying were interrelated (Table 3). Earlier test holes were correlated wth earlier

Table 1. Presence of suitable, unused sites in nesting area clearings and in adjacent forest (after data in Burger and Zappalorti 1986)

Characteristics	Usable sites	
	Percent of random sites in clearing that fall within mean ±1 SD of sites used by snakes	Percent of random sites in forest that fall within mean ±1 SD of sites used by snakes
Percent tree cover	29 (9)	3 (1)
Percent ground cover	23 (7)	0 (0)
Distance from forest edge	87 (27)	74 (23)
Sand compaction	48 (15)	61 (19)
Sand type	23 (7)	10 (3)
Suitable with respect to all five characteristics	23 (7)	0 (0)

Sample size is 31 for each place (number of suitable sites in parentheses). We used the characteristics of snake nest sites to examine whether random points had the same values, or fell outside the limits of sites used by snakes

Table 2. Nesting phenology of pine snakes from 1978 to 1989 in the pine barrens of New Jersey

Year	1st date of test holes	Number of nests[a]	1st egg-laying date	Mean date egg-laying (±SD in days)	Last egg-laying date
1977	15 June	12	20 June	24.5 June ± 7.5	30 June
1978	18 June	12	28 June	1.1 July ± 3.3	12 July
1979	15 June	9	18 June	26.1 June ± 6.6	6 July
1980	18 June	16	22 June	1.5 July ± 5.5	9 July
1981	15 June	16	17 June	23.6 June ± 4.3	1 July
1982	22 June	13	27 June	2.9 July ± 2.4	6 July
1983	18 June	24	23 June	30.6 June ± 3.6	6 July
1984	17 June	15	21 June	27.7 June ± 3.1	3 July
1985	14 June	25	18 June	23.7 June ± 4.4	1 July
1986	14 June	33	17 June	22.7 June ± 5.7	3 July
1987	20 June	15	25 June	30.1 June ± 2.9	6 July
1988	23 June	17	29 June	4.8 July ± 4.6	14 July
1989	24 June	21	27 June	3.3 July ± 2.7	10 July

[a] Where the female was in the nest and/or eggs were still unattached (indicating they were recently laid)

Table 3. Relationships among temporal variables, and of temporal variables of test hole construction and egg-laying with mean monthly temperatures

	Date of first test hole	Number of nests	Date of first clutch	Mean date of clutches	SD of mean clutch date	Date of last clutch
Temporal variables						
Date of first test hole	–	NS	0.79 (0.0003)	0.82 (0.0002)	−0.49 (0.02)	0.61 (0.0007)
Number of nests		–	NS	NS	NS	NS
Date of first clutch			–	0.80 (0.002)	−0.38 (0.05)	0.68 (0.002)
Mean date of clutches				–	NS	0.68 (0.002)
Variation in clutches[a]					–	NS
Date of last clutch						
Mean monthly temperatures						
April	−0.44 (0.04)	NS	−0.51 (0.01)	−0.51 (0.01)	−0.34 (0.05)	−0.43 (0.04)
May	NS	NS	NS	NS	0.35 (0.06)	NS
June	NS	NS	NS	NS	−0.41 (0.05)	NS
April–June (cumulative)	NS	0.43 (0.04)	−0.42 (0.05)	−0.36 (0.06)	NS	−0.40 (0.06)
May–June (cumulative)	NS	0.56 (0.008)	NS	NS	NS	NS

[a] Standard deviation of egg laying

Kendall τ correlation coefficients (with levels of significance) are shown. NS = not significant

first clutches, mean date of egg-laying and earlier last clutches, but were negatively correlated with the standard deviation of egg-laying date. Similarly, date of first clutch, mean clutch date and last date of egg-laying were positively correlated. Standard deviation of egg-laying was negatively correlated with date of first test hole and first clutch. Thus when egg-laying is earlier, there is a longer period of egg-laying.

We examined the timing of test hole initiation and egg-laying in relationship to mean monthly temperatures (from National Oceanographic and Atmospheric Administration 1977–1989) for January through June (Table 3). Although temperature is not expected to influence test hole construction itself, test hole construction is an indication that females are searching for nest sites and indicates a readiness to lay. There were no significant correlations between mean temperatures and temporal patterns of pine snake egg-laying for January, February and March. However, mean temperatures for April were negatively correlated with all temporal characteristics of snake egg-laying (Table 3). That is, when April temperatures were higher than normal the snakes nested earlier. Mean May and June temperatures did not correlate with temporal patterns except that they were related to the standard deviation of mean date of egg-laying. Cumulative temperatures for April through June were positively correlated with number of nests and negatively correlated with date of first, mean, and last clutch. The number of nests we found was positively correlated with the cumulative mean temperatures for May and June (Table 3). Taken altogether these data indicate that mean April temperatures are critical for the timing of egg-laying in pine snakes, but that cumulative temperatures from April through June are also important.

Nest philopatry

Over the 13 years of this study we always found gravid and nesting females in the same general nesting area. We defined a nesting area as a clearing bounded by dense trees (see Burger and Zappalorti 1986). Nesting areas were separated by at least 1 km, and some were separated by several kilometers. The separation between nesting areas is due to lack of habitat: pine snakes require open patches for nesting (Burger and Zappalorti 1986). Some nesting areas were small (only a few meters square), others were large abandoned fields (100 × 50 m), and others were long and narrow (a 5-m wide strip along an abandoned railroad). Of the 45 marked females recaptured during this study, only two were found nesting in a different nesting area from their initial capture site.

Many nests had old egg shells from the previous year (73% of 102 nests) and the incidence of old shells increased with the number of active clutches per nest. Most nests (66%) with old shells had only one such clutch. However, since these were often found by digging farther in a tunnel where it felt soft (but was not an open tunnel), old egg shells from previous clutches could easily be missed. Further, egg shells disintegrate in 3–4 years or are eaten by ants.

The presence of old, hatched shells in nests (Kauffeld 1957) indicates that pine snakes use the same nest site from year to year, but not that the same female uses the nest. Our data on female philopatry to specific nest sites include the following incidents from marked females. From 1978 to 1988 we branded 98 females at the nesting sites we rechecked in most years (an additional nine new females marked in 1989 had no opportunity for recapture), and 45 (42%) were recaptured at least once at exactly the same nest site. Of these 45, 30 marked females have been captured in exactly the same nest site for 2–3 consecutive years (Table 4) although the nest site was occupied for more years.

Table 4. Philopatry and nest site use by pine snakes

Number of years female located	Years nest site used consecutively whether a female was recaptured or not										Number of females represented[f]
	2	3	4	5	6	7	8	9	10	11	
Philopatry											
Consecutive use											
2 years	5	3	5	4	4	1		1			23
3 years		3		1	2	1					7
Non-consecutive use[a]											
2 years			1	3	1	2		1	1[c]		9
3 years[b]				1		1					2
4 years[b]				1						1[d]	2
Non-philopatry[e]						2					2

[a] Eggs present at the site each year, but snake not always found in nest every year
[b] At least 2 years were consecutive
[c] Female found at nest in 1978 and 1987
[d] Female found in 1978, 1979 and 1988 and 1989
[e] Two females nested together in same site for 3 years, at a 2nd site for 1 year: original site used for 7 years
[f] A total of 98 females were branded from 1977 to 1988 at the sites where these data were collected. Additional 9 were branded in 1989, but we had no opportunity to recapture them

Each female is included only once. "Use" means we found a clutch of eggs or a gravid female at the site

There is only a brief period of 1 day–2 weeks when a nest can be located because high winds or rain may result in the dump pile filling in the nest-opening. Given the difficulty of finding any female pine snake in a nest when we open it, it is remarkable that we have found such a high number of females in consecutive years.

We also found 13 females in the same nest for 2 or 3 non-consecutive years (Table 4). In the intervening years the snakes were not located, although the nest site was used by pine snakes for nesting. Only 2 of 45 females were ever found at a different nest site. These two females nested together in the same nest for four seasons, using one site in 1983, a different site 55 m NW in 1984, and the original site again in 1986 and 1987. In 1983 the nest was destroyed and the eggs eaten by fox, and a nearby nest was also destroyed there in 1984, the year the pair of females moved. The predator was identified by tracks, and a characteristic dump pile and tooth marks on the eggs (Burger and Zappalorti 1986).

These data indicate that: (1) exactly the same nest sites can be used up to 11 years in a row; (2) some females lay for at least 2 or 3 years in a row; (3) some females lay for 2 or 3 years in a row in exactly the same nest site; (4) sites were used by the same female as much as 10 years apart; and (5) 95% of females are only found in the same nest site from year to year; if they are not found in their previous site, they are not found at all.

Discussion

Egg-laying synchrony

Obtaining sufficient data on egg-laying in snakes is difficult without the aid of radio-telemetry because their nest sites are usually hard to find. Accurate data on egg-laying in *Pituophis melanoleucus* is rare because they lay eggs in burrows where it is difficult to determine laying date. In other parts of its range, *Pituophis melanoleucus* use the burrows of pocket gophers *Thomomys* spp. (Neill 1974; Parker and Brown 1980; Carpenter 1982), thirteen-lined ground squirrel *Citellus tridecemlineatus*, and woodchucks *Marmota monax* (Vogt 1981). Since the mammal systems exist, it is difficult to ascertain when and where females enter or oviposit. However, female pine snakes in New Jersey dig their own nests, and these can be located when females were excavating them or shortly thereafter.

Egg-laying of New Jersey pine snakes usually occurred over a 2-week period, and was relatively synchronous for a reptile. Synchronous nesting has been reported as an antipredator strategy for snapping turtles (*Chelydra serpentina*; Robinson and Bider 1988). Nesting synchrony was the only strategy that could decrease nest predation because predators required a short period before they reached their maximum efficiency in destroying nests. Predation rates declined 6 or 7 days after egg-laying (Robinson and Bider 1988), perhaps due to decreases in odors on the sand surface. Overall 84% of nests were destroyed (Robinson and Bider 1988). On the contrary, Burger (1977) found that losses due to predation were evenly spaced throughout the developmental period in diamond-backed terrapin (*Malaclemys terrapin*). Wiewandt (1983) noted the importance of nesting synchrony as an antipredator mechanism for adult and offspring iguanine lizards. Thus the pattern of predation may be critical to the evolution of synchrony.

Predation rates for pine snakes are relatively low since 73% of our nests had old hatched shells from successfully hatched clutches. Predation may be low because the eggs are located an average of 1.4 m from the entrance hole, although they average 15 cm from the soil surface (Burger and Zapplorti 1986). Thus a predator that uses olfaction to cue in to the entrance (where presumably the female's odor is strongest) may stop digging before it reaches the eggs. Although foxes (*Vulpes fulva*) prey upon some nests, humans are a greater threat (although they are more recent) because they dig up nests and remove the eggs and females for their collections or for illegal sale.

We suggest that in pine snakes temperature may be a more critical synchronizer of egg-laying than predators. Pine snake eggs in nature require a minimum of about 60 days to hatch. Given that development time is related to nest temperature, it is adaptive to time egg-laying so that eggs are exposed to optimum temperature throughout development. Although there are suitable nest sites nearby (see (Table 1, Burger and Zappalorti 1986), there are also many non-suitable sites. Thus once a suitable site is selected (where eggs hatch successfully), it is adaptive for the snake to continue to use this site rather than search for another one nearby. For the 13 years studied, the mean temperatures of July and August, taken together, (after NOAA 1977–1989) were always warmer than those of June and July ($\bar{x}=4.5\pm$ 2.8° C colder on average), or August and September ($\bar{x}=$ 8.4 ± 2.1° C colder on average). Nonetheless, pine snakes nesting in the New Jersey Pine Barrens are at the northern extreme of their range in eastern North America (Wright and Wright 1957). Nests initiated and placed so that eggs are exposed to low temperatures may experience biased secondary sex ratios and the young may be behaviorally disadvantaged (Burger and Zappalorti 1988; Burger 1989).

Temporal patterns of egg-laying

The temporal pattern of pine snake egg-laying was negatively correlated with mean April temperatures and not significantly so with May and June temperatures. In the New Jersey Pine Barrens pine snakes emerge from their hibernacula in late March to late April (most years in early April; Burger et al. 1988). The time they emerge may determine the timing of egg-laying, perhaps through the mechanism of the total time females have available to obtain food resources.

One aspect bearing comment is the positive correlation between the number of nests we found and cumulative mean temperatures for April through June and May to June. This suggests that not all females may lay each year. Our data clearly show that more than half of the recaptured females did lay in consecutive years (see below), but it is not certain that all do.

Nest site philopatry

The use of the same nests occurs in some lizards, because old egg shells have been found in iguanid nests (Wiewandt 1983), but this does not indicate that the same female is using the same nest site. In some cases female iguanas are attracted to the shallow depressions in the sand left from the previous season (Wiewandt 1983), but no such indentation occurs in the Pine Barrens of New Jersey.

In this study female pine snakes always nested in the same general cleared area. Females may return to the same general nesting area (e.g. open clearing, railroad bed) where they first emerged as hatchlings because they were imprinted on the site upon emerging from their nests, or they learned to associate the characteristics of the area with nesting. Thereafter, females may simply continue to return to the same area to nest in successive years.

The presence of the same female at the same nest site in successive years indicates that female pine snakes can lay every year (in contrast to some viviparous snakes; Blem 1982; Reinert and Zappalorti 1988), and that they exhibit nest site philopatry. When we dig up nests we obliterate the tunnels and chambers. Nonetheless, in successive years nests were re-excavated. Nests that we excavated had higher hatching success than those we did not dig up because predation rates were lower on excavated nests. We attribute this difference to our masking the snake's odor, and leaving a human odor that may be less attractive to predators.

Although only 42% of the females used the same spot in successive years, it is likely that most reused the same sites because: (1) Only 2 of 45 females were ever found in a different site (and these females returned the next year to their original site); (2) the same sites were used every year by pine snakes even though we did not always find the females; (3) females often are removed from our population by poachers (accounting for the disappearance of marked females); and (4) some sites were used by the same female as much as 8, 9, and 10 years apart.

New Jersey pine snakes are prized by collectors because of their unique patterns and their ability to adapt well to captivity; and eggs and gravid females are poached. In 1988 8 of 20 nest sites with previously-marked females were excavated by poachers; and in 1989, 7 of 19 sites were destroyed by poachers. Some of these nests may have had within them gravid females or females that had recently laid eggs. Further, poachers could have found gravid females searching for nest sites, removing them permanently from our sample. The taking of pine snakes from the New Jersey Pine Barrens is not a new phenomenon (Courier 1897; Kauffeld 1957).

Females leave before eggs hatch, thus they are not simply returning to a safe nesting site where they observed that their eggs hatched. Females may be returning to their natal area to nest the first time, and then returning in successive years to the same sites. It is also possible that they use olfactory cues from the presence of old egg shells to identify their previous nest sites and to ascertain if the eggs hatched successfully. Old egg shells are strewn around on the ground when fox or skunks have preyed upon them, in contrast to hatched nests where the egg shells are in the egg chamber below ground. Females selecting where to dig spend several minutes tongue-flicking on the soil surface and on the old shells (Burger and Zappalorti 1989). Test holes may simply be used to locate the correct site that is laced with their scent from previous years. Although it is difficult to follow searching females, we have observed two marked females make several test holes within a nesting clearing that was 40 × 15 m, and then dig nests only when they reached their previous year's site.

In birds, nest and colony site philopatry confers familiarity with landmarks, resources, and predators, and allows them to continue to nest where they have previously been successful (see Burger 1984). Birds tend to shift sites when they have not successfully raised young. Thus there are immediate benefits (avoidance of predators and environmental stress), as well as the long-term benefit of using sites where young were produced.

In pine snakes, nest site philopatry allows females to return to a familiar place where landmarks, resources and predators are known, where they know suitable basking sites, resting locations, and hiding places from predators. Females spend 2–3 days digging nests, and during this phase they are especially vulnerable to predators and thermal stress. Presumably using the same nest site, if it was successful, results in higher reproductive success than switching sites. Whether females can ascertain if a nest was successful (by the presence of hatched shells in the nest or the lack of preyed-upon shells on top) is unclear. The data support the hypothesis that females can locate their previous nest site, and continue to use it in successive years.

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