*Journal of Herpetology*, Vol. 25, No. 2, pp. 152–160, 1991

# Nesting Behavior of Pine Snakes (*Pituophis m. melanoleucus*) in the New Jersey Pine Barrens

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ABSTRACT.—**We studied the excavation and nesting behavior of pine snakes (*Pituophis m. melanoleucus*) in the New Jersey Pine Barrens from 1977–1989. Females excavate a tunnel and nest chamber for egg laying. Females initially make slight depressions in the sand (pre-test holes, 22%), then construct small test holes (16%), and finally excavate long tunnels leading to nest burrows (62%). Test holes and nests did not differ in most external characteristics (dump pile size, entrance size), although they did differ in soil moisture at the end of the tunnel, mean tunnel length, and number of turns. Mean clutch size was 9.5 ± 0.3 (range 4–16), and was related to female snout-vent length ($r = 0.60$, $P < 0.001$).**

Female vertebrates exert control over the growth, development, and survival of embryos either by having internal development (i.e., most mammals), impregnable eggs (i.e., most birds), or by depositing their eggs in environmental conditions suitable for their development. For some egg-laying vertebrates, selecting nest and egg-deposition sites is the limit of parental care. In reptiles, females exhibit parental care ranging from simple nest site selection to the guarding of nests, eggs, and offspring (e.g., *Alligator mississippiensis;* Garrick and Lang, 1977). Most species of snakes lay their eggs under rotting logs or leaves, or in mounds, burrows, or crevices (Wright and Wright, 1957). Bull snakes, *Pituophis melanoleucus sayi,* usually lay their eggs in the burrows of small mammals (Parker and Brown, 1980; Gutzke and Packard, 1987). However, in the New Jersey Pine Barrens there are few small mammals that regularly dig appropriately-sized burrows (e.g., star-nosed mole, *Condylura cristata,* and common hairy-tailed mole, *Parascalops breweri;* Van Gelder, 1984). Pine snakes in the New Jersey Pine Barrens excavate their own nests, tunnels, and egg chambers (Moore, 1893; Trapido, 1937; Zappalorti et al., 1983; Burger and Zappalorti, 1986), and are morphologically equipped to do so (Knight, 1986). In this paper we describe their excavating and nesting behavior.

Some other reptiles dig their own nests in sand, including turtles (*Malaclemys terrapin,* Burger and Montevecchi, 1975; *Macroclemys temmincki,* Ewert, 1976; *Caretta caretta,* Ackerman, 1981), iguanas (*Iguana iguana,* Rand, 1968) and other lizards (*Phrynosoma solare,* Van Devender and Howard, 1973), and crocodiles (*Crocodylus acutus,* Lutz and Dunbar-Cooper, 1984). Although many reuse the same general nesting area every year (Congdon et al., 1983), only a few reptiles reuse the same nest in successive years (Lutz and Dunbar-Cooper, 1984). Parker and Brown (1980) report that female bull snakes lay in the same general area year after 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, 1988). They select sites with soft, moist sand where there are few roots to impede digging. Although we have previously described nest site selection, we have not described the nesting process. In this paper we describe how females excavate nests; describe the tunnels, nest chambers, and nest temperatures; and examine the relationship between clutch size, female size, and nest characteristics. The pine snakes nesting in the New Jersey Pine Barrens are distributionally disjunct from other pine snakes (Sweet and Parker, 1990).

## METHODS

We searched snake nesting areas in Atlantic, Ocean, and Burlington counties in the Pine Barrens of New Jersey from mid-May through July from 1977–1989 for gravid females, digging females, and nesting burrows. Pine snakes nest in open clearings in pitch pine (*Pinus rigida*) and blackjack oak (*Quercus marilandica*) forests (Burger and Zappalorti, 1986).

Snake holes can be recognized because of their small size and a distinctive pile of excavated sand (here termed a dump pile) on one side of the opening. Snake holes lead to nests, or are either "pre-test holes" (hole but no tunnel) or "test holes" (short tunnels with no eggs and no digging females). 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 (with hatched egg shells).

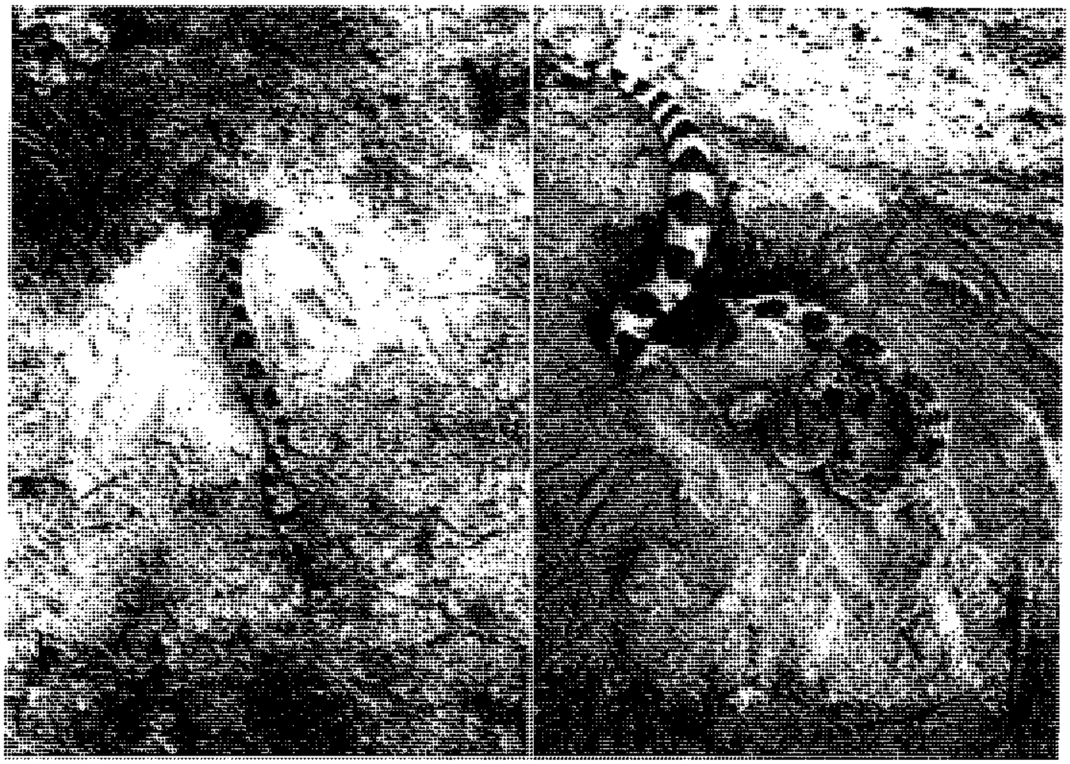

FIG. 1. Nest site of pine snake (*Pituophis m. melanoleucus*) showing characteristic deposit (dump pile) of excavated sand (left) and female pine snake pulling sand from burrow (right). Note dump pile, and that female is obviously gravid.

The following information was recorded at each snake hole: date, time, location, general habitat, length and width of the dump pile (after Carpenter, 1982), width and height of the opening, compass direction the opening faced, soil moisture in the nest, total tunnel length, number of turns (greater than 45°), and the locations of all clutches, hatched eggs and females. During tunnel excavation we drew scale maps noting every turn, the lengths of all segments, and the locations of all clutches, old hatched shells, and females. Soil moisture was measured using an Instamatic Moisture Meter (AMI Medical Electronics Inc.) that registers between 1 and 8 (1 = low moisture, after Reinert and Kodich, 1982).

Females located in nests were measured (total length, and snout–vent length, SVL), and some gravid females were removed to the laboratory. We used these gravid females and those still remaining at the nest site to determine the minimum interval between nest construction, burrow use, and egg-laying. Previous experience indicated that females will lay eggs in laboratory conditions when provided with ample space and damp sand. All females were branded (Clark, 1971) and released after egg-laying. Gravid females located away from known nesting areas were also taken to the laboratory, measured, marked, and allowed to lay eggs before being returned to their capture site.

We used Kruskal-Wallis $\chi^2$ tests to determine differences among means, and correlation coefficients to determine significant relationships among the distribution of variables. In this paper we provide means and standard errors unless otherwise noted.

## RESULTS

*Nest Site Characteristics.*—Females move to the nesting area in mid-June, and we observe them testing the sand in mid- to late June. From 1977 to 1989 we located 119 places where snakes had excavated: Pre-test holes (22%, N = 26), test holes (16%, N = 19), and nests (62%, N = 74). Pre-test holes were difficult to locate unless they were found immediately after they were made because wind or rain obliterated them. Pre-test holes are small indentations in the sand where female pine snakes had pressed their snouts to the ground several times, and sometimes removed a little sand, but without making a hole more than 2 cm deep.

TABLE 1. Comparison of nest structure as a function of stage in pine snakes. Given are means ± one standard error; all dimensions in cm, units for moisture are on a scale from 1 (dry) to 8 (wet).

| Characteristic | Test holes | Completed nests: Prior to oviposition | Completed nests: After oviposition | Kruskal-Wallis $\chi^2$ ($P$) |
|---|---|---|---|---|
| Number | 26 | 19 | 74 | |
| Dump pile length | 44 ± 4 | 55 ± 2 | 49 ± 2 | 4.34 (NS) |
| Dump pile width | 35 ± 4 | 53 ± 5 | 54 ± 3 | 7.26 (0.05) |
| Entrance moisture | 1.1 ± 0.1 | 1.3 ± 0.5 | 1.2 ± 0.3 | 2.57 (NS) |
| Entrance height | 7.4 ± 1 | 5.2 ± 4 | 6.0 ± 3 | 1.94 (NS) |
| Entrance width | 9.1 ± 2 | 7.9 ± 8 | 14.0 ± 7 | 0.98 (NS) |
| Tunnel length | 47 ± 14 | 146 ± 7 | 140 ± 7 | 18.4 (0.0001) |
| Tunnel number of turns | 0.4 ± 0.01 | 1.7 ± 0.2 | 1.9 ± 0.2 | 19.9 (0.0001) |
| Chamber length | | 18 ± 2 | 20 ± 9 | 1.99 (NS) |
| Chamber width | | 11 ± 7 | 11 ± 5 | 1.07 (NS) |
| Chamber height | | 8 ± 1 | 7 ± 5 | 0.99 (NS) |
| Depth to top of chamber | | 13 ± 2 | 12 ± 2 | 0.33 (NS) |
| Depth to bottom of chamber | | 22 ± 2 | 21 ± 3 | 1.71 (NS) |
| Tunnel/Chamber Moisture | 1.0 ± 0.1 | 1.3 ± 0.3 | 1.4 ± 0.2 | 6.86 (0.05) |
| Temperature (C) bottom of egg chamber | | 23 ± 2 | 27 ± 1 | 6.54 (0.05) |
| Temperature (C) at top of egg chamber | | 26 ± 2 | 29 ± 2 | 4.64 (NS) |

Test holes are places where a female started to excavate a nest, but did not continue. These were distinguished from nests by their small dump piles, short tunnel length, and lack of eggs, females, or egg chambers. Females were not found within them, and on subsequent visits they were not further excavated by female pine snakes. Holes initially designated test holes that were later finished and used for egg deposition were re-measured and removed from the test hole category. Nest sites had large dump piles (Fig. 1), long tunnels with one or more chambers, and often contained new clutches, and old, hatched egg shells.

We examined 25 pretest holes, 18 test holes, and 93 nests during the study (Table 1). Pretest holes, mere depressions in the sand, were easily distinguished because they lacked dump piles and an opening that went into the ground. The external appearance of test holes and nests did not differ with respect to dump pile length and moisture. However, the dump piles of test holes were narrower, tunnel length was less, and there were fewer turns in the tunnel than for nests (Table 1).

Nests with and without eggs were similar in construction (Table 1). Tunnel length varied from 39–228 cm, with 0–6 turns (median = 2). For nests making more than one turn, 40% made all turns in the same direction as the previous turn. Nest openings faced in all compass directions ($\bar{x}$ direction = 188 ± 57°). Only about 13% of the 93 nests were straight and involved no turn greater than 30°. When females encountered tree roots they shifted directions. Examples of nests are shown in Fig. 2.

Tunnels usually slanted downward for a third to a half of their length, and then slanted upwards. Thus, mean tunnel depth (32.8 ± 1.3 cm) was significantly deeper than mean egg chamber depth below ground (21.8 ± 0.8 cm, $\chi^2 = 16.2, P < 0.01$). In some cases we found females in nest chambers with no eggs. Oddly, chamber length ($r = -0.35, P < 0.06$) and width ($r = -0.48, P < 0.001$) were negatively correlated with SVL, suggesting that smaller (and perhaps younger) snakes are less efficient at making a compact chamber and laying eggs in it.

Completed nests did not always contain both eggs and females, although about 10% contained eggs with females that already laid. Over half of the nests without eggs had females within the nest, and females remained in nests until they laid eggs. We did not always find females immediately after nest construction, but even so the mean interval between finding a female in a completed nest and egg-laying was 5.5 ± 1.2 days (N = 48).

*Excavation Behavior.*—Female nesting can be divided into phases: (1) exploratory, (2) testing, (3) digging, (4) resting, (5) egg-laying, and (6) post-laying resting. During the exploratory phase females move over the ground in search of suitable habitat. They pause periodically, and move from place to place. Females seek nest sites by probing for a suitable site. Such pretest holes may be only a depression in the ground. Over the years we watched females make about 20 depressions.

Females then begin digging, abandoning the site if it is not suitable (test hole), or continuing to dig if it is. We have watched about 30 females

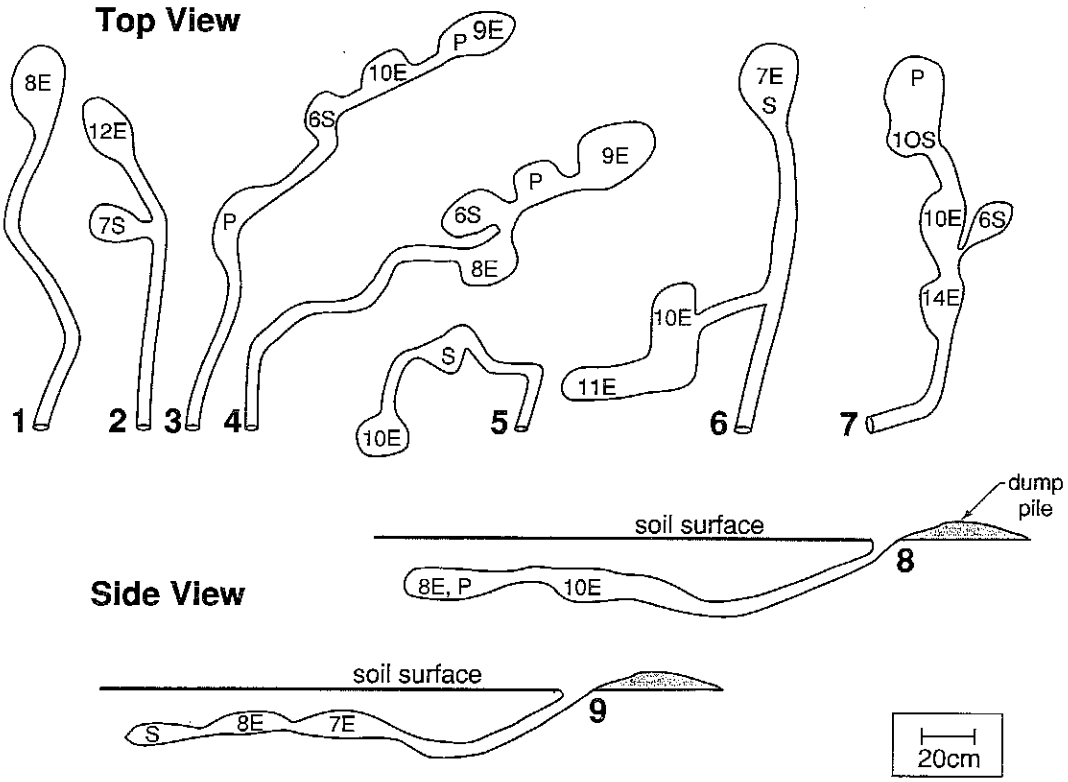

FIG. 2. Diagrams of nine representative nests showing the locations of eggs (E), old shells from previous years (S), and female pine snakes (P).

abandon a hole, and move to a new site; and about 25 females dig at various stages on a future nest. Digging females typically face in a southerly direction when digging. The direction of 87% of the nests was southeast to southwest. Assuming an equal probability of nests facing in the four cardinal directions, this difference was significant ($N = 46$, $\chi^2 = 59.3$, df = 1, $P < 0.001$).

Females dig tunnels by pushing forward with their snout and head, crooking the neck, capturing sand in the crook, and bringing sand out of the nest to deposit it on the dump pile (Fig. 1). They then return to the burrow to bring out more sand. When they encountered thick roots ($N = 26$) they shifted tunnel directions to avoid the root.

Typically females begin digging in the morning (0830–1030 h); when it becomes too hot they rest. They continue the digging process from 1530 until dark, resting for periods of up to 3 min while actively digging. Digging a nest usually takes from two to four days (based on about 25 females). Female pine snakes are most vulnerable to predators (birds, mammals, man) and heat stress when they are first excavating the opening. When the tunnel is long enough, they can rest within (Fig. 3). As mentioned above, eggs are not laid immediately. Usually females found digging nests or occupying nest chambers are noticeably gravid (Fig. 1). However, this is not always the case, and some females in nests do not appear gravid. One such female captured in a partially completed nest was branded, released, and recaptured in the nest 7 days later when she did appear gravid. She laid eggs 2 days later in the laboratory.

Moisture conditions clearly affect the digging behavior of females. In 1988, an exceptionally dry year, four of 23 nests were located under logs (1), shingles (2), or other debris (1). Additionally, two females nested under pine trees where the sand was damper. It appeared that the snakes had difficulty excavating burrows that did not collapse. In other years all nests were underground and in clearings.

*Egg-laying, Egg Position and Moisture.*—Female pine snakes dig nests prior to egg-laying, and the egg-laying period from 1977 to 1990 ranged from 17 June to 14 July. In any one year the egg-laying period was usually only about two weeks in duration (Burger and Zappalorti, unpubl. obs.).

Only 21% of clutches were in side chambers;

most were in egg chambers within the main nest tunnel. Egg chambers were oblong and were only 7 to 8 cm high. Most (81%) clutches were placed with the eggs horizontal, with no eggs on top of one another. There was an open air space above the eggs (eggs are 3–4 cm wide, $\bar{x} = 3.9 + 0.1$ cm). After 1–2 days the eggs stick together and they no longer will break apart until they are ready to hatch.

Nest temperatures were lower in nests before the eggs were laid than after, and were generally lower at the bottom rather than the top of the nest chamber (Table 1). Similarly, soil moisture was less in test holes compared to nests.

*Clutch Size and Female Size.*—Mean clutch size was 9.5 ± 0.3 (range = 4–16), and related to female SVL ($r = 0.60, P < 0.001$) and total body length ($r = 0.46, P < 0.01$; Fig. 4). Gravid females located during the study ranged in SVL from 91–143 cm ($\bar{x} = 121 \pm 1.8$ cm, N = 98). Thirty-eight percent of the nests contained more than one clutch, and 4% had four clutches. Overall 73% of the nests had old, hatched shells present.

## DISCUSSION

*Nest Construction.*—Nesting females move to the nesting areas to bask in mid-June, and begin testing the sand in mid to late June. Several spots are probed (1–6) before the female even begins to excavate. Often a test hole is excavated several cm before it is abandoned. This extensive behavioral process indicates that the females are indeed selecting nest sites, and are assessing sand quality and possibly nest and tunnel suitability. Females may also be trying to locate the exact site they used in previous years since they show nest site philopatry from year to year (Burger and Zappalorti, unpubl. obs.).

Test holes and nests are distinguishable only with respect to tunnel length, number of turns, and chamber (or tunnel) moisture. If the site is suitable and the snake completes the nest the length should be greater, and more turns would be expected. Moreover, moisture in the tunnels or chambers differed: nests had higher moisture than test holes. It is not surprising that moisture is crucial, given the importance of hydric conditions to the development of reptile eggs (Tracy et al., 1978; Packard et al., 1981, 1982; Gutzke and Packard, 1987; Thompson, 1987). Gutzke and Packard (1987) in an experimental study on *Pituophis melanoleucus sayi* showed that although the hydric environment does not affect hatching success, eggs exposed to wet or moist hydric conditions produce larger hatchlings than do eggs exposed to dry conditions. Thus maintenance of a moist environment may be a critical factor in the selection of sites and construction of burrows.

Whenever digging pine snakes encounter a particularly dense root system or a large root they shift directions or abandon the site. Many of the shifts in tunnel direction reported in Table 1 reflected the presence of roots. If the change in direction still results in dense roots they may abandon the site and move elsewhere. We suggest that this behavior may be a result of the requirement for the nests to be in the open where there can be full sun penetration to the soil surface. Large roots or a dense root system may indicate to the gravid female that there is too much shade as well as being difficult conditions for excavation. Pine snakes nesting in the New Jersey Pine Barrens are at the northern limit of their range in eastern North America, and to prevent thermal stress on eggs, females may be required to place egg chambers in full sun. In northern Utah, Parker and Brown (1980) reported *Pituophis* eggs in mammal burrows at 34 cm. Since they hatched, the conditions were suitable. However, in New Jersey no clutches were as deep as 34 cm, added evidence that thermal conditions may be critical. Female pine snakes in New Jersey can clearly dig deeper, since tunnels frequently were deeper than 30 cm even though the egg chambers averaged only 21–22 cm deep. Further, the shallowness of nests (none below 25 cm) in New Jersey is not due to an inability to dig deeper because pine snakes dig hibernacula that are below 100 cm (Burger et al., 1988).

Tunnels angled downward until they reached an average depth of 33 cm, and then angled upward for an average egg chamber depth of 21–22 cm. We believe this structure may serve to eliminate standing water in the egg chamber. Since pine snakes do not cover their nests, the hole remains open until heavy rains collapse the entrance. During this time rain water could enter the egg chamber through the opening, except that it falls to the low tunnel spot, and then filters down through the sand. Excessive standing water can kill developing embryos in some reptiles (Lutz and Dunbar-Cooper, 1984). Alternatively, females may simply be assessing soil moisture, moving higher to reach optimum conditions; or shifting burrow direction to confuse predators into assuming there are no eggs in the tunnel system.

Most nest tunnels were over 100 cm long (39–228 cm), raising the question of why snakes excavate such a long tunnel rather than simply digging down the required 15–25 cm and depositing their eggs directly. Excavating a tunnel allows them to leave a substantial air space above the eggs. It also removes the eggs (with their associated odor) a substantial distance from the opening. Perhaps eggs deposited closer to the tunnel opening are more easily detected by

FIG. 3. Pine snake in an almost completed burrow (top) and exposed pine snake nest (bottom). Note large dump pile and that only the rear end of the snake protrudes from the opening while she is digging.

mammalian predators, but we have no evidence of this. Clearly human poachers give up more easily on long tunnels, often missing a second or third clutch. With increasing length, it is easy to miss a sudden turn and lose the tunnel completely. Further, the disruption of the soil by digging females would deposit odors in the sand, and disrupting the sand directly over the nest may leave more odor than presently exists. It is also possible that the open air space above the eggs is essential for the hatching process. Pine snakes take 20–40 h to hatch once the egg shell

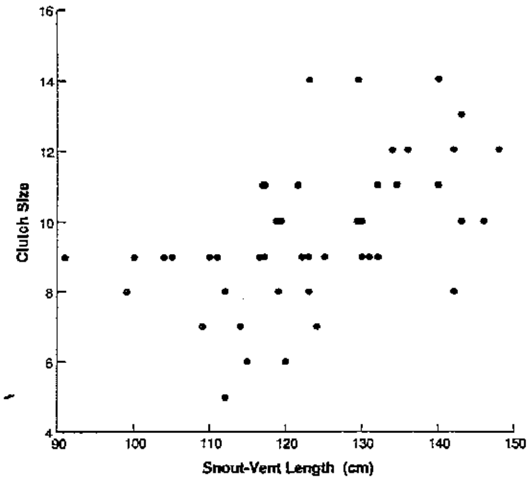

FIG. 4. Relationship of clutch size to female pine snake snout-vent length.

is slit, and during much of this time only the head emerges (pers. obs.). It may be essential for them to be in open air rather than soft sand so they can clear their lungs and begin breathing.

*Female Behavior.*—Observations of females indicated that the process of nest site selection and excavation is not as short as is usual for most reptiles. Small turtles may take 30 min to 2.5 h to excavate nests and lay eggs (Burger, 1977; Congdon et al., 1983), whereas for large sea turtles the process may take much longer (Bustard and Greenham, 1969). However, sea turtles that spend a long time on land digging either do so nocturnally, or nest in large groups or arribadas. In the former case thermal stress is reduced, and in the latter there is some protection in numbers. Lizards may be exposed for little time as they deposit eggs within logs (Cooper et al., 1983) or for a much longer period of days (Rand, 1968). Female *Iguana iguana* spend days excavating burrows that are 1–2 m in length, but they do so in groups that might provide some protection from predators (Rand, 1968).

Most species of snakes merely deposit eggs under logs, leaves, or in other tunnels and burrows (see Wright and Wright, 1957). Thus they incur only laying costs and not construction costs. Pine snakes are the only snake we know of that spends two to three days digging their own burrows, remaining near or in the nest throughout. During much of the process the female has her head and part of her body underground while leaving her posterior end out and exposed to predators (including poachers). Females usually reuse the same site from year to year (Burger and Zappalorti, unpubl. obs.). Presumably a place that was safe for the excavation phase in previous seasons may continue to be safe. Further, females surely learn the places where they can bask in partial shade during the hot part of the day.

It is unclear to us how females locate the exact nest site used in previous years, but the possibilities include odors remaining from the past, using the presence of hatchling shed skins or old egg shells, or using landmarks to determine the site. The latter seems unlikely since in 1989 two females placed nests where they had been previously (1985–1989), despite the previously pristine pine barrens site having been completely overturned by bulldozers, leaving exposed soil with no trees for 30 m around. Surely the physiognomy looked entirely different.

Another possibility explaining nest site philopatry is that females come back to the same general nesting area or clearing, and then seek appropriate digging conditions. Appropriate digging conditions might include compactness of sand, absence of roots, and adequate soil moisture (Burger and Zappalorti, 1986). This seems unlikely, because when three or four females nest in the same area, each female selected her own site rather than switching among sites. Thus, the mechanism for nest site fidelity is at present undetermined.

*Communal Nesting.*—In the New Jersey Pine Barrens pine snakes often nest communally. Trapido (1937) suggested that pine snake burrows may be used from year to year by more than one female, and Kauffeld (1957) reported finding a gravid female in a burrow already containing eggs. Nonetheless, the extent of communal nesting in pine snakes has not been recorded previously. Communal nesting has been reported for a number of reptiles including snakes (Brodie et al., 1969; Covacevich and Limpus, 1972; Parker and Brown, 1972), iguanas (Drummond and Burghardt, 1983; Wiewandt, 1983), and other lizards (Magnusson and Lima, 1984). Wright and Wright (1957) reported clutches of 7–41 for New Jersey pine snakes. However, we feel these large clutches may actually have been double or triple clutches from 2 or 3 females that nested communally. We often found clutches adjacent to one another, but they could be distinguished by differences in color (freshly laid eggs are bright white), and by the degree of adhesiveness. Eggs stick to one another and cannot be separated after 1–2 days. Snakes we captured just prior to laying had a maximum clutch size of 16 (N = 70). Thus it is likely that the very large clutches reported by Wright and Wright (1957) were from more than one female.

Communal nesting may occur because suitable sites are limiting, or because chemical cues from conspecifics serve as attractants indicating safe nesting sites (Magnusson and Lima, 1984). In iguanine lizards communal nesting may be adaptive because choosing a site already worked by others makes digging easier, allows usurpation of an already constructed hole, and may lower the risk of predation to the female or her hatchlings by nesting in synchrony with others (Wiewandt, 1983). Further, lizards are often forced to compete for limited space (soil is scarce on rocky islands; Wiewandt, 1983). Suitable sites seem not to be lacking for pine snakes in New Jersey, because they could simply dig other nests nearby. However, digging is energetically costly and time consuming, and it may be adaptive to simply parasitize the efforts of another female.

It is intriguing to ponder whether the females nesting in a communal nest are related (mother-daughter, or siblings) but we have no data concerning this point. In successive years the same females nest together in communal nests, but their initial relationship is unknown.

*Acknowledgments.*—We gratefully acknowledge D. Bertrand, J. Bockowski, W. Callaghan, J. Dowdell, R. Ford, T. Georgiadis, M. Gochfeld, Otto Heck, D. Bertrand, Z. Leszczynski, P. Mooney, G. Rocco, and P. Vargas for their continued field assistance, logistical support and helpful comments, and Z. Leszczynski for some of the photographs of the digging female. We thank M. Gochfeld, S. Sweet and anonymous reviewers for clarifying comments on the ms. Our research was partially funded by the Endangered and NonGame Species Program of the New Jersey Department of Environmental Protection, Division of Fish, Game and Wildlife, and the Charles and Johanna Busch Fund of Rutgers University. Our field research station was provided by the Ocean County Department of Emergency Services and the Ocean County Planning Board, through the courtesy of the Ocean County Board of Chosen Freeholders.

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Accepted: 4 November 1990.