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Nest Site Selection by Pine Snakes, *Pituophis melanoleucus*, in the New Jersey Pine Barrens

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We examined nest site selection by 31 female pine snakes that excavated and laid eggs at 22 nest sites in the Pine Barrens of southern New Jersey. All nests occurred in large clearings with less than 10% tree cover in pitch pine-scrub oak uplands. Nest sites differed from randomly selected points adjacent to nests with respect to vegetation cover and composition, distance to clearing edges and soil characteristics. Nests were in soft sand in open, unvegetated sections of clearings. There were few differences between solitary and communal nests except that more solitary nests were in Pennsylvania sedge than in grass in areas with greater tree cover and closer to roads.

NEST site selection in reptiles and amphibians has been studied for only a few species (Heatwole, 1977): alligators (*Alligator mississipiensis*, Garrick and Lang, 1977), salamanders (*Ambystoma opacum*; Petranka and Petranka, 1981), iguanas (*Iguana iguana*; Rand, 1968) and turtles (*Malaclemys terrapin*; Burger and Montevecchi, 1975; *Macroclemys temmincki*; Ewert, 1976; *Caretta caretta*; Stoneburner and Richardson, 1981). Descriptions of nest sites of snakes are largely cursory or based on small sample sizes. Snakes usually oviposit beneath logs, leaves, or under other debris (Wright and Wright, 1957). Most studies on snake nests report on no more than two or three oviposition sites. There are several reports of communal nests, but again they refer to only one or two sites (Cook, 1964; Brodie et al., 1969; Covacevich and Limpus, 1972; Palmer and Braswell, 1976; Swain and Smith, 1978). Most authors quantify neither the nest site nor the surrounding habitat, and none examines selection.

Pine snakes in New Jersey excavate and oviposit in nests in sandy locations in forests of pitch pine, *Pinus rigida*. Since the snakes actually excavate the nests (Moore, 1893; Zappalorti et al., 1983), they provide an excellent opportunity to determine physical and social factors that contribute to their choice of particular locations. We present data on nest site requirements of an uncommon species whose natural habitat is under intense pressures from developers.

The genus *Pituophis* is widely distributed throughout the United States (Parker and Brown, 1980). The pine snake, *Pituophis m. melanoleucus*, is largely limited to the southeastern Atlantic States (Stull, 1940). New Jersey contains a disjunct population at the northern limit of its range. Little is known of the breeding biology of pine snakes in nature. Western populations of *P. melanoleucus* have been known to oviposit communally with several other species (Brodie et al., 1969), particularly with *Masticophis taeniatus* (Parker and Brown, 1972, 1980). Published accounts of nests are limited to general descriptions of the habitat (talus slopes, grassy open areas) or nest site (cavities in talus, burrow systems) but there are no quantitative data on nest site characteristics from which one could determine factors influencing their selection of sites. Further, in all cases fewer than four oviposition sites were recorded (Parker and Brown, 1980). In no case are there data comparing the nest site choices of the snakes with the available habitat. Selection implies a choice from available habitat. Ours is the first study on snakes to examine a large number of nests of one species in a limited geographical area.

METHODS AND STUDY AREA

We studied nest site selection as part of a larger study on the ecology and behavior of pine snakes. We and our associates spent about 250 man-h searching for snake nests in Ocean, Monmouth and Burlington counties, New Jersey in June and July 1982. The study area included undeveloped areas of the Pine Barrens in these counties.

The habitat in the study area is primarily pitch pine, *Pinus rigida* and black jack oak, *Quercus marylandica*, in uplands and Atlantic white cedar, *Chamaecyparis thyoides*, in lowland bogs. We did not expect snakes to nest in all locations but we searched all areas. We searched by driving sand roads and by walking and looking under logs, trees, debris and leaves in forests. All known nesting areas were searched at least three times a week and other suitable sites were checked regularly from early May until late July. Since the snakes leave an open burrow entrance with "dump piles" of excavated sand we feel confident that we did not miss any snake nests in the areas that we searched systematically. We searched the study area before any predicted rains since heavy rain can obscure the openings.

Each nest was marked, then excavated to determine the number of snakes or clutches within the length of the tunnel and the relative location of the burrow and nest chamber(s).

Data were recorded on distance of the burrow entrance to the nearest edge of the clearing; distance of the burrow entrance to the closest road, house and hibernaculum; distance and species of the closest vegetation; percent of ground cover over the nest entrance, nest chamber and entire burrow; percent aerial cover; slope of the nest (with an inclinometer); type of sand; and sand resistance. Sand type was graded according to a scale: 0 = very hard packed sand (some humus), 1 = hard packed sand, 2 = soft packed sand and 3 = loose, or sugar sand (so loose that a car gets stuck). We measured sand resistance by dropping a surveyor's arrow (mass of 85 g) held 1 m above the ground and recording depth it penetrated from the surface. Percent vegetation cover was visually estimated in a 1 m^2 area around the nest or random point. For vegetation we recorded the most abundant plant in the 1 m^2 sample area around each nest or random point.

We also measured the maximum length and width of the clearing, the slope in the clearing and estimated the percent of tree cover in the clearing and in a 10 m radius area surrounding the clearing.

We recorded similar data at randomly selected sites located in the open clearing with nests (to test for microhabitat selection within clearings) and at forest sites in areas immediately surrounding clearings (to test for differences between clearings and surrounding habitat). We selected random sites by choosing two numbers from a random table; one to indicate direction (in degrees) and the other to indicate distance from the nest. We used the same procedure for the surrounding habitat, but used the boundary of the clearing as a reference point and selected random numbers from 0–100 m. For comparative purposes we estimated the percent ground cover, percent aerial cover and the species composition in an area immediately adjacent and parallel to the snake burrow.

Some of the snake burrows contained single clutches and some had as many as four snakes nesting in the same burrow. We recorded the number of snakes using a particular burrow and compared the characteristics of solitary burrows with communal ones.

Initially we used a multivariate analysis of variance (MANOVA) to determine whether there were significant differences among the three habitat types (nest sites vs random clearing sites and random forest sites). We used Arcsin transformations for the percentage data. After establishing that there were significant differences among types we then tested for type differences for each characteristic using Duncan's multiple range test.

We compared random points and nests with ANOVA for unequal variances using SAS (Barr et al., 1976). Where appropriate, χ^2 tests determined if there were differences in non-numeric variables (such as sand type and vegetation species) among sites. Means ± one standard deviation are given in the text.

Results

We located 22 nests containing eggs from 31 clutches. Almost half of the snakes nested communally. Sixteen snakes nested solitarily, eight nested communally in double clutches, three snakes laid communally in one nest and four laid communally in another nest.

Pine snake females excavated burrows that ranged in length from 90–305 cm (mean = 187.6 ± 75.5). The egg chambers were 14.0 ± 2.9 cm wide. The mean surface of the eggs was 15.2 ± 7.6 cm below the surface. Burrows were often straight although they curved whenever the digging female encountered large roots.

All snake nests were located in clearings (N = 22) with few trees, in recently-cleared, or in burned areas with open, exposed sand. Clearings used for nesting were 166.1 ± 58 m long by 79.2 ± 55 m wide, with slopes of less than 14°. Overall, the percent of trees in the clearings was 2.4 ± 2.6%. Areas surrounding clearings averaged 47.5 ± 20.2% tree cover.

There were significant differences among the three site types (nest sites, random sites in clearings and random sites in forests) when all environmental variables were considered together ($F = 19.0$, $df = 18{,}68$, $P < 0.0001$, MANOVA). In general, all three sites were significantly

TABLE 1. CHARACTERISTICS (MEAN ± STANDARD DEVIATION) OF PINE SNAKE NESTS, RANDOM POINTS LOCATED WITHIN THE CLEARING AND ADJACENT AREAS OUTSIDE THE CLEARINGS.

Characteristic	Nests	Random clearing[b]	Random nonclearing[c]	F	P
Percent ground cover					
Entire nest	4.7 ± 14	54.9 ± 37	84.7 ± 25	70.81	.0001
Mouth	1.5 ± 4	36.4 ± 35	82.4 ± 26	80.46	.0001
Chamber	3.9 ± 14	52.1 ± 38	79.7 ± 29	53.79	.0001
Percent of ground cover					
Trees	1.2 ± 2.4[a]	10.8 ± 18[a]	28.5 ± 27	16.15	.0001
Area	2.4 ± 3	4.1 ± 5	1.85 ± 115	44.76	.0001
Adjacent	47.5 ± 26	49.1 ± 20	45.2 ± 21	0.26	n.s.
Distance from point to (m)					
Edge	29.3 ± 22[a]	26.3 ± 21[a]	13.0 ± 6	7.24	.001
Hibernacula	46.0 ± 37	32.5 ± 21	29.2 ± 27	0.79	n.s.
Houses	73.1 ± 48	74.9 ± 53	91.0 ± 42	0.64	n.s.
Road	67.3 ± 61	56.3 ± 52	72.6 ± 60	0.46	n.s.
Spike penetration (cm)[a]	6.2 ± 0.6	4.6 ± 1.7[a]	5.2 ± 1.7[a]	8.74	.0003
Sand type[d]	2.0 ± 0	1.4 ± 0.7[a]	1.0 ± 0.6[a]	9.34	.0003

[a] If there are no significant differences among the three groups, results are listed as n.s. in probability column. For factors that varied significantly, "a" indicates the groups that were not significantly different from each other. Otherwise all three are significantly different.
[b] In the same clearing as snake nests.
[c] In the surrounding forest.
[d] χ^2 test used for this comparison.

different from each other. We then used ANOVAs and χ^2 tests to determine differences among site types for each environmental characteristic.

Ground cover averaged less than 5% over the entire nest and was less over the mouth and the egg chamber (Table 1). Nest sites had significantly less cover than random sites within clearings and forest (random non-clearing) sites had significantly more ground cover than random sites within clearings. Nests had significantly less ground cover (4.7 ± 14%) than areas immediately adjacent to them ($\bar{x}$ = 22.3 ± 25.7%; t = 3.34, df = 42, $P < 0.001$). Species composition of the ground cover, however, did not differ significantly. Nests had significantly less mean aerial cover (1.2 ± 2.4%) than areas immediately adjacent to them (4.3 ± 5.2%; t = 3.00, df = 42, $P < 0.004$). Above ground cover was least at nest sites and greatest in the forest points (Table 1).

The species composition of the dominant vegetation near nests differed significantly from that at randomly selected sites in clearings (χ^2 = 65.3, df = 20, $P < 0.0001$). Grasses and Pennsylvania sedge, *Carex pensylvanica*, were most abundant at nest sites; grasses, Pennsylvania sedge and heather (*Hudsonia* sp.) at random clearing sites; and blueberry (*Vaccinium* sp.), pitch pine and heather at forest sites (Fig. 1). Species composition did not differ between nest sites and adjacent areas. There were few trees close to the nests and random points in the clearing and more trees in the random points in the forest. Within clearings there was significantly less tree cover within 20 m of the nest; whereas in the forest there were no differences in the tree cover within 20 m of the random site and outside the 10 m radius (Table 1).

Many of the clearings used for nesting were adjacent to roads and housing developments. Sixty-eight percent of nests were 16–48 m from the edge of clearings. In general, snake nests were farther from clearing edges than random points within the clearing (Table 1).

Ten nests were within 32 m of roads, although many of these were infrequently used dirt roads. Three nests were within 100 m of heavily used paved roads. Similarly, seven nests were located near houses or hunting lodges. Although many of the buildings were abandoned or used infrequently, one snake nest was only 50 m from an occupied house.

Snake nests (73%) were often located within 64 m of a known hibernaculum located in the same clearing. Only a few (9%) of known nest sites were beyond 100 m of a hibernaculum, but this could result from our failure to locate some hibernacula.

Pine snakes always nested in soft packed sand,

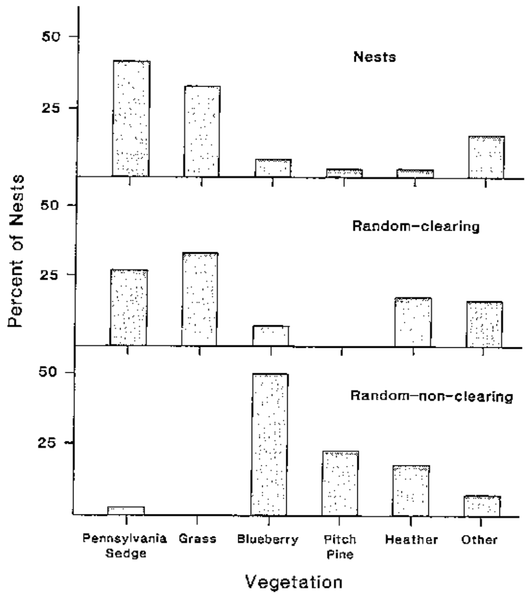

Fig. 1. Percent of nests (and random points in the clearing and non-clearing) in which the plant species shown were dominant.

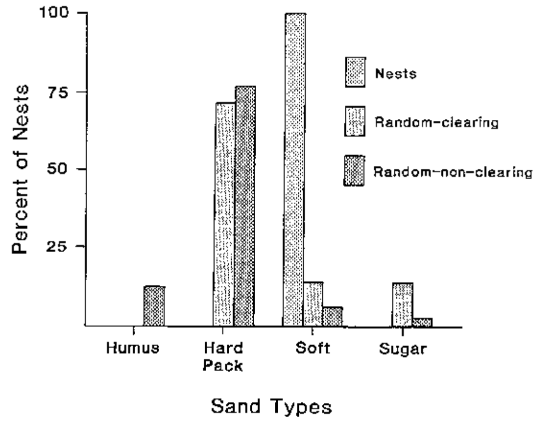

Fig. 2. Percent of nests (and random points in the clearing and non-clearing) having particular sand types.

whereas random sites within clearings consisted primarily of hard-packed sand, with fewer points in soft sand (Fig. 2). Forest random points contained some sand mixed with humus (Fig. 2). Sand penetration also differed significantly among nests and randomly selected sites (Table 1). At nest sites the spike penetrated between 5 and 7.5 cm, whereas in the random points the spike penetrated from 1.0–9 cm. Thus snakes used sand allowing a particular penetration and avoided harder or softer sand, even when in clearings.

Communal nests had significantly less aerial vegetation cover ($\bar{x} = 1.0 \pm 1.8\%$) than solitary nests ($\bar{x} = 3.6 \pm 2.6\%$, $t = 3.08$, $df = 22$, $P < 0.004$), although there were no differences in either ground cover or tree cover in adjacent areas. Most communal nests (46%) were iu grass, whereas most solitary nests were closest to Pennsylvania sedge (56%; $\chi^2 = 11.5$, $df = 5$, $P < 0.04$). Communal nests (27%) were often located near other forbs. Thus the closest vegetation to communal nests was never blueberry, heather, or pitch pine, even though 25% of solitary nests were adjacent to them. Communal and solitary nests did not differ in distance from houses or hibernacula, although solitary nests were significantly closer to roads ($\bar{x} = 37.5 \pm 57$ m) than were communal nests ($\bar{x} = 94.7 \pm 58$ m; $t = 2.59$, $df = 22$, $P < 0.01$).

Only one of the 22 nests sites was destroyed, presumably by a mammalian predator that dug up the eggs. Snakes hatched and emerged from all other nests.

Discussion

Nest site selection may function to reduce predation or exposure to severe weather. Thus, nest site selection often involves choosing sites that are cryptic (Tinbergen et al., 1967; Joern and Jackson, 1981) or are protected from wind (Becker and Erdelen, 1982), storm tides, flooding (Bergman et al., 1970; Bongiorno, 1970) and sun and heat stress (Walsburg, 1983). Also important are social factors such as avoidance of nest parasitism (Gochfeld, 1979), avoidance of theft of nest material (Burger, 1979) and presence of group benefits such as antipredator behavior (Burger, 1981).

In reptiles, nest site selection may reflect wind avoidance (as in sea turtles, Bustard and Greenham, 1969), the need for soft substrate for digging (Burger and Montevecchi, 1975; Garrick and Lang, 1977), antipredator considerations (Burger and Montevecchi, 1975), or beneficial temperature relationships (Burger, 1976; Stoneburner and Richardson, 1981). These relationships have not been examined in snakes. Indeed, it has not been shown whether snakes select nest sites or nest randomly in appropriate habitats. Recently Porter and Tracy (1983) pointed out the importance of the interaction of nest site selection, potential nest environments viviparity and delayed oviposition.

In our study, pine snakes selected nest sites in open clearings with less than 5% tree cover. Specific nest sites had less ground cover and aerial cover, were farther from the edge of the clearing and had softer sand than randomly selected points inside and outside of clearings. There were few differences between solitary and communal nests. Choice of nest sites seemed to relate primarily to digging conditions and site temperature.

By selecting nest sites in open clearings with little vegetation cover snakes avoid obstacles to digging. That root obstructions were important was indicated by changes in burrow direction for above-ground vegetation. Nonetheless, females usually avoided nest sites with no ground cover, suggesting that plant roots stabilize the burrow roof. Some burrows made sharp turns (sometimes almost 150°) when roots were encountered.

We never found nests in humus (type 0). Penetration in sand with humus was low (<4 cm); presumably it would be difficult for snakes as well. Similarly, snakes avoided packed sand (type 1) with penetrations below 5 cm. Indeed, choice of sand for burrowing was rather narrow; snakes selected soft sand ranging from 5–7.5 cm sand penetration. They did not nest in loose sand with penetrations over 7.5 cm. Although such sand would be easy to penetrate, it could collapse on the digging snake and eggs. Hatchlings may have difficulty escaping from soil substrates susceptible to collapse or with dense root structures. The sand used for nest sites was moist below about 15 cm and moisture may be another critical nest site characteristic.

Females selected nest sites that maximized exposure to the sun. Placement below the soil surface presumably buffers extremes in environmental temperature and moisture. Parker and Brown (1972) similarly reported one *Pituophis* nest on an open grassy slope facing SE and Brodie et al. (1969) reported sites on open, SE-facing talus slopes.

Snake nests were farther from clearing edges than expected from random points. This may reflect avoidance of edges where vegetation cover was more dense. The snakes were not avoiding edges because of the presence of roads or houses since the snakes nesting in solitary nests dug close to them. Further, there were no significant differences between the nests and random points with respect to the distances to houses and roads.

Communal nests had significantly less aerial cover, were more often located in grass rather than Pennsylvania sedge and were farther from roads than solitary nests. Either such nests were preferred because they offer ideal physical conditions for incubation, or their use avoided the cost of burrowing (e.g., energetic expenditures, exposure to predators). Presumably predators such as large hawks or foxes could prey on a digging female. Humans prey on digging females, collecting them for private collections or for sale. Historically Indians may have used them for food or ritual purposes.

The differences between solitary and communal nests relate directly to potential temperature relationships: less above ground cover would provide less shading. Grass might be selected over sedge because it has fewer, weaker roots than sedge. Both species are the same height above ground and equally dense. Nesting farther from the road may be preferred for communal nests because it decreases disturbance to the snake during burrow excavation. Although cars did not seem to disturb snakes, the presence of people often resulted in cessation of digging and departure of the female. The use of an already-excavated burrow may reflect the parasitism of another snake's labors as well as the choice of optimal burrow conditions. Further, if females home to their place of hatching then females that lay in the same burrow are related.

Pine snake nests were located in clearings, or along road or railroad beds. Clearings used by snakes were usually man-made. Only 1 of 20 clearings selected by nesting females appeared to be natural and created by fire. The man-made clearings seem to be crucial to the nesting ecology of *Pituophis* and indeed may have improved nesting habitat for the snakes. Although such clearings do not appear to be typical of the pine barren localities they may be essential for successful pine snake reproduction. Possibly clearings created by natural fires or by Indian burns (Russell, 1981) also improved habitat for pine snake nesting.

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