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MOVEMENT PATTERNS AND HABITAT SELECTION BY NATIVE AND REPATRIATED LOUISIANA PINE SNAKES (*PITUOPHIS RUTHVENI*): IMPLICATIONS FOR CONSERVATION

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Abstract. The Louisiana pine snake, *Pituophis ruthveni*, is an uncommon and poorly known snake that currently lacks federal protection. To learn more about the natural history of *P. ruthveni*, ten adults and one juvenile were studied by radiotelemetry during 1995–97 in north-central Louisiana. In addition, one adult and seven juvenile captive-bred individuals of *P. ruthveni* were released on the study site and studied by radiotelemetry during 1996–97. All snakes were usually present in mammal burrows year-round and were most frequently observed above-ground during late morning and mid-afternoon and during spring and fall. Native snakes moved longer distances and occupied larger home ranges than did repatriated snakes. Native snakes preferred the interiors of pine forests and pine plantations and repatriated snakes preferred the edges of pine plantations. Native and repatriated snakes frequented areas with an abundance of pocket gopher (*Geomys breviceps*) mounds, few trees, and an open canopy. *Pituophis ruthveni* depends on pocket gophers directly (as a source of food) and indirectly (by using pocket gopher burrows for shelter). Therefore, habitat selection by snakes appears to be largely determined by the distribution of pocket gophers. Based on short term survival rates, the results of this study indicate that repatriation may be used to restock natural populations of *P. ruthveni*. However, the long-term survival of *P. ruthveni* will ultimately depend on the maintenance of an understory of herbaceous vegetation that supports pocket gophers (as a food source) and, in turn, pine snakes.

Key Words. *Pituophis ruthveni*; Movement patterns; Habitat selection; Conservation; Telemetry; Repatriation.

The genus *Pituophis* (Serpentes: Colubridae) contains three species in the United States: *P. catenifer*, *P. melanoleucus*, and *P. ruthveni* (Collins 1997). The Louisiana pine snake, *P. ruthveni*, was recently elevated to specific status (Reichling 1995) and is endemic to northern and western Louisiana and eastern Texas (Conant and Collins 1991; Reichling 1995; Thomas et al. 1976). Few data have been collected on the natural history of *P. ruthveni* since its original description (Stull 1929). The paucity of data on *P. ruthveni* is due to the snake's limited distribution (Reichling 1995; Thomas et al. 1976), low population density

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(Jennings and Fritts 1983; Reichling 1989), and secretive nature (Reichling 1988*a*).

Today, *P. ruthveni* is confined to three disjunct areas: north-central Louisiana, west-central Louisiana, and east-central Texas. Clearcut logging of the original pine forest in the western Gulf Coastal Plain during the 1920s (Boyer 1980; Conant 1956) coincided with considerably fewer sightings of *P. ruthveni* according to Fitch (1949), who suggested that logging negatively affected populations of *P. ruthveni*. Logging practices, as well as suppression of the historic fire regime, continue to threaten the long-term survival of *P. ruthveni* (Reichling 1989; Rudolph and Burgdorf 1997; J. Himes, pers. obs. 1996, 1997).

Pituophis ruthveni is not legally protected by the state of Louisiana. Although populations of this species in the Angelina, Kisatchie, and Sabine National Forests receive protection, many records of *P. ruthveni* today are from privately owned sites in Louisiana (Reichling 1988*a*). Thus, the continued survival of this species in the wild is questionable. A better understanding of the natural history (e.g., habitat and spatial requirements) of *P. ruthveni* will help biologists plan conservation strategies for dwindling natural populations of this species.

Most conservation strategies involve habitat management and therefore affect the populations of those species occupying the managed habitat. Although habitat management may be important for conservation of some species, additional strategies may be needed to conserve species such as *P. ruthveni*, which occur at low population densities or are locally extirpated (Dodd 1987, 1993). One additional strategy is to restock captive-bred individuals into their original natural populations.

Release of captive-bred snakes into the wild is a rare practice and results are inconclusive (Dodd and Seigel 1991; Speake et al. 1987). Release of captive-bred indigo snakes (*Drymarchon corais*) in 18 areas by Speake et al. (1987) resulted in the successful reestablishment of only two populations. However, the origin of some released snakes was unknown and thus the genetic composition of the reestablished populations was possibly altered.

A captive breeding colony of *P. ruthveni* was established at the Memphis Zoo and Aquarium (MZA) in 1987 (Reichling 1988*b*, 1993) with two snakes from the same gene pool of *P. ruthveni* that we studied during 1995–97 (S. Reichling, pers. comm. 1995). In 1996, the MZA donated nine individuals of *P. ruthveni* from this colony to us for release within the parental population currently under study. These snakes comprised three litters born in consecutive years (1994: one snake; 1995: four; 1996: four) and each litter was produced from the same two snakes used to establish the breeding colony.

We studied movement patterns and habitat selection of naturally occurring and captive-bred individuals of *P. ruthveni* that were released on the study area during May 1996–December 1997. To determine the feasibility of restocking for conserving natural populations of *P. ruthveni*, data were compared between naturally occurring and captive-bred snakes. If naturally occurring and captive-bred pine snakes in the same area exhibit similar natural histories, it is possible that captive-bred snakes will reproduce among themselves and with naturally occurring pine snakes, thus increasing the population size, total reproductive capacity, and the diversification of the local gene pool.

MATERIALS AND METHODS

Study Site

The approximately 5000 ha study site, located in Bienville Parish, Louisiana, consists of low sandy hills divided by ravines. The soil is clayey at the bottom of the ravines, where temporary creeks form during rainy weather. The only permanent creek has been dammed to form a 3000 ha lake that borders the study site to the north and west. Pine forest (with an understory that contains considerable herbaceous vegetation dominated by grasses and a diversity of forbs) is the dominant plant formation on the hills and oak forest is dominant surrounding the creek bottoms. Portions of the native forest have been clearcut and subsequently planted in young pines (2–3 m height in 1996). Two transmission line easements that pass through the study site are periodically mowed and are dominated by herbaceous vegetation.

Snake Collection

Fifteen snake traps were set at the study site during 1995–96. Traps were constructed of plywood and hardware cloth (6 mm mesh) that formed boxes (1.3 x 1.3 x 0.3 m) with a funnel entrance on each side. Hardware cloth drift fences (height = 0.5 m) extended 16 m from each funnel entrance, thereby enhancing trapping success. Fresh water was available in each trap. During the months of

March–October, all traps were checked and the water was replaced twice weekly.

Pine snakes were captured in the traps during 1995 ($n = 6$; one adult female, five adult males) and 1996 ($n = 2$; one juvenile female, one adult female). Four additional pine snakes (two adult females in 1995, one adult female in 1996, one adult male in 1997) were captured by hand 5 km west of the study site. In November 1996, the MZA donated nine individuals of *P. ruthveni* (six juvenile females, two juvenile males, one adult male) from its captive breeding colony to be released on the study site. Prior to shipping from Memphis, these snakes were inspected by an accredited veterinarian from the American Association of Zoo Veterinarians and were determined to show no signs of disease.

Snakes that were captured in traps or by hand and returned to their natural population were termed naturally occurring (NAT). Snakes born in captivity from parents captured from the natural population and obtained from the MZA for release into the natural population were termed captive-bred (CAP). Specific identification numbers were assigned to each snake, and sex, length, and mass were recorded of all snakes immediately before and after the study (see Table 1 in Himes et al. 2002).

Experimental Protocol and Radio Implantation

Pine snakes were surgically implanted with radiotransmitters. When not in surgery, one or two snakes were housed in fiberglass and plastic cages (56 x 30 x 23 cm) at 20–25°C, with an approximate 12 h:12 h light:dark photoperiod. Additional heat was supplied by lamps and heating pads. Fresh water was available *ad libitum* and freshly killed mice were offered as food once a day. Cages were washed with soap and rinsed clean every other day and were covered with paper to minimize disturbance.

NAT snakes and four of the five largest CAP snakes were implanted with transmitters within a week of capture or receipt (the other large CAP snake died in surgery). The four smallest CAP snakes were maintained in captivity for approximately 6 mo before implantation to enable them to increase in size and avoid exceeding a transmitter mass/initial snake mass value of 0.060 (see Table 1 in Himes et al. 2002), making implantation easier and minimizing inhibition of locomotory performance.

Snakes were implanted intraperitoneally with SI-2T transmitters (dimensions 44 x 10 mm, weight 12 g; Holohil Systems Ltd., Carp, Ontario, Canada), each of which was equipped with a 20-cm whip antenna (see Reinert and Cundall [1982] for description of implantation procedure). The native juvenile snake was similarly implanted with a 2.5-g transmitter (constructed by P. Blackburn, Stephen F. Austin University, Nacogdoches, Texas, USA, and not commercially available; projected battery life of 6 mo at expected operational temperatures). Anesthesia was achieved by inhalation of halothane (Ayerst Labs, Inc., New York, USA).

Snakes were allowed a 2-d recovery period before release on the study site. NAT snakes captured on the study site were released at their points of capture. NAT snakes captured off the study site and CAP snakes were individually released on the study site (≥ 100 m from the nearest NAT snake) at habitat edges to test habitat choice by the snakes. At the midpoint of the study in August 1996, radio-carrying snakes were refitted with new transmitters. At the end of the study in December 1997, radio-carrying snakes were retrieved and radios were removed. After radio replacement/removal and a 5-d recovery period, snakes were returned to their points of capture.

Radiotracking

Each radio emitted a frequency-specific, pulsing signal of 150–151.999 Mhz, detectable at distances up to 1–2 km. The signal was detected by a three-element Yagi antenna and an R2100 receiver (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA).

Radiotracking took place from May 1995–December 1997. Snakes were located once a week during the winter, two–five times a week (different days) during the spring and fall, and four–seven times a week during the summer. During the summer and fall of 1996 and the fall of 1997, snakes were located twice a day, except during one week in the fall of 1997, when snakes were located three times a day. Consecutive trackings of individual snakes took place > 5 h apart. Snakes were occasionally tracked at night. To prevent equipment damage, tracking did not take place during rain.

Data Collection

The site of located snakes was flagged and coordinates were recorded with a Global Positioning System (Trimble Navigation Limited, Sunnyvale, California, USA). Snake position was recorded as in a stump, under debris, in the open,or in a mammal burrow. Habitat data were collected in an 11.2 m radius (area = 0.04 ha) from each snake location (= NAT and CAP plots for naturally occurring and captive-bred snakes, respectively) and 100 random locations (= RAN plots), as selected from 15-min series topographical maps (U.S. Geological Survey, Denver, Colorado, USA). RAN plots were considered to contain the expected habitat. These plots provided the control by which the null hypothesis (snakes did not select a specific habitat type) was tested. If there was a significant difference between the frequencies of habitat types in which snake plots (NAT or CAP) and RAN plots were located, then snakes were considered to be selecting a specific habitat. When a snake was tracked to a site < 5 m from its last location, new habitat data were not collected. Habitat data were usually collected immediately after locating the snake. However, when a snake was located in the open, habitat data were collected the following day to minimize disturbance of the snake.

All live trees ≥ 25 cm in diameter at breast height (DBH) on habitat plots were counted. All logs (≥ 10 cm diameter) on a plot were counted and categorized as pine vs. hardwood, hollow vs. nonhollow, and freshly decayed (most of log surface covered with bark) vs. highly decayed (< 50% of log covered with bark). A one-factor metric prism (General Supply Corp., Jackson, Mississippi, USA) was used to determine the basal area of canopy and midstory trees. Canopy closure percentage was determined from a cardboard sighting tube (James and Sugart 1970). Understory cover (foliage, branches, leaf litter) was estimated visually. The number of pocket gopher mounds, open mammal burrows, and stems (trees < 25 cm DBH) was counted. The habitat type (pine forest, pine-hardwood forest, hardwood-pine forest, hardwood forest, pine plantation, grassland, or clearcut) of each plot was determined and the distances to different habitat types within 200 m of a plot were measured.

Replicated soil samples ($n = 4$) were individually taken with a soil auger under all the pine species on the study site (shortleaf—*Pinus echinata*; slash—*P. elliottii*; longleaf—*P. palustris*; loblolly—*P. taeda*) and a hardwood (sycamore—*Platanus occidentalis*) and tested for pH following EPA Test Methods (SW-846, Method 9045C [Soil and Waste pH]). Particle composition of the soil samples was determined with a soil texture test (LaMotte Chemical Products Co., Chestertown, Maryland, USA). A soil mineral particle density triangle was used to determine the classification of each soil sample based on sand:silt:clay ratio (Buckman and Brady 1969).

Data Analysis

GPS coordinates were entered into the program Calhome (J. Kie, 1994, MS-DOS Version 1.0, Fresno, California, unpublished) to calculate the distance between snake locations on consecutive days and the home range size by year for each individual with at least ten consecutive day locations (distances between nonconsecutive day locations were not calculated because movement was unknown for intervening days). Home ranges were individually enclosed with a 100% minimum convex polygon. The area (ha) of a polygon represented the size of the enclosed home range.

Comparisons of data for individual snakes were made using a Chi-square (χ^2) goodness of fit, with $P < 0.05$ (for purposes of brevity and simplicity; however, pooled data on NAT and on CAP snakes are illustrated on graphs). Yates correction for continuity was applied to χ^2 calculations when $df = 1$. To prevent pseudoreplication, significant differences between NAT (or CAP) snake plot data and the corresponding RAN plot data were only indicated when individual data for all NAT (or CAP) snakes significantly differed from RAN plot data. To prevent biased habitat analyses due to radically uneven sample sizes, a minimum of ten plots for an individual snake was required for analysis of that snake's habitat data.

RESULTS

The entire study consisted of 2063 observations on 720 habitat plots (new habitat data were not collected during the 1343 observations on snakes that had moved < 5 m since the immediately preceding observation on each respective snake). A total of 1358 and 705 observations were made on NAT and CAP snakes, respectively, resulting in 535 and 185 habitat plots. Movements and home range sizes were calculated for the six NAT and three CAP snakes that were tracked for at least ten days. Habitat data were analyzed for the 519 and 179 plots from the nine NAT and six CAP snakes, respectively, that each contributed at least ten plots.

Movement Patterns

Within all seasons, NAT and CAP snakes were found most frequently in mammal burrows, mostly

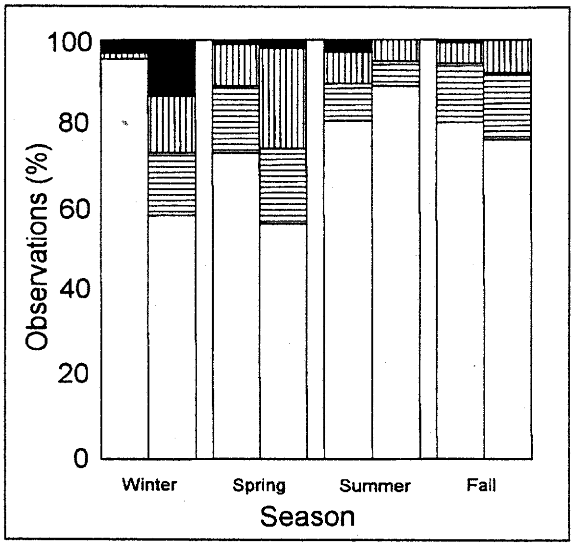

Figure 1. Frequency of positions of naturally occurring (NAT; *n* = 1358) and captive-bred (CAP; *n* = 705) pine snakes by season. Positions are in a hollow stump or log (black bars), under debris (leaves, pine needles, branches, or log; vertical bars), in the open (horizontal bars), and in mammal burrows (open bars).

of pocket gophers (where, for all seasons combined, an average of 74 and 70%, respectively, of all observations of snakes occurred; Fig. 1). NAT snakes were observed in the open (and presumably were active) most frequently from March–May (when 13% of observations were of snakes in the open) and September–November (17%; Fig. 2A), and from 1000–1100 h (19%) and 1400–1600 h (16%; Fig. 2B). NAT snakes were not observed in the open (and presumably were inactive) from December–February (Fig. 2A), and from 0100–0600 h and 1900–2300 h. CAP snakes were observed in the open most frequently from March–April (28%) and November–December (23.5%), and from 0900–1200 h (19%) and 1400–1500 h (15.5%; Fig. 2B). CAP snakes were observed in the open least frequently during February (7%) and from June–August (7%; Fig. 2A), and were not observed in the open from 0100–0600 h and 2000–2300 h.

NAT snakes moved significantly greater distances on consecutive days ($P < 0.05$) and maintained significantly larger home ranges ($P < 0.05$) than did CAP snakes: mean (± 1 SE; range and sample size in parentheses) distances moved (m) on consecutive days were 118.0 ± 20.9 (1.6–1158.6, *n* = 9) and 33.7 ± 7.7 (1.9–414.9, *n* = 3) for NAT and CAP snakes, respectively, and mean (± 1 SE; range and sample size in parentheses) home range sizes (ha) were 33.2 ± 11.1 (6.5–107.6, *n* = 9) and 5.1 ± 2.3 (2.4–9.7, *n* = 3) for NAT and CAP snakes, respectively (Table 1).

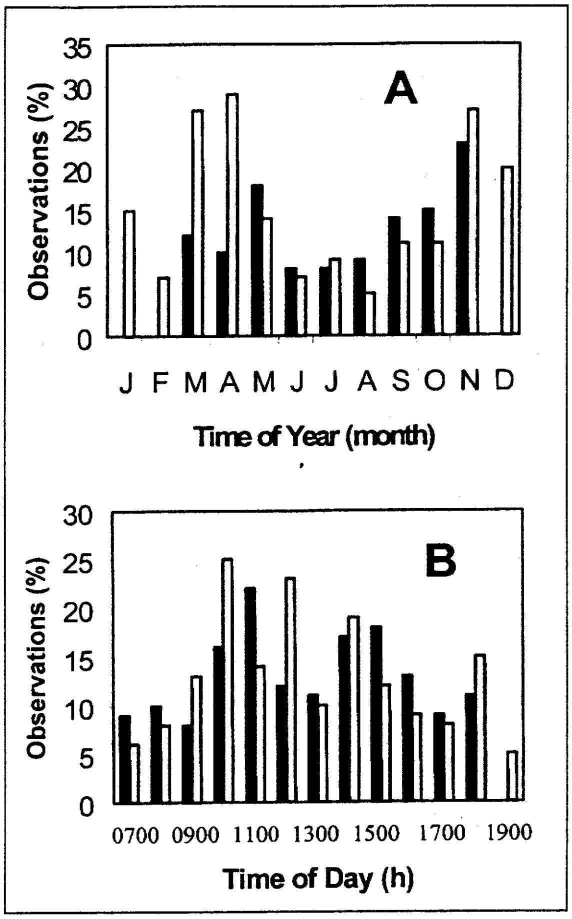

Figure 2. Frequency of NAT (*n* = 173, closed bars) and CAP (*n* = 93, open bars) snakes located in the open by month (A) and hour (B). Hours during which no snakes were located in the open (0100–0600 h and 2000–2300 h) are not shown.

Macrohabitat

NAT snake plots were more frequent in pine forests (where 56% of all NAT snake plots were located) than expected (RAN plots; Fig. 3). NAT and CAP snake plots were more frequent in pine plantations (23 and 38%, respectively) and grasslands (6 and 5%, respectively), and were less frequent in pine-hardwood, hardwood-pine, and hardwood forests (5 and 13%, respectively, for all three habitats combined) than expected ($P < 0.05$ [hardwood forests]; RAN plots; Fig. 3). Of the six CAP snakes with a minimum of five expected locations per habitat, one individual each was found signifi-

TABLE 1. Mean (± 1 SE; range and sample size in parentheses) distance (in m) per move and home range size (in ha) for individuals of *Pituophis ruthveni* tracked for at least ten consecutive days (includes data from nine of 19 snakes in the study; a minimum of ten consecutive days per snake was required for statistical analysis). Snakes originated from natural populations (NAT) or were captive-bred (CAP).

Snake ID No.	Origin	Mean Distance per Move		Home Range Size	
		1996	1997	1996	1997
11	NAT	36.4 ± 10.0 (1.6–282.1, $n = 39$)	96.7 ± 16.9 (3.8–434.1, $n = 44$)	7.5	9.3
15	NAT	219.9 ± 32.4 (4.4–1158.6, $n = 58$)	–	107.6	–
18	NAT	108.1 ± 21.2 (3.3–768.5, $n = 54$)	107.2 ± 17.9 (3.2–1018.1, $n = 74$)	22.6	43.8
25	NAT	–	40.1 ± 5.7 (3.5–145.0, $n = 48$)	–	6.5
30	NAT	111.6 ± 23.1 (3.2–379.1, $n = 23$)	138.9 ± 14.4 (4.7–439.0, $n = 80$)	17.0	22.3
33	NAT	–	203.5 ± 43.4 (7.1–677.4, $n = 24$)	–	61.8
34	CAP	–	30.6 ± 2.2 (1.9–102.0, $n = 61$)	–	3.2
35	CAP	–	22.1 ± 3.3 (3.2–54.6, $n = 46$)	–	2.4
36	CAP	–	48.4 ± 13.9 (3.7–414.9, $n = 33$)	–	9.7
mean	NAT	118.0 ± 20.9* (1.6–1158.6, $n = 9$)	33.2 ± 11.1** (6.5–107.6, $n = 9$)		
mean	CAP	33.7 ± 7.7* (1.9–414.9, $n = 3$)	5.1 ± 2.3** (2.4–9.7, $n = 3$)		

*Means are significantly different ($t = 2.24$, $df = 10$, $P < 0.05$)
**Means are significantly different ($t = 2.47$, $df = 10$, $P < 0.05$)

cantly more often ($P < 0.05$) in a forest, pine plantation, and clearcut (Table 2). Of the remaining three CAP snakes, one individual each was found relatively more often ($P \geq 0.05$) in a forest, grassland, and clearcut (Table 2).

NAT snake plots were > 200 m from the nearest habitat edge more frequently (51%) than expected, whereas CAP snake plots were ≤ 100 m more frequently (56 and 28% at distances of ≤ 50 and 50–100 m, respectively) and > 200 m from the nearest habitat edge less frequently (7%)than expected (RAN plots; Fig. 4A). NAT and CAP snake plots were nearer forests more frequently (55 and 52%, respectively) than expected and the former and latter plots were respectively nearer clearcuts and pine plantations less frequently (19.5 and 6%, respectively) than expected (RAN plots; Fig. 4B).

Microhabitat

Most NAT and CAP snake plots (80 and 88%, respectively) contained relatively few (< 10) trees as expected (RAN plots; Fig. 5A). Moreover, nearly 50% of all CAP snake plots lacked trees (Fig. 5A). NAT snake points (point = center of NAT snake plot where snake was located) were more frequently nearer loblolly pines (40%) than expected, and nearer longleaf (12%) and slash pines (33%) as expected (center of RAN plot; Fig. 5B). CAP snake points were more frequently nearer longleaf (23%) and slash pines (46%) than expected (center of

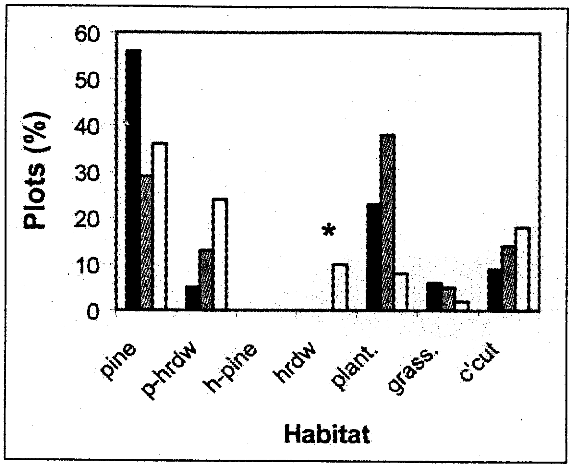

Figure 3. Habitats where NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots (radius = 11.2 m) were located compared to available habitats (random plots [RAN]; n = 100, open bars). Abbreviations used are pine (pine forest), p-hrdw (pine-hardwood forest), h-pine (hardwood-pine forest), hrdw (hardwood forest), plant. (pine plantation), grass. (grassland), and c'cut (clearcut). Above the bars (hrdw only), significant differences (at $P < 0.05$) compared to random plots are labeled using asterisks (*).

RAN plot; Fig. 5B). NAT and CAP snake points each were more and less frequently nearer shortleaf pines (9 and 7%, respectively) and hardwoods (5 and 8%, respectively), respectively, than expected (center of RAN plot; Fig. 5B).

NAT and CAP snake plots contained fewer canopy hardwoods (mean number of trees ± 95% CI on NAT and CAP snake plots, respectively, 0.22 ± 0.09, range = 0–8.5, n = 519; 0.49 ± 0.24, 0–5.0, n = 179) than expected (RAN plots; Fig. 5C). NAT and CAP snake plots also contained fewer midstory hardwoods (mean number of trees ± 95% CI on NAT and CAP snake plots, respectively, 0.32 ± 0.25, 0–14.5, n = 519; 0.37 ± 0.14, 0–6.0, n = 179) than expected (RAN plots; Fig. 5C). NAT snake plots contained more canopy pines than did CAP snake plots (mean number of trees ± 95% CI on NAT and CAP snake plots, respectively, 8.9 ± 0.95, 0–34.0, n = 519; 6.4 ± 0.99, 0–36.0, n = 179; Fig. 5C).

NAT and CAP snake plots contained the expected (RAN plots) number of logs and thus there were no significant differences ($P \geq 0.05$) in the number of logs on NAT and CAP snake plots and on RAN plots. Most NAT and CAP snake plots (58 and 59%, respectively) contained less than four logs and few plots (23 and 22%, respectively) contained more than five logs). NAT snake plots contained a higher percent of pine logs (82.5%) than expected (RAN plots; Fig. 6). NAT and CAP snake plots contained a high percent of highly decayed logs (81 and 76%, respectively) and a low percent of hollow logs (14 and 24%, respectively) as expected (RAN plots; Fig. 6). NAT and CAP snake plots contained the expected (RAN plots) percent of foliage (25 and 26%, respectively) and branches (8 and 9%, respectively), and less leaf litter (58 and 55%, respectively), canopy closure (25 and 17%, respectively; Fig. 7), and number of stems (3 and 5%, respectively) than expected (RAN plots; Fig. 8A).

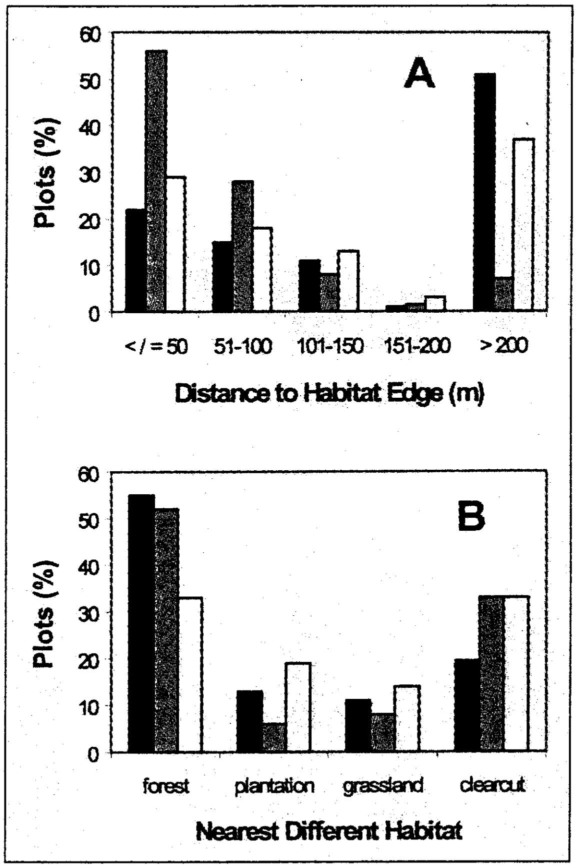

Figure 4. (A) Proximity of NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots to nearest habitat edge compared to RAN plots (n = 100, open bars). (B) Nearest different habitat (≤ 200 m; all forest types grouped together) to NAT (n = 265, black bars) and CAP (n = 172, grey bars) snake plots compared to RAN plots (n = 100, open bars). Abbreviation used is plantation (pine plantation).

Pocket Gopher Mounds and Open Mammal Burrows

NAT and CAP snake plots contained more pocket gopher mounds (mean number of mounds ± 95% CI on NAT and CAP snake plots, respectively, 31 ±

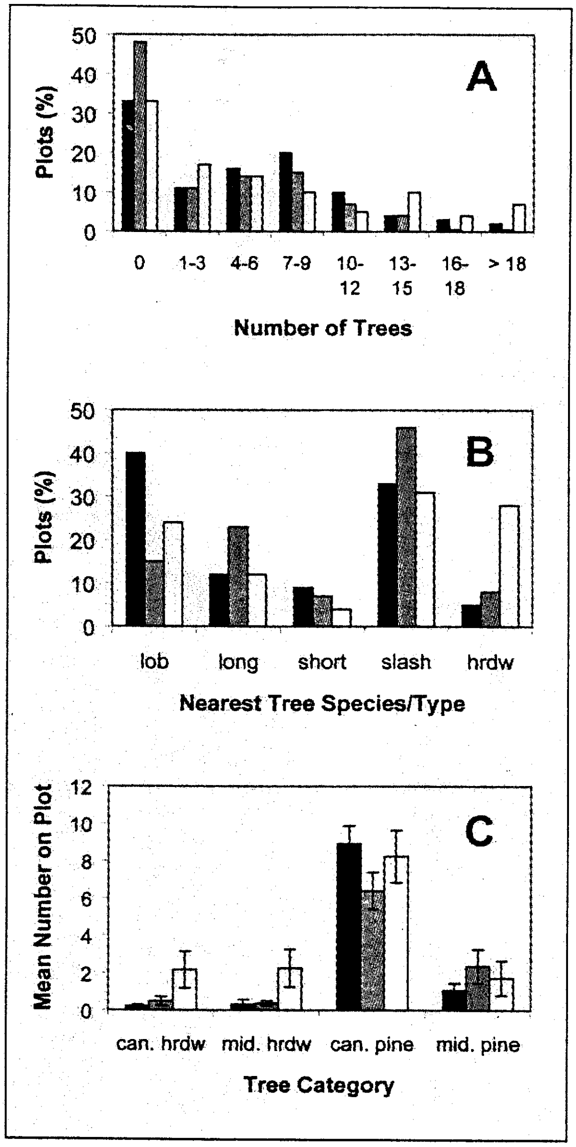

Figure 5. (A) Mean number of trees on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots compared to RAN plots (*n* = 100, open bars). (B) Nearest tree species/type (≤ 15 m; all non-pines grouped together) to NAT (*n* = 349, black bars) and CAP (*n* = 92, grey bars) snake points compared to random points (*n* = 67, open bars). Points represent the center of plots. Abbreviations used are lob (loblolly pine), long (longleaf pine), short (shortleaf pine), and slash (slash pine). (C) Number of trees (by size class and type) on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots compared to RAN plots (*n* = 100, CI = 0.95, open bars). Abbreviations used are can. hrdw (canopy hardwood), mid. hrdw (midstory hardwood), can. pine (canopy pine), and mid. pine (midstory pine). Canopy trees have a DBH (diameter at breast height) ≥ 25 cm, and midstory trees have a DBH < 25 cm.

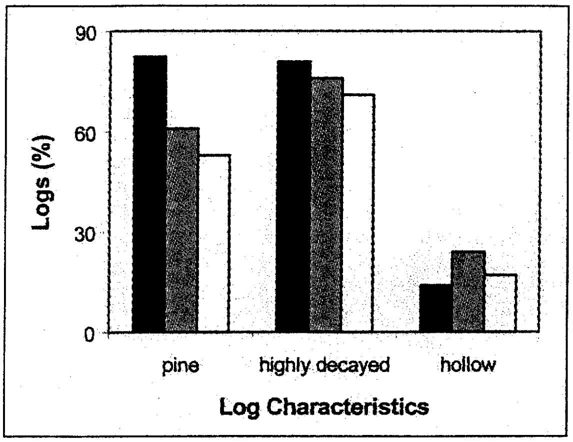

Figure 6. Characteristics of logs on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots compared to RAN plots (*n* = 100, open bars). Abbreviation used is highly decayed (< 50% of bark remaining on log).

2.5, range = 0–211, *n* = 519; 27 ± 4.2, 0–104, *n* = 179) than expected, but few open mammal burrows (mean number of burrows ± 95% CI on NAT and CAP snake plots, respectively, 3 ± 0.1, 0–24, *n* = 519; 4 ± 0.1, 0–23, *n* = 179) as expected (RAN plots; Fig. 8A). Pocket gopher mounds were less frequently located on NAT and CAP snake plots in clearcuts (3 and 1%, respectively, of plots containing mounds) than expected (RAN plots; Fig. 8B). Mounds were more frequent on CAP snake plots in pine plantations (45%) and less frequently in pine forests (35%) than expected (RAN plots; Fig. 8B). Mounds were more frequent than expected on NAT and CAP snake plots where the most abundant trees were loblolly

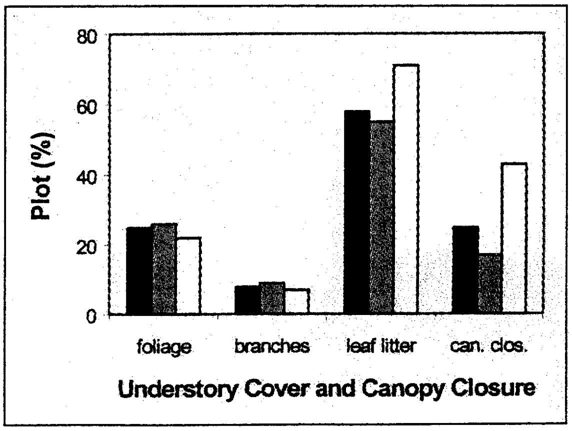

Figure 7. Understory cover percents on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots and canopy closure percent over the center of NAT and CAP snake plots compared to RAN plots (*n* = 100, open bars). Abbreviation used is can. clos. (canopy closure).

TABLE 2. Habitat selection of captive-bred individuals of *Pituophis ruthveni* after release at study area. All snakes were individually released at one point at the edge of the specified habitats. After Release locations were recorded the day after release (when snakes were first radiotracked) and thereafter. All forests are pine-dominated. An asterisk (*) indicates habitats in which snakes are found significantly more often ($P < 0.05$) than in other habitats. All locations for each snake are ≥ 5 m from the immediately preceding location for each respective snake. A minimum of five expected locations in all habitats that were present (as edges) at each snake's point of release was required for statistical analysis. A Chi-square (χ^2) goodness of fit tested the null hypothesis that snakes are to be expected in each habitat with equal frequency. See Fig. 3 for mean percent of snake locations by habitat.

Snake ID No.	Habitat		*df*	χ^2
	Point of Release	After Release (% of snake locations)		
34	forest, grassland, pine plantation	forest (14%), grassland (0%), pine plantation (86%)	2	79.71*
35	clearcut, forest	clearcut (2%), forest (98%)	1	40.20*
36	clearcut, forest, grassland	clearcut (70%), forest (30%), grassland (0%)	2	27.62*
37	forest, pine plantation	forest (41%), grassland (6%), pine plantation (53%)	1	0.24
38	clearcut, forest	clearcut (0%), forest (100%)	–	–
39	clearcut, forest, grassland	clearcut (0%), forest (80%), grassland (20%)	–	–
40	forest, grassland, pine plantation	forest (57%), grassland (14%), pine plantation (29%)	2	2.00
42	clearcut, forest, grassland	clearcut (11%), forest (22%), grassland (67%)	2	4.67

(37 and 34%, respectively, of plots containing mounds and trees) and shortleaf pine (7 and 3%, respectively), and less frequent than expected where slash pines were most abundant (47 and 33%, respectively; RAN plots; Fig. 8C). Mounds were also less frequent than expected on NAT snake plots where the most abundant trees were longleaf pine (8%) and hardwoods (1%; RAN plots; Fig. 8C).

Soil

Although not significant, more sand than silt and clay particles were present in the soil samples under loblolly pine (sand:silt:clay = 7.0:1.7:1.3; $df = 3$, $\chi^2 = 6.07$, $P \geq 0.05$) and under longleaf, shortleaf, and slash pines (7.0:2.3:0.7; $df = 3$, $\chi^2 = 6.43$, $P \geq 0.05$). Relatively fewer sand and clay particles and relatively more silt particles were present in the soil samples under sycamore (sand:silt:clay = 4.7:5.0:0.3) than in the samples under pines ($P \geq 0.05$). Soil pH (6.6–7.0) did not significantly differ between tree species ($df = 4$, $\chi^2 = 0.02$, $P \geq 0.05$).

DISCUSSION

Movement Patterns

NAT snakes were most active from 15 March–27 November, with a short period of dormancy from December–February. By contrast, CAP snakes were active throughout the year, which may have been a response to surgery performed during November. Snakes undergoing surgery after September were more frequently found in the open during the initial months after release, perhaps in an attempt to enhance their rates of healing from surgery by basking in the sun (Rudolph et al. 1998). All snakes, regardless of whether they were dormant or active, were usually in mammal (mostly pocket gopher) burrows. Mammal burrows provide safety from predators and the mammals themselves are the snakes' main food source (Brown and Parker 1982; Vandeventer and Young 1989; Wright and Wright 1957). In addition, extreme surface temperatures can be

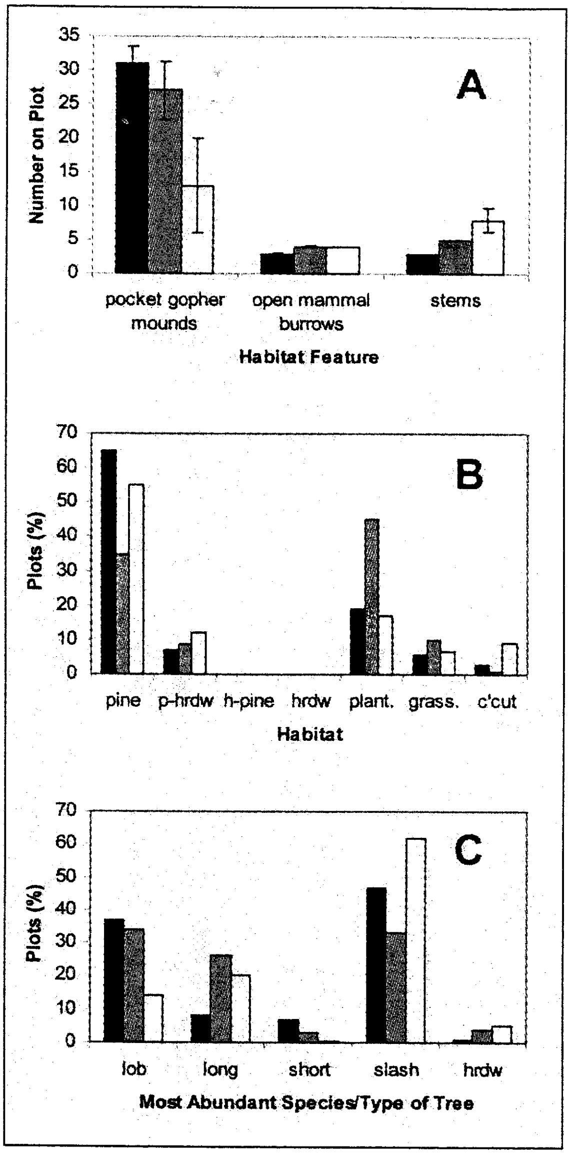

Figure 8. (A) Mean number of pocket gopher mounds, open mammal burrows, and stems (= trees with DBH < 25 cm) on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots compared to RAN plots (*n* = 100, CI = 0.95, open bars). (B) Habitats where pocket gopher mounds were located on NAT (*n* = 519, black bars) and CAP (*n* = 179, grey bars) snake plots compared to RAN plots (*n* = 100, open bars). See Fig. 3 for habitat abbreviations. (C) Pocket gopher mound abundance according to most abundant tree species/type (all non-pines grouped together) on NAT (*n* = 349, black bars) and CAP (*n* = 92, grey bars) snake plots compared to RAN plots (*n* = 67, open bars). See Fig. 5B for tree species/type abbreviations.

avoided by sheltering underground, where temperatures are less variable.

The higher overall number of observations of *P. ruthveni* in the open during the spring and fall than during the summer and winter may indicate a bimodal pattern of seasonal activity. Bimodal seasonal activity patterns have been observed in several other species of snakes in warm temperate climates (e.g., *Diadophis punctatus*, *Heterodon platirhinos*, *H. simus*, *Virginia valeriae* [Gibbons and Semlitsch 1987]). Seasonal activity is determined by three essential natural history components: survival, reproduction, and feeding (Gibbons and Semlitsch 1987). Subterranean snakes such as *Pituophis* may be more active in spring and fall if above-ground movement is associated with reproductive activity such as mating or searching for oviposition sites (Gibbons and Semlitsch 1987). Decreased above-ground activity in summer and winter may be due to avoidance of hot and cold surface temperatures, respectively, which may be life-threatening to ectotherms such as snakes (Cowles and Bogert 1944).

Likewise, the higher overall number of observations of *P. ruthveni* in the open during the late morning and mid-afternoon than during the early afternoon and night may indicate a bimodal pattern of daily surface activity. Bimodal daily activity patterns have also been reported for *Crotalus atrox* (Landreth 1973), *Heterodon platirhinos* (Platt 1969), and *Thamnophis radix* (Heckrotte 1962). Daily activity may be a function of searching for food or a mate, predator avoidance, or thermoregulation (Gibbons and Semlitsch 1987). For subterranean snakes such as *Pituophis*, which maintain lower active body temperatures than do more terrestrial snakes (Brattstrom 1965; Parker and Brown 1980), a bimodal daily activity pattern allows the maintenance of lower body temperatures through avoidance of higher midday temperatures (Bogert 1949, 1959).

The lower vagilities and smaller home ranges of CAP snakes may have been due to the snakes' introduction into an unfamiliar habitat after a lifetime in captivity, as well as to their levels of endurance, which are typically lower in younger and smaller snakes (Pough 1978). Alternatively, the smaller size of CAP snakes may have enabled them to access more mammal burrows, particularly of small rodents, thereby potentially increasing the snakes' foraging success within a relatively small area. Also, because smaller individuals of *P. ruthveni* are more vulnerable to predation than are larger individuals (J.

Himes and L. Hardy, pers. obs. 1996, 1997), the smaller snakes may limit the extent of their movements to lessen their conspicuity to predators.

Habitat Relations

By comparing the habitats used by *P. ruthveni* to the frequencies of the different habitats throughout the study area, we can determine habitat preferences. Pine snakes were most frequent in pine habitats (pine forests and pine plantations for NAT snakes, pine plantations for CAP snakes) and less frequent in the remaining forest types and clearcuts.

Pituophis ruthveni is closely associated with pocket gophers (Rudolph and Burgdorf 1997; Vandeventer and Young 1989), as evidenced by the frequency of individuals of *P. ruthveni* immediately adjacent to pocket gopher burrow systems, the propensity of snakes that are disturbed on the surface to retreat to nearby pocket gopher burrows, the exclusive occurrence of hibernation sites in pocket gopher burrow systems, and the use of pocket gophers as food (Rudolph and Burgdorf 1997). Indeed, individuals of *P. ruthveni* in this study were consistently found in areas containing an abundance of pocket gopher mounds.

Pocket gopher mounds on NAT snake plots were more frequent in pine forests and were less frequent in all other forest types and in clearcuts. Pocket gopher mounds on CAP snake plots were more frequent in pine plantations and were less frequent in clearcuts. This similarity in frequented habitats between pocket gophers and pine snakes indicates that habitat selection by pine snakes is determined in turn by habitat selection by pocket gophers.

NAT snakes were > 200 m from the nearest habitat edge most frequently; the interior of pine forests and pine plantations were especially frequented. Individuals of *P. m. melanoleucus* in New Jersey also showed no preference for habitat edges, possibly because the snakes fed on small mammals not limited to ecotones (Burger and Zappalorti 1988). By contrast, CAP snakes were ≤ 100 m from the nearest habitat edge most frequently. However, this was probably because CAP snakes were released at habitat edges and moved shorter distances than did NAT snakes. Monitoring of CAP snakes over a longer period may have been necessary to determine whether they would select the habitat interiors as well.

NAT and CAP snakes that were located outside a forest, but < 200 from the nearest habitat edge, were usually nearest a forest and in a pine plantation, further exemplifying the importance of piney habitats to pine snakes. The general absence of NAT snakes in or near clearcuts may be caused by the scarcity of pocket gophers in this habitat. Workers from International Paper Company, who managed the study site for timber, sprayed the clearcuts with herbicides (Accord® and Arsenal®) to prevent herbaceous plant growth and natural tree succession. The reduction of herbaceous plant growth results in less forage for pocket gophers (Rudolph and Burgdorf 1997), which may account for the avoidance of these areas by pocket gophers and, in turn, pine snakes. In addition, many pesticides cause direct and indirect mortality of reptiles and mammals (e.g., Clark 1988).

NAT and CAP snakes were on plots containing few large (≥ 25 cm DBH) trees. Moreover, CAP snakes were frequently on plots lacking trees. Selection for areas containing few large trees (e.g., pine plantations) accounted for the less canopy closure on snake plots than expected. Less canopy closure allows greater sunlight penetration, leading to more sunlight striking the forest floor and, as a result, increasing the growth of herbaceous vegetation in the understory. This vegetation, which is the main component of pocket gopher forage (Lowery 1974), supports more pocket gophers and, in turn, pine snakes. The few stems (trees < 25 cm DBH) on snake plots also led to greater sunlight penetration; an abundance of stems forms a dense midstory that blocks out light. In addition, areas on the surface receiving greater sunlight intensity may offer suitable nesting sites to female pine snakes by attaining warmer soil temperatures, thus enhancing egg incubation (e.g., *P. m. melanoleucus* [Burger and Zappalorti 1986]).

NAT snakes were nearer loblolly and shortleaf pines more frequently and nearer hardwoods less frequently than expected. Similarly, pocket gopher mounds on NAT snake plots were nearer loblolly and shortleaf pines more frequently and nearer hardwoods less frequently. This similarity in frequented microhabitats between pocket gophers and NAT snakes further indicates that habitat selection by naturally occurring pine snakes is determined in turn by habitat selection by pocket gophers. A clear relationship between microhabitat selection by CAP snakes and by pocket gophers was not evident. Seven of the eight CAP snakes were juveniles and thus pocket gophers may not constitute as essential a food source as do smaller rodents (e.g., woodland voles [*Microtus pinetorum*] and cotton rats [*Sigmodon hispidus*]). In addition, *Microtus* and *Sigmodon* excavate or use burrows that may provide refugia for juvenile pine snakes as well (Lowery 1974; J. Himes, pers. obs. 1996, 1997).

NAT and CAP snakes were on plots containing few canopy and midstory hardwoods, exemplifying the scarcity of pine snakes in hardwood-dominated forests. However, NAT and CAP snakes were on plots containing the expected number of canopy and midstory pines. Thus, the number of pines by canopy class is probably unimportant to pine snakes. In addition, NAT and CAP snakes were rarely located under debris or in logs and thus log abundance and characteristics are probably also unimportant to pine snakes, which preferentially shelter in pocket gopher burrows (Rudolph and Burgdorf 1997; J. Himes and L. Hardy, pers. obs. 1996, 1997). Nonetheless, NAT snakes were on plots containing an abundance of pine logs, probably because these snakes preferred pine forests. Lastly, NAT and CAP snakes were located where understory cover was relatively sparse.

Soil under all pine species at the study site contained more large particles (sand) compared to soil under sycamore. Excavation is probably facilitated by larger particle size and thus obligatory and facultative burrowers such as pocket gophers and *P. ruthveni*, respectively, may prefer the sandy soils associated with pine forests. Moreover, female pine snakes may prefer to nest in soft sand of (e.g., *P. m. melanoleucus* [Burger and Zappalorti 1986]).

Conservation

Rangewide habitat destruction and human persecution have reduced natural populations of *P. ruthveni* to the point that this is arguably the rarest endemic species of snake in the U.S. (Jennings and Fritts 1983; Reichling 1988*a*, 1989; Vandeventer and Young 1989). Lacking federal protection, *P. ruthveni* will probably become threatened further if conservation steps are not taken. Most records of *P. ruthveni* since 1980 have come from private property in Bienville Parish that is managed for timber (D. Rudolph, pers. obs. 1995). At the study site alone, 359 ha were clearcut in 1997 and 219 ha were to be clearcut in 1998 (both combined = 13% of an approximately 4450 ha area). The long-term impact of this habitat alteration on pine snakes remains to be seen. However, because pine snakes frequent pine forests and avoid clearcuts, the effects will probably be negative.

Another potentially harmful type of habitat alteration has been caused by suppression of the historic fire regime. An earlier study on *P. ruthveni* in eastern Texas indicated that pine snakes (as well as their pocket gopher prey) are most common where a lush understory of herbaceous vegetation is maintained by fires (Rudolph and Burgdorf 1997). However, the effects of wildfires have been limited due to fire suppression; by comparison, prescribed fires are generally less intense and are concentrated in the late winter and early spring. Thus, the extensive growth of herbaceous vegetation, which depends on sunlight penetrating the forest canopy and reaching the understory, has been largely replaced by hardwoods that block out the incoming sunlight (Rudolph and Burgdorf 1997). Fire suppression and consequential hardwood encroachment have also been prevalent at the Bienville Parish study site (J. Himes, pers. obs. 1996, 1997).

Unless the extent of this habitat alteration in areas containing populations of *P. ruthveni* is lessened or stopped, strategies besides habitat preservation may be needed to prevent this species from becoming further threatened. The release of captive-bred individuals of *P. ruthveni* into areas containing naturally occurring conspecifics may bolster natural populations. In this study, NAT and CAP snakes exhibited similar activity patterns. CAP snakes were less frequent in pine forests and more frequent in clearcuts than were NAT snakes. In addition, at least one CAP snake each was found most frequently in a pine forest, pine plantation, grassland, and clearcut, indicating that these snakes were not restricted to one habitat.

Himes et al. (2002) found that during their second year of life, CAP snakes experienced higher winter survivorship and had growth rates nearly identical to *P. c. deserticola* of the same age and sex (Parker and Brown 1980). Moreover, three CAP snakes were observed in the field to contain a large midbody bulge that probably indicated recent prey consumption. Thus, it appears that CAP snakes were able to survive and obtain enough food to grow at a normal rate.

Although the initial results of this study are encouraging, to accurately assess the applicability of repatriation, repatriated snakes should be monitored over several-year periods (Dodd and Seigel 1991) and their natural history data compared to naturally occurring snakes in the same area. The results, however, should be considered directly applicable only to the population under investigation. Ultimately, in order for repatriation to be a successful conservation strategy, relocated snakes need to reproduce with naturally occurring snakes and not vacate the general area of their release. Lastly, snakes to be repatriated should be free of disease (Dodd and Seigel 1991) and only released into their original gene pool to prevent outbreeding depression (Reinert 1991).

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