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June 14, 2002.

FA-TEXAS

GRANT: E-1

Joyce Johnson, Chief
Division of Federal Aid, Region II
U.S. Fish and Wildlife Service
P.O. Box 1306
Albuquerque, New Mexico 87103

Attention: Penny Bartnicki

Dear Joyce:

Enclosed is a Final Report for Project 71 (Radio-telemetry Study of Louisiana Pine Snakes in Eastern Texas and Western Louisiana). It is a late report from Segment 1 of the above grant. The primary investigator was unable to meet one of the objectives (develop a phylogenetic cladogram), but is currently working on it for late year publication. If you have further questions, please contact me at 512-389-4641.

Sincerely,

Neil (Nick) E. Carter
Federal Aid Coordinator

NEC: ne

cc: Krishna Gifford
John Herron
Paul Robertson
Gareth Rowell
Robert Wommack

*To manage and conserve the natural and cultural resources of Texas for the
use and enjoyment of present and future generations.*

FINAL REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. E-1-10

Endangered and Threatened Species Conservation

Project WER ²⁵60(71): Radio-telemetry Study of Louisiana Pine Snakes in
Eastern Texas and Western Louisiana

Prepared by: D. Craig Rudolph



John Herron
Program Director, Wildlife Diversity

Robert Cook
Executive Director

April 30, 2002

FINAL REPORT

STATE: Texas

GRANT NO: E-1-10

PROGRAM TITLE: Endangered and Threatened Species Conservation

PERIOD COVERED: September 1, 1995 - August 31, 1998

PROJECT NUMBER: WER²⁵68(71)

PROJECT TITLE: Radio-telemetry Study of Louisiana Pine Snakes in
Eastern Texas and Western Louisiana

PROJECT OBJECTIVE:

To improve knowledge of the biology and status of the Louisiana pine snake.

To determine the home range size and characteristics of Louisiana pine snake in longleaf pine/bluestem savannah habitat.

To develop a detailed characterization of habitat use compared to available habitat.

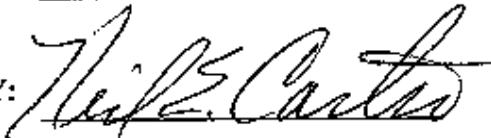
To determine prey composition and availability.

To refine knowledge of the status of the taxon and assess potential threats.

To develop a phylogenetic cladogram for the genus *Pituophis* based on mitochondrial DNA for comparison with morphological data.

PROJECT COSTS (Last Segment): \$ 0.00

PREPARED BY: D. Craig Rudolph DATE: January 30, 2002

APPROVED BY:  DATE: June 14, 2002
Neil E. Carter
Federal Aid Coordinator

Preface

The attached manuscripts and reprints resulted from this project and are submitted in partial fulfillment of the Federal Aid final report requirement.

Significant Deviation

The last objective "to develop a phylogenetic cladogram for the genus *Pituophis* based on mitochondrial DNA (mDNA) for comparison with morphological data" was not addressed in the manuscripts and reprints. This work is currently underway. mDNA analysis should be completed by this summer of 2002 with a finished manuscript ready for publication by December 1, 2002.

List of Manuscripts and Publications

1. Rudolph, D. C. and S. J. Burgdorf. 1997. Timber Rattlesnakes and Louisiana Pine Snakes of the West Gulf Coastal Plain: Hypotheses of Decline. Texas Journal of Science 49(3) Supplement: 111-122.
2. Rudolph, D.C., S. J. Burgdorf, J. C. Tull, M. Ealy, R.N. Conner, R. R. Schaefer, and R. R. Fleet. 1998. Avoidance of Fire by Louisiana Pine Snakes, *Pituophis melanoleucus ruthveni*. Herpetological Review 29(3): 146-148.
3. Rudolph, D.C., S. J. Burgdorf, R. N. Conner and R. R. Schaefer. 1999. Preliminary Evaluation Of The Impact Of Roads And Associated Vehicular Traffic On Snake Populations In Eastern Texas. IN Evink, G. L., P. Garrett and D. Zeigler, eds. Proceedings of the Third International Conference on Wildlife Ecology and Transportation. September 13 - 16, 1999, Missoula, Montana. Pp. 129 - 136.
4. Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. In press. Growth Rates And Mortality Of The Louisiana Pine Snake (*Pituophis Ruthveni*). Journal of Herpetology.
5. Rudolph, D.C., S. J. Burgdorf, R. N. Conner, C. S. Collins, D. Saenz, R. R. Schaefer, T. Trees, C. M. Duran, M. Ealy, and J. G. Himes. Submitted. Prey Handling And Diet Of Louisiana Pine Snakes, (*Pituophis Ruthveni*) And Black Pine Snakes (*Pituophis Melanoleucus Lodingi*) With Comparisons With Other Selected Colubrid Taxa. Herpetological Natural History.

TIMBER RATTLESNAKES AND LOUISIANA PINE SNAKES
OF THE WEST GULF COASTAL PLAIN:
HYPOTHESES OF DECLINE

D. Craig Rudolph and Shirley J. Burgdorf

Wildlife Habitat and Silviculture Laboratory

(Maintained in cooperation with the College of Forestry, SFASU)

Southern Research Station, USDA Forest Service

Nacogdoches, Texas 75962

Abstract.—Timber rattlesnakes (*Crotalus horridus*) and Louisiana pine snakes (*Pituophis melanoleucus ruthveni*) are large-bodied snakes occurring on the West Gulf Coastal Plain. Both species are thought to be declining due to increasing habitat alteration. Timber rattlesnakes occur in closed canopy hardwood and pine-hardwood forests, and Louisiana pine snakes in pine forests on sandy, well drained soils. While various factors are probably involved in population declines, this study examined one factor for each species that may have widespread consequences for population viability. Results obtained in this study support the premise that timber rattlesnakes are vulnerable to mortality associated with roads and vehicular traffic. Data and discussion are presented suggesting that populations are negatively impacted in areas of eastern Texas having a high road density. Conversely, Louisiana pine snakes appear to be affected by changes in the fire regime which has altered vegetation structure resulting in decreases in pocket gopher (*Geomys breviceps*) density. Decreases in gopher densities are further hypothesized to result in decrease or extirpation of pine snake populations.

Timber rattlesnakes (*Crotalus horridus*) and Louisiana pine snakes (*Pituophis melanoleucus ruthveni*) are large-bodied snakes with low reproductive rates. Thus, they are vulnerable to population decreases due to habitat modifications and increased mortality rates. Anecdotal evidence suggests that both species are declining on the West Gulf Coastal Plain (Conant 1956; Young & Vandeventer 1988; Brown 1991). Consequently, the Texas Parks and Wildlife Department has listed the timber rattlesnake as threatened and the Louisiana pine snake as endangered in Texas (TPWD 1992). In an effort to understand the biology of these two species and elucidate factors that are potentially responsible for the presumed population declines, radio-telemetry studies of both species were initiated.

Both species are undoubtedly subject to a variety of human induced impacts that have reduced populations and resulted in extirpation of local populations. However, this study focuses upon two hypotheses, one for each species, that the authors suspect are of importance in causing

Table 1. Annual home range size (ha) of adult timber rattlesnakes in eastern Texas.

Snake	Minimum Convex Polygon	Harmonic Mean 95% Contour
TX 1 (male) 1993	105.4	123.7
TX 1 (male) 1994	113.6	148.8
TX 2 (male)	212.6	256.7
TX 3 (female)	19.5	22.1
TX 4 (female)	20.2	15.3

declines on a landscape level.

Timber rattlesnake ecology.—Timber rattlesnakes on the Gulf Coastal Plain are typically associated with hardwood and mixed pine-hardwood forests (Martin 1992). Extensive areas dominated by longleaf pine (*Pinus palustris*) are generally not occupied (Mount 1975; Dundee & Rossman 1989). This general pattern is consistent with observations made in eastern Texas during this study.

Timber rattlesnakes are classic ambush predators, often spending up to several days in a given position waiting for prey to pass within striking distance. Foraging snakes frequently assume positions adjacent to logs, tree trunks or other structures that may be used as travel corridors by prey species (Reinert et al. 1984; Brown & Greenberg 1992). Juveniles occasionally climb trees to heights of 15 m, and may remain in trees for several days (Saenz et al. 1996). Prey typically consists of small mammals up to the size of squirrels (*Sciurus* spp.) and rabbits (*Silvalagus* spp.) (Klauber 1956).

Preliminary radio-telemetry results document the large home ranges of adult male timber rattlesnakes in eastern Texas (Table 1). Adult females have substantially smaller home ranges. The average annual home range size (Harmonic Mean 95% contour) for adult females (19 ha) is much smaller than that of adult males (176 ha). Juvenile snakes have generally smaller home ranges than adult females. The difference in home range size between adult females and adult males is primarily due to differences in movement patterns associated with breeding activities.

Table 2. Average daily distance moved (m) by adult male and female timber rattlesnakes during the mating and non-mating season.

Snake	Non-mating (1 Mar.-15 Aug)	Mating (16 Aug.-1 Nov.)
TX 1 (male) 1993	27.2	71.0
TX 1 (male) 1994	31.5	59.8
TX 2 (male)	25.0	85.6
TX 3 (female)	10.3	18.3
TX 4 (female)	17.7	15.9

Based on observations of pairs in close association, actual mating, and movement patterns, the mating season of timber rattlesnakes in eastern Texas is from mid-August until movement to the hibernacula, generally late October to November. A marked change in movement patterns of adult males, but not adult females, occurs at the initiation of the breeding season. Prior to the breeding season adult snakes move relatively short distances and spend extensive periods, often several days, at a given location. Females continue this behavior throughout the active season. This pattern is presumably driven by the ambush predation strategy employed by this species (Reinert et al. 1984).

Commencing with the initiation of the mating season, the movement patterns of adult males change dramatically. Throughout the mating season adult males move more frequently and move longer distances than adult females, or adult males prior to the mating season. This pattern is documented by the average distances moved per day by males and females prior to, and during the mating season (Table 2). Based on approximately once per week telemetry locations of individuals, males move substantially greater distances during the mating season than prior to the mating season (72.1 vs 27.9 m per day). Females' movement distances do not differ substantially between these two periods (17.1 vs 14.0 m per day). This behavior of adult males during the mating season results in movements of 1-2 km per week, traversing loops up to 2 km in diameter.

Causes of mortality and population decline.—Many factors undoubtedly contribute to mortality and population declines of timber rattlesnakes (Brown 1993). Factors associated with human development have pre-

sumably had a detrimental impact on timber rattlesnake populations, especially in recent decades (Brown 1993).

Habitat alteration due to changes in land use patterns have had a generally negative impact on timber rattlesnake populations throughout their range. Urbanization and agricultural development have eliminated the species from much of its historic range (Brown 1993). In eastern Texas urbanization is not as extensive as in some areas, and agriculture (pasture and row crops) have declined in recent decades. Commercial timber production lands are subject to harvesting-related disturbances, often on short rotations, that have unknown impacts on timber rattlesnake populations.

Anecdotal evidence suggests that direct killing by humans is substantial on the West Gulf Coastal Plain, but data are lacking. Rattlesnake roundups, important sources of mortality for some rattlesnake populations, probably have little impact on timber rattlesnake populations in Texas due to legal protection and the difficulty of collection compared to other rattlesnake species. Most human-related mortality reported to the authors is associated with timber harvest activities, incidental encounters during various outdoor activities, and especially with snakes encountered on roads.

Northern populations are subject to massive mortality through direct killing by humans at communal hibernacula (Galligan & Dunson 1979; Brown 1993). Mortality at the den sites is higher on adult females due to the tendency of gravid females to remain in the den vicinity during gestation (Brown 1991). In eastern Texas typical hibernacula consist of armadillo (*Dasypus novemcinctus*) burrows, decayed stump holes and associated root channels, and beneath the root masses of wind tilted trees. No instances of more than one individual at a hibernation site was observed during this study. Consequently, hibernating rattlesnakes in eastern Texas are not particularly vulnerable to human predation at their hibernacula.

The road mortality hypothesis.—Road networks and substantial vehicle traffic are significant causes of vertebrate mortality (Ehmann & Cogger 1985; Bennett 1991). In the United States Lalo (1987) estimated vertebrate mortality on roads at one million individuals per day. Rattlesnakes are particularly susceptible to road associated mortality since they suffer

from intentional killing due to their economic value and humans' general negative opinions of snakes (Adams et al. 1994).

Encounters between timber rattlesnakes and humans in eastern Texas frequently occur on roads. Of 36 individuals recorded in that study, 16 were of snakes crossing or dead on roads.

Aspects of timber rattlesnake biology influence the patterns of road associated mortality. Human encounters with timber rattlesnakes in eastern Texas, in general and on roadways, are more frequent in late summer and fall. This corresponds with the mating season, suggesting that the increased movements of adult males during this period are responsible for this pattern. Of 21 individuals of known sex recorded by the authors from roads during a three year period, 15 were adult males. This pattern is a potential cause of the skewed sex ratio in favor of adult females at the radio-telemetry study site. Although the sample size is small, adult females captured to date greatly outnumber adult males (8 females, 2 males).

Recent records of timber rattlesnakes were obtained from an 18 county area in eastern Texas. These records indicated that their distribution in the region is primarily associated with the floodplains and adjacent uplands of rivers and permanent streams. Preliminary radio-telemetry results indicate that the snakes are primarily using the uplands adjacent to floodplain habitats. Extensive areas of similar upland habitat not adjacent to rivers and permanent streams currently support few timber rattlesnakes. Differences in density of roads show a similar pattern; i.e., road networks are most dense in the upland areas not adjacent to permanent rivers and streams.

These observations suggest that timber rattlesnakes were more widespread on the landscape in the recent past. It is therefore proposed that development of dense road networks and associated vehicular traffic have resulted in the extirpation or major reduction in timber rattlesnake populations over much of the eastern Texas landscape.

This hypothesis was tested by comparing total lengths of roads within 2 and 4 km of recent rattlesnake locality records with random points. This analysis was first accomplished for the entire 18 county area in eastern Texas. It is possible that timber rattlesnakes are always

Table 3. Total road lengths (km) within 2 and 4 km of all snake collection points and random points, and snake collection points and random points within 3 km of permanent streams.

	Snake Points	Random Points	Prob.
<u>All Points</u>			
Total Roads w/in 2 km	4.09	7.01	$t = -8.94$ $P < 0.0001$
Total Roads w/in 4 km	13.43	21.44	$t = -2.68$ $P < 0.0088$
<u>Points w/in 3 km of Permanent Streams</u>			
Total Roads w/in 2 km	4.20	7.82	$t = -3.87$ $P < 0.0003$
Total Roads w/in 4 km	13.22	23.70	$t = -6.78$ $P < 0.0001$

restricted to forested habitats adjacent to rivers and permanent streams, although the preliminary radio-telemetry results suggest otherwise. To avoid the necessity of the assumption that timber rattlesnakes were once widespread on the eastern Texas landscape, the data was reanalyzed restricting consideration to the subset of the data (snake locations and controls) located within 3 km of rivers and permanent streams. In both analyses (Table 3) a highly significant relationship was found. Recent timber rattlesnake locations have a lower density of roads within 2 and 4 km than do random points. These results support the hypothesis that development of dense road networks and resulting vehicular traffic have significantly reduced timber rattlesnake populations in eastern Texas.

Louisiana pine snake ecology.—The Louisiana pine snake is possibly the least understood of any large snake of the United States due to their limited range, extreme rarity and secretive behavior. They are large, semi-fossorial constrictors with a range restricted to eastern Texas and western Louisiana (Conant 1956). Louisiana pine snakes are generally associated with open pine forests, especially longleaf pine (*Pinus palustris*), and sandy, well drained soils (Young & Vandeventer 1988). An association with pocket gophers (*Geomys breviceps*) is frequently noted in the literature (Young & Vandeventer 1988; Sweet & Parker 1991). Data derived from captive breeding programs indicates a remarkably small clutch size (3-4), the lowest of all the subspecies of *Pituophis melanoleucus* (Reichling 1990).

Preliminary results of on-going radio-telemetry studies in Louisiana and Texas indicate a moderate home range size averaging 27.7 hectares. In the pine upland habitats dissected with a network of small drainages, pine snake activity is heavily concentrated on the low broad ridges overlain with sandy well drained soils. Vegetation typically consists of a pine overstory with moderate to sparse midstory, and a well developed herbaceous understory dominated by grasses.

An extremely close association with pocket gophers is supported by observations made during the course of this study. The distribution of Louisiana pine snakes on the landscape, concentration on sites with sandy well drained soils, matches that of pocket gophers (Davis et al. 1938; Sulentic et al. 1991). Most Louisiana pine snake telemetry locations (approximately 90% of 500+ records) are of snakes in or immediately adjacent to pocket gopher burrow systems. Individuals disturbed on the surface frequently retreat to nearby pocket gopher burrows. In addition, all hibernation sites located to date ($n = 27$) have been in pocket gopher burrow systems. Finally, Louisiana pine snakes are thought to prey heavily on pocket gophers (Vandeverter & Young 1989).

Causes of mortality and population decline.—Louisiana pine snake populations are thought to have declined in recent decades (Jennings & Fritz 1983; Young & Vandeverter 1988; Reichling 1995). Lack of baseline population data, rarity, and secretive behavior make any conclusions speculative. Intensive trapping efforts conducted during this study within the historic range suggest that current populations are very low with local pockets of higher density.

Louisiana pine snake populations are subject to many of the impacts common to other large snake species. Speculation in the literature as to causes of decline has included habitat alteration, direct human predation, collection for the pet trade and road mortality (Young & Vandeverter 1988). Data are lacking to evaluate the relative impacts of these potential causes of population decline.

Alteration of the fire regime hypothesis.—Most of the historic range of the Louisiana pine snake is still forested. However, essentially the entire historic range has been extensively altered by forestry practices (Frost 1993; Outcalt & Outcalt 1994). All but a few hectares of the

original pine forests of the region have been harvested at least once. Most of the original longleaf pine habitat has been converted to other pine species, primarily loblolly pine (*Pinus taeda*) and slash pine (*P. elliottii*), due to alteration of the fire regime or direct planting. Rotation ages under current silvicultural practices preclude the regeneration of old growth forests, and short rotation silviculture for pulp production is dominant on private lands.

The impact of these habitat alterations on Louisiana pine snake populations is not known. Studies currently in progress are designed to answer questions concerning habitat use in relation to silvicultural practices. What is obvious from preliminary data is the close association of these snakes with pocket gophers. It is therefore hypothesized that factors that influence pocket gopher distribution and abundance also influence Louisiana pine snake distribution and abundance, specifically that pocket gopher declines precipitate Louisiana pine snake declines. It is further proposed that the distribution and abundance of pocket gophers is determined in part by the fire regime, and that changes in the historic fire regime have had a negative impact on pocket gopher abundance.

West Gulf Coastal Plain pine forests, especially longleaf pine, have evolved as fire climax communities due to effects of frequent, low intensity ground fires (Komarek 1964; Platt et al. 1988). Frequently burned sites on sandy, well drained soils typically support a pine dominated overstory, minimal midstory, and a well developed herbaceous understory (Bridges & Orzell 1989). Alteration of the historic fire regime has been widespread (Frost 1993). Fire suppression has reduced the frequency of fire, and the substitution of prescribed fire for wildfire has changed the seasonal occurrence. The result has been a widespread encroachment of woody vegetation forming a dense midstory, and the suppression or virtual elimination of the previously well developed herbaceous understory (Frost et al. 1986; Bridges & Orzell 1989).

Pocket gophers feed primarily on subterranean portions of herbaceous plants (English 1932; Sulentic et al. 1991). The widespread decline of herbaceous vegetation in West Gulf Coastal Plain pine communities has presumably reduced pocket gopher abundances. Although there may be problems with this approach (Andersen 1987), this study used pocket gopher mound densities as an index of pocket gopher abundance. Pre-

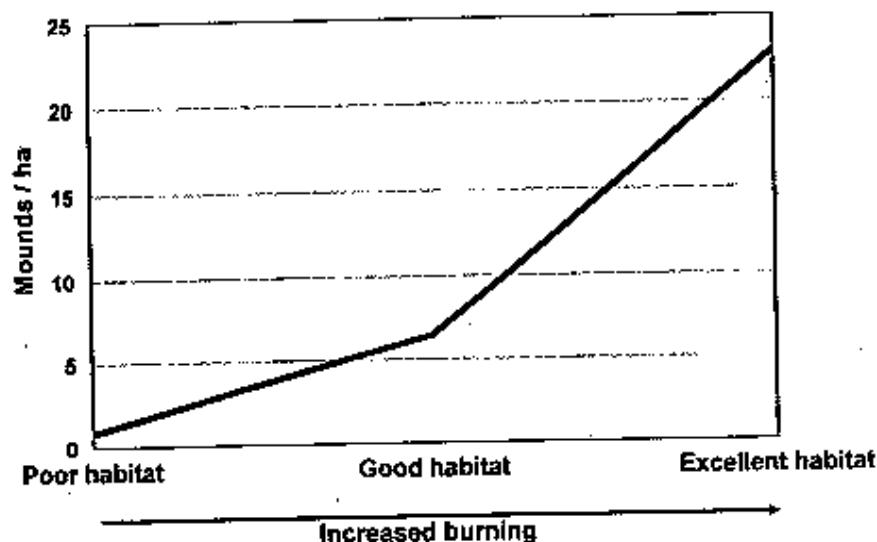


Figure 1. Hypothesized relationship between effectiveness of burning and pocket gopher (*Geomys breviceps*) density based on preliminary data on mound density.

liminary data suggest that habitats that have a vegetation structure typical of fire climax conditions (well developed herbaceous stratum) support higher gopher densities than sites where fire has not been sufficient to suppress woody vegetation and prevent reduction of the herbaceous stratum (Fig. 1).

Further confirmation of the relationship between pocket gopher densities and the fire regime would support the hypothesis that pocket gopher population declines in West Gulf Coastal Plain pine habitats have resulted in the apparent decline of Louisiana pine snake populations.

CONCLUSIONS

Two hypotheses have been presented for the apparent population declines of two large snake species on the West Gulf Coastal Plain. The first is that development of a dense road network and associated vehicular traffic have led to the elimination or decline of timber rattlesnake populations throughout the region. In the case of Louisiana pine snakes,

it is proposed that changes in the fire regime have reduced pocket gopher densities and thereby led to a decline in pine snake populations. Preliminary data were discussed to test these two hypotheses. Hopefully, additional data will be forthcoming to critically test these hypotheses.

ACKNOWLEDGMENTS

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breeding season, males searched for mates while on migration routes to the stream (Tsuiji and Kawamichi 1996a), and they also occasionally waited for females on shore around the pool at night. Such males may be able to intercept newly arriving females to the pool. In general, the males of explosive breeders occur widely around the edges of ponds until spawning commences, whereupon they concentrate around oviposition sites (e.g., *Bufo bufo*, Davies and Halliday 1979; *Rana sylvatica*, Howard 1980). Although this was seen occasionally in *B. torrenticola*, males more often searched and struggled for mates in the deeper parts of the breeding pool. However, lone females commonly were found in shallow water near shore, and paired females were most often found at the communal oviposition site.

Breeding adult *B. torrenticola* showed predominantly nocturnal activity; both sexes were more abundant (Tsuiji and Kawamichi 1996a) and more widely distributed in the pool at night than during the day, and almost all toads at the surface or on land were found at night. During the day, however, many toads were found in the relatively deeper parts of the pool. The diurnal breeding activity of *B. torrenticola* may be associated with the early breeding in spring, color dimorphism in visual mate recognition (see discussion in Tsuiji and Kawamichi 1996a), and/or underwater breeding.

Besides *B. torrenticola* and members of Pipidae living in the water, underwater breeders are known for the tailed frog, *Ascaphus truei* (Jameson 1955), and the Japanese steam-breeding frog, *Rana sakuraii* (Kusano and Fukuyama 1989), both breeding in fast-flowing streams. Thus, underwater breeding behavior is considered to have evolved independently among anuran groups. The possible benefits of breeding on the bottom of fast-flowing streams include: 1) richly oxygenated waters; 2) low metabolic demands in relatively cold water; 3) relatively stable water temperature; 4) no danger of drying; and 5) predator avoidance (see Olson 1989). On the other hand, possible costs are restricted activity in the water and risk of the eggs being washed away. For two Japanese underwater breeders, *B. torrenticola* and *R. sakuraii*, the most striking adaptation to underwater breeding is enlarged dorsal skin of males (Maeda and Matsui 1989; pers. observ.) that might assist cutaneous respiration in the water and allow them to be vigorously active there.

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Avoidance of Fire by Louisiana Pine Snakes, *Pituophis melanoleucus ruthveni*

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Wildfire and prescribed fire are important influences on pine ecosystems in the southeastern United States (Komarek 1968, 1974; Platt et al. 1988). Although considerable research on the impact of fire on vertebrates due to changes in vegetation structure has been reported, the direct impact of fire on vertebrates is not well known (Means and Campbell 1981). The Louisiana pine snake (*Pituophis melanoleucus ruthveni*) occupies a limited range in eastern Texas and western Louisiana (Conant 1956; Reichling 1995). Within this range it is generally found on sandy soils in longleaf pine (*Pinus palustris*) savannas (Young and Vandeverter 1988). Historically these longleaf pine savannas were maintained by frequent, low intensity ground fires (Komarek 1968; Platt et al. 1988, 1989). In recent decades wildfire frequencies have declined severely due to suppression efforts, and maintenance of these fire climax communities is currently dependent on prescribed fire (Conner and Rudolph 1989; Landers 1987; Platt et al. 1988; Van Lear 1985).

The association of Louisiana pine snakes with longleaf pine savannas and the dependence of these savannas on frequent fire suggests that Louisiana pine snakes have adapted to frequent fire. The influence of wildfires has declined precipitously in recent decades and prescribed fires have only maintained a substantial ecosystem role in limited situations. We have previously hypothesized that these alterations in the fire regime have resulted in apparent declines and local extirpations of Louisiana pine snakes (Rudolph and Burgdorf 1997). The massive increase in woody midstory vegetation and consequent decline of herbaceous vegetation are hypothesized to have had a detrimental impact on pocket gopher populations (*Geomys brevicauda*) and ultimately on Louisiana pine snakes.

Since 1993, radio-transmitters (Hörsihl Systems Ltd., SI-2T transmitters) have been implanted in Louisiana pine snakes at a variety of sites in Texas and Louisiana using the protocol of Weatherhead and Anderka (1984). These transmitters provide a location signal that varies with temperature, providing an estimate of snake body temperature. Preliminary results of ongoing studies demonstrate that Louisiana pine snakes are associated with sandy soils, savanna habitats with abundant herbaceous vegetation, and presence of Baird's pocket gophers (*G. breviceps*). Louisiana pine snakes spend substantial amounts of time underground, primarily in pocket gopher burrow systems, or coiled on the surface adjacent to entrances to pocket gopher burrow systems (Rudolph et al., unpubl.).

Sites where instrumented snakes were located were periodically prescribed-burned by land managers, providing an opportunity to observe snake behavior during exposure to fire. Habitat at all sites consisted of a longleaf pine overstory with a well developed herbaceous understory dominated by bluestem (*Schizachyrium* spp.) and other grasses. Nine snakes were located in burn areas during 1994–97. All nine snakes survived exposure to the prescribed fires with no apparent damage. Six of the snakes were known to be in the burned areas, but were not under observation during the course of the prescribed burns, and it is not known if they were above or below ground at the time of the fires. Three snakes were under observation during the course of the prescribed fires and observations are detailed below.

A prescribed fire on 25 February 1994 burned the area where an adult female Louisiana pine snake was located. At 1155 h the snake was coiled on the surface 1 m downslope from the burrow it used to access a pocket gopher burrow system where it had hibernated. It remained in this position until the approach of the fire at 1438 h. Immediately prior to the passage of the fire the air temperature was 25°C and the transmitter temperature was 27.5°C. The approaching fire was backing downslope at approximately 5 m per min, with flame heights of 0.5–0.8 m. When the fire front was approximately 15 m from the snake, it began moving downslope away from the fire and the burrow entrance. After progressing approximately 2 m the snake reversed direction and moved toward the approaching fire and into the burrow. The fire was 10 m distant as the snake moved underground. The transmitter temperature immediately began to drop from 27.5°C toward the burrow temperature of approximately 11–14°C. Burrow temperatures for this and other observations were estimated from transmitter temperatures of instrumented snakes located in pocket gopher burrows during the general period of the prescribed fire in question.

A prescribed fire on 10 March 1997 burned the area where two Louisiana pine snakes were located. One snake, an adult female, was coiled on the surface at 1145 h. Numerous pocket gopher mounds were evident but, to avoid disturbing the snake, they were not investigated in detail. The snake was in the same position at 1300 h, as the fire approached. Air temperature was 24°C and transmitter temperature was 27.5°C as the backfire with 0.3–0.6 m flame heights moved downslope at approximately 1 m per min. The snake began moving when the fire was 2 m distant and entered a burrow approximately 5 m distant. The burrow presumably allowed access to the pocket gopher burrow system. The fire passed over the snake's burrow entrance at 1352 h. Transmitter temperature at 1400 h was 22°C and dropping toward the burrow temperature of approximately 12–16°C.

The second snake observed on 10 March 1997, an adult male, was located at 1150 h, moving out of a debris pile. It was inadvertently disturbed in the process of being located and rapidly

moved approximately 30 m and sought shelter under grass cover. It was still in this location at 1504 h, as the fire approached. The snake was not visible and was not approached closely because of the risk of disturbing it again. As the fire approached the snake, air temperature was 24°C and the transmitter temperature was 23.5°C. The fire was a backfire moving downslope at approximately 2 m per min with 0.4–0.8 m flame heights. The snake maintained its position under grass cover until the flames were within 20 cm at 1516 h. The snake then emerged from beneath the grass cover and moved rapidly across the slope, parallel to and approximately 1.5 m in front of the fire. After moving 15 m the snake reversed direction and moved 95 m in the opposite direction still paralleling the fire front. When relocated at 1524 h, the snake was underground approximately 2 m in front of the advancing fire. The fire passed over the snake's position at 1533 h. The transmitter temperature was unchanged at this time, but began dropping immediately and had reached 18.5°C by 1715 h. After the passage of the fire, no evidence of an entrance to a burrow was located, although numerous pocket gopher mounds were in the immediate vicinity.

These observations suggest that Louisiana pine snakes are not at excessive risk of death or injury because of frequent fire in fire climax pine communities. Snakes located on the surface near known burrow systems simply retreat underground, even if this requires moving toward the advancing fire. Once underground, presumably at the 10–20 cm depth typical of pocket gopher burrows, they are insulated from the effects of the passing fire. Results of our telemetry studies (Rudolph et al., unpubl.) demonstrate that Louisiana pine snakes are underground, or on the surface within a few meters of known burrows, a large majority of the time. Given the large differences at which the snakes apparently detected the advancing fires, it is impossible to reasonably speculate on the possible cues that they might be using to detect fires. It is very possible that different cues are used in different situations.

Snakes on the surface and not near known burrows may be at greater risk. This would occur primarily when snakes were moving substantial distances; i.e. between pocket gopher burrow systems, or had sought temporary surface shelter during moves. The third snake discussed above fits this scenario. Even in this situation, behavior of the pine snake served to minimize risk. The snake's immediate behavior was to move a safe distance away from the fire and then initiate what appeared to be rapid searching for a subterranean retreat. This behavior did not cease until the snake gained an underground retreat, even though movement of just a few meters directly away from the advancing fire would have temporarily removed the risk.

The prescribed fires that have largely replaced wildfires in Louisiana pine snake habitat differ substantially from historical fires (Frost 1993; Komarek 1968). Prescribed fires are typically conducted in late winter-early spring whereas wildfires are/were more frequent later in the growing season. In addition, due to a number of concerns, prescribed fires seldom achieve the intensity of many wildfires. These differences presumably influence the interaction of Louisiana pine snakes and fires, however, comparative data are lacking.

The observed behaviors of these Louisiana pine snakes are sufficient to reduce the risk of mortality or injury to a low level from all but the most rapidly advancing fires that occur in the longleaf pine ecosystem. In all of the observed instances the fires were relatively slowly advancing backfires. The potential for mortality or injury to snakes due to rapidly advancing headfires is presumably greater, especially for snakes without immediate access to a

burrow. Wildfires, due to their greater intensity, may pose more of a risk than prescribed fires.

Erwin and Stasiak (1979) and Seigel (1986) reported mortality and injury to several snakes, including *P. melanoleucus*, as a result of prescribed fires conducted in prairie habitats in Nebraska and Missouri. These observations demonstrate that snakes are susceptible to death or injury during fires. The authors of both studies suggested that the timing of fires probably influenced their impact on snakes. Means and Campbell (1981) reported significant mortality of eastern diamondback rattlesnakes (*Crotalus adamanteus*) due to prescribed fires in a longleaf pine ecosystem. All reported instances were of snakes in ecdysis and it was hypothesized that reduced mobility and sensory abilities were associated with the mortality. Similar effects are possible with Louisiana pine snakes, but relevant observations are not available.

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Diel and Monthly Variations in Capture Success of *Phrynosoma cornutum* via Road Cruising in Southern Texas

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Road cruising may be a time-efficient capture method for Texas horned lizards (*Phrynosoma cornutum*) and may yield better capture success per unit effort than systematic searches and funnel and pitfall trapping (Fair and Henke 1997). However, it is unknown if road cruising can be used to assess activity patterns of *P. cornutum*. *Phrynosoma* may show changes in their activity patterns due to season (Fair 1995; Potter and Glass 1931) or ambient temperature (Prieto and Whitford 1971). We hypothesize that *P. cornutum* would be most active and, therefore most vulnerable to collection, during the warmest months, and that *P. cornutum* in southern Texas would exhibit one daily peak in activity during spring and autumn and two daily peaks in activity during summer as suggested by Potter and Glass (1931). We sought to test this hypothesis by collecting information on the success of sighting and capturing *P. cornutum* during road cruising searches throughout a four year period.

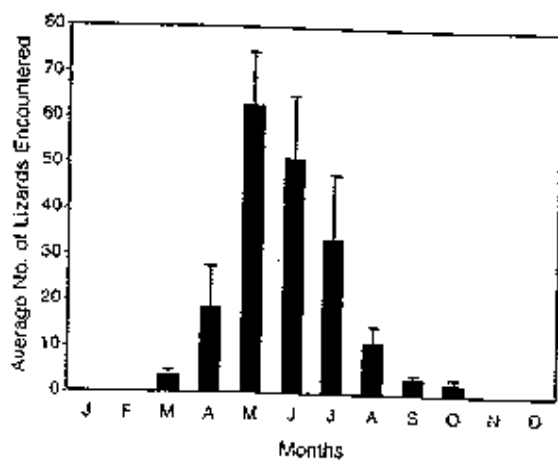


FIG. 1. Average number of *P. cornutum* collected monthly via road cruising during March 1991 to October 1994 in southern Texas. Bars extending above the means are the standard errors of the means. Average number of *P. cornutum* for January, February, November, and December was calculated using three years of data; the average number of *P. cornutum* for the remainder of the months was calculated using four years of data.



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PRELIMINARY EVALUATION OF THE IMPACT OF ROADS AND ASSOCIATED VEHICULAR TRAFFIC ON SNAKE POPULATIONS IN EASTERN TEXAS

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Abstract

Roads and associated vehicular traffic have often been implicated in the decline of snake populations. Radio-telemetry studies have documented vehicle related mortality as a factor in Louisiana pine snake (*Pituophis ruthveni*) and timber rattlesnake (*Crotalus horridus*) populations in eastern Texas. The hypothesis that existing road networks depress populations of large snake species was tested using a trapping protocol to sample snake populations at five distances from road corridors: 50, 250, 450, 650, and 850 m. Results suggest that populations of large snake species are reduced by 50% or more to a distance of 450 m from roads with moderate use. There was no indication that trap captures had reached an asymptote at a distance of 850 m. On a landscape scale, quantification of the density of the road network suggests that populations of large snakes may be depressed by 50% or more across eastern Texas due to road associated mortality.

Introduction

Roads and associated vehicular traffic have increased enormously during the last several decades. Adams and Geis (1983) estimated that the United States contained 6.3 million km of roads occupying 8.1 million ha. The impact of these very high densities of roads and vehicular traffic on vertebrate populations is poorly known, but presumed to be substantial (Bennett 1991). Lalo (1987) estimated vertebrate mortality on roads in the U. S. at one million individuals per day.

Reptiles, including snakes, are particularly vulnerable to mortality associated with roads due to their slow locomotion, their propensity to thermoregulate on road surfaces, and intentional killing by humans when observed on road surfaces. The magnitude of reptile mortality is high (Ashley and Robinson 1996, Fowle 1996, Rosen and Lowe 1994, Ruby et al. 1994), but the population impacts of this mortality are not well known. Impacts are presumably species specific. Species exhibiting low reproductive rates and low adult mortality are often identified as being particularly vulnerable to population consequences of road associated mortality (Fowle 1996, Rosen and Lowe 1994, Ruby et al. 1994, Rudolph et al. 1998).

Road mortality of snakes has been identified as constituting a "sink" for local populations (Rosen and Lowe 1994). In eastern Texas road mortality has been suggested as the primary factor in the local extirpation of timber rattlesnake (*Crotalus horridus*) populations (Rudolph et al. 1998) and a significant cause of mortality in the Louisiana pine snake (*Pituophis ruthveni*). In order to quantify the magnitude of road associated mortality on snake populations in eastern Texas, we initiated a trapping survey of snakes adjacent to roads.

Study Area

This study was conducted on the Angelina National Forest (Angelina and Jasper Counties) in eastern Texas. The general habitat is pine forest (*Pinus palustris*, *P. taeda*, *P. echinata*) managed for timber production. A variable mixture of angiosperm tree species occurs, especially along drainages. A dense road network exists consisting of state highways, secondary highways, and U. S. Forest Service system roads.

Methods

The trapping protocol consisted of transects perpendicular to a roadway. Transects were selected, to the extent possible, to minimize habitat differences within a given transect. Traps were placed at 50, 250, 450, 650, and 850 m from the edge of the road right-of-way. Due to the density of the road network existing on the Angelina National Forest 850 m was the maximum length of transect that could be established. The entire length of each transect was at least 850 m from other roads to minimize confounding impacts to the extent possible. On occasion unmaintained "woods" roads with minimal traffic (<1 vehicle/day) crossed the transect line or were within 850 m of the line. Average vehicle traffic volumes were obtained from the Texas Department of Transportation and the U. S. Forest Service.

Two transects (A and B) were established adjacent to Forest Service System Road 303 and a unsurfaced county road. These are gravel roads that are graded and maintained, and include cleared rights-of-way with drainage structures and contours. Average traffic volumes were less than 100 vehicles per day. Three transects (C, D and E) were established adjacent to Texas State Highway 63 in Angelina and Jasper Counties. Highway 63 is a paved two lane highway with paved shoulders. Average traffic volume is approximately 2400 vehicles per day.

Traps consisted of a plywood top and bottom 1.2 m X 1.2 m supported by wooden uprights 0.45 m tall. The sides were screened with hardware cloth (3.2 mm mesh). A hinged door in the top allowed access. Four funnel entrances were constructed of hardware cloth and wired into the midpoint of each side of the trap. Minimum funnel diameter was approximately 4 cm. Hardware cloth (3.2 mm mesh) drift fences were constructed of 61 cm wide strips buried approximately 10 cm in the soil. Drift fences extended 15.2 m from each funnel entrance. A water source was placed in each trap.

Four transects (A-D) were installed in January-February 1997 and a fifth transect (E) was installed in February 1998. Transects were operated during 1997 and 1998 from approximately 1 March to 31 October. Traps were checked once per week and all animals were removed. All snakes were returned to the laboratory where species, total length, and sex were recorded. PIT tags (Avid, Inc.) were implanted and snakes were returned to the capture site and released 50 m from the capture trap the week following capture. All subsequent recaptures were recorded. Recaptured individuals were included in the analyses because nearly all recaptured individuals were subsequently captured in different traps, including captures spanning the total range from traps 50 m to 850 m from road rights-of-way. For all other vertebrates, species and number were recorded, and they were released immediately.

A series of habitat measurements were taken at each trap location. Basal areas of canopy trees were determined with a 1-factor metric prism. Canopy closure was measured at the endpoint of each drift fence with a spherical densiometer and values averaged for each trap location. Percent cover of herbaceous and woody understory vegetation (to 1 m in height) was visually estimated within a 11.3 m radius circle centered on the trap midpoint. Foliage density (horizontal cover) was estimated using a density board (MacArthur and MacArthur 1961).

The distribution of snake captures among transects was compared within years by heterogeneity χ^2 . If transects were similar, we pooled data within and across years and compared trap distances with a pooled χ^2 . If the pooled χ^2 indicated differences among trap locations, we used simple linear regression to look for a trend (positive or negative).

Results

Because the drift fences and traps were constructed using 3.2 mm mesh hardware cloth, very small species and individuals were not captured. A total of 156 individual snakes (including 18 recaptures) of 11 species was captured in 1997 (4 transects) and 156 individuals (including 21 recaptures) of 13 species were captured in 1998 (5 transects) for a total of 312 captures (Table 1). Heterogeneity χ^2 analysis indicated that within years the distribution of snake captures was similar among transects and consequently transects were pooled within and across years. In all three cases (1997 snake captures, 1998 snake captures, and all snake captures) the pooled χ^2 analysis indicated highly significant differences among traps at different distances from roads (Table 2). Simple linear regression was used to search for linear trends in these data. In 1997 snakes and total snakes there was a significant linear trend of positive slope (Table 2). The data for 1998 did not reach significance at the 0.05 level, however the slope was positive.

A total of 397 individuals of 28 species of other vertebrates were captured, 260 in 1997 and 137 in 1998 (Table 3). Anurans, lizards, and rodents (71, 73, and 173 individuals respectively) were the primary taxa captured. An extreme drought presumably resulted in fewer individuals being captured in 1998. These data were analyzed in the same way as the snake data (Table 2). Heterogeneity χ^2 indicated that the transects could be pooled, and the pooled χ^2 analysis was not significant at the 0.05 level indicating no significant differences among traps at different distances from roads. Simple linear regression did not detect a significant linear trend in these data.

The number of individuals captured in relation to distance from road rights-of-way for snakes in 1997 and 1998, and other vertebrates in both years combined, are presented graphically in Fig. 1.

Habitat data are summarized in Table 4. The variation in habitat measures between trap locations is substantial. Regression analyses revealed only three significant linear trends in relation to distance from road corridors among the 25 instances examined (5 transects \times 5 habitat variables). The significant regressions were scattered among three habitat variables and three transects, and the numerical differences within these transects were not large.

Discussion

The data support the hypothesis that snake mortality associated with roads and vehicle traffic reduces the abundance of larger snakes for substantial distances from road corridors. Snake abundance, inferred from the trap success measured in this study, is reduced by more than 50% adjacent to roads compared with the abundance 850 m from roads. For all data combined, trap success remained low up to a distance of 450 m from road corridors and then increased substantially.

The combined data did not show any evidence of reaching an asymptote at the maximum distance (850 m) from road corridors. Due to the existing road density we were unable to locate transects suitable for quantifying trap success at distances greater than 850 m. Consequently, we were unable to measure the full impact of road corridors on snake populations on the Angelina National Forest.

The combined data for other vertebrate species suggests that roads and associated vehicular traffic are not having a significant impact on populations of these other species. However, these data are numerically dominated by rodents, anurans and lizards, species characterized by short generation time, rapid recruitment, and small home ranges compared to large snakes. It is not surprising that we did not detect major impacts on these taxa given the scale at which we were sampling. These data also suggest that the effect that we observed was due to direct mortality on larger snakes, rather than an indirect impact on the prey base of snake populations.

Although substantial habitat variation occurred among trap sites, patterns paralleling the increase in snake captures with increasing distance from road corridors were not strong. Only three significant linear regressions among the 25 examined suggests that habitat differences are not responsible for the pattern of snake captures. Despite the variation in habitat, not generally correlated with distance from road corridors, significant patterns were still detected in the snake trap data.

The magnitude of the impact on snake populations was relatively similar for the high traffic volume state highway and the lower traffic volume forest service system and county roads. The reason for this similarity is not immediately apparent. It may be that snakes are so susceptible to road related mortality that even moderate traffic volumes effectively remove nearly all of those individuals whose home range, or at least core areas, include the road corridor. Traps at 50 m, and even greater distances, may only be sampling those surviving individuals whose home range did not include the road corridor. In the case of larger snakes, it may be that essentially the full impact of vehicle related mortality along road corridors occurs at relatively low traffic volumes, on the order of a hundred vehicles per day. Additional data are required to address this hypothesis in more detail.

The observed deficit in snake captures, approximately 50% out to distances of 450 m from road corridors, and the lack of any indication of reaching an asymptote at the maximum distance sampled (850 m) suggests a very substantial impact on snake populations at the landscape level. Quantification of the road system on the southern portion of the Angelina National Forest revealed that 79% of the landscape is within 500 m of a highway or Forest Service System Road. This suggests that a substantial proportion of the expected snake fauna has been eliminated across the landscape due to road related mortality.

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TABLE 1. Numbers of snakes trapped by transect and year at 50, 250, 450, 650, and 850 meters from edge of road right-of-way.

Transect	Year	Trap Distance from Road (m)					total
		50	250	450	650	850	
A	1997	6	12	14	11	17	60
	1998	9	9	10	5	12	45
B	1997	8	1	2	10	13	34
	1998	1	2	2	2	7	14
C	1997	3	0	9	12	12	36
	1998	1	7	6	14	14	42
D	1997	5	10	1	4	6	26
	1998	3	6	0	5	8	22
E	1998	6	8	6	7	7	34
Total	1997	22	23	26	37	48	156
Total	1998	20	32	24	32	48	156
Total	1997/98	42	55	50	69	96	312

TABLE 2. Trend analysis of snakes and other vertebrates trapped at various distances from edge of road right-of-way.

Category	Heterogeneity χ^2	Pooled χ^2	Linear Trend ¹
Snakes 1997	19.6 (P = 0.080)	15.9 (P = 0.003)	P = 0.02
Snakes 1998	13.7 (P = 0.602)	14.8 (P = 0.005)	P = 0.08
Total Snakes	39.1 (P = 0.001)	28.9 (P = 0.001)	P = 0.03
Total Other Vertebrates	3.9 (P = 0.426)	9.4 (P = 0.052)	P = 0.75

¹ Probability associated with test of slope equal to zero using simple linear regression.

TABLE 3. Numbers of non-snake vertebrates trapped by year at 50, 250, 450, 650 and 850 meters from edge of road right-of-way.

Year	<u>Trap Distance from Road (m)</u>					total
	50	250	450	650	850	
1997*	55	55	30	55	65	260
1998	29	27	26	28	27	137
Total	84	82	56	83	92	397

* Transects A-D only.

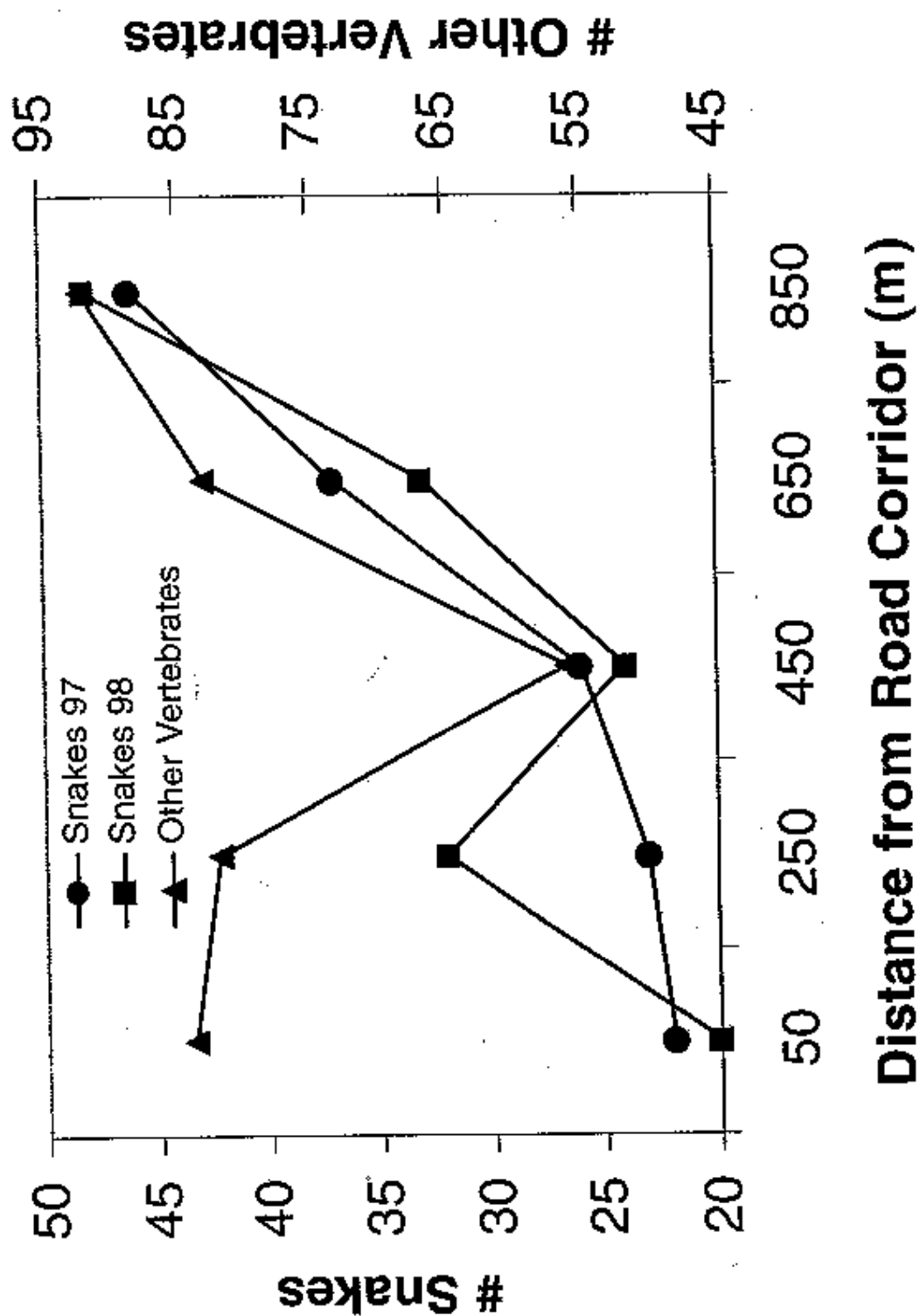


Figure 1.
Number of snakes and other vertebrates captured at 50, 250, 450, 650, and 850 m from road corridors.

TABLE 4. Probabilities associated with regression coefficients between habitat variables and distances from road rights-of-way.

Habitat Variable	A	B	Transect C	D	E
Canopy Basal Area	.3316	.3393	.3871	.0273*	.3542
Canopy Closure	.2580	.8361	.1942	.6042	.0351*
Foliage Density	.9256	.2509	.9785	.0974	.3373
% Woody Vegetation	.1553	.1933	.5594	.2920	.2075
% Herbaceous Vegetation	.6376	.5890	.3081	.0435*	.0596

* Significant regression ($P < 0.05$).

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LRH: J. Himes et al.

RRH: Growth and mortality of Louisiana pine snakes

GROWTH RATES AND MORTALITY OF THE LOUISIANA PINE SNAKE (PITUOPHIS RUTHVENI)

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Abstract: The Louisiana pine snake, Pituophis ruthveni, is an uncommon and poorly known snake. To learn more about the natural history of P. ruthveni, data on growth rates were collected on 29 adults and 1 juvenile by radiotelemetry during 1993-1997 in western Louisiana and eastern Texas. In addition, data on growth rates were collected on 1 adult and 7 juvenile captive-bred P. ruthveni that were released on the study site in north-central Louisiana and studied by radiotelemetry during 1996-1997. Growth rates were greater for juveniles than for adults. The three captive-bred juveniles had growth rates similar to the native juvenile. Adult males reach larger sizes (mean initial SVL = 119.0, $N = 7$) than adult females (mean = 95.6, $N = 7$). Total length/mass ratios are general health indicators and probably can be used to identify sexual maturity. Known-age growth curves suggest that the earliest sexual maturity occurs at about three years of age and at a total length of 120 cm or more.

The genus Pituophis (Serpentes: Colubridae) contains three species of snakes in the United States: P. catenifer, P. melanoleucus, and P. ruthveni (Collins, 1997). The Louisiana pine snake, P. ruthveni, was elevated to specific status by Reichling (1995) and is endemic to western Louisiana and eastern Texas (Conant and Collins, 1991; Reichling, 1995; Thomas et al., 1976). Rodríguez-Robles and De Jesús-Escobar (2000) agree with the recognition of specific status for P. ruthveni. 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 (Jennings and Pritts, 1983; Reichling, 1989), and secretive nature (Reichling, 1988).

An extensive radiotelemetry study initiated in 1993 (Rudolph and Burgdorf, 1997; Rudolph et al., 1998) is increasing our knowledge of the ecology of P. ruthveni. Results confirm the basic conclusions obtained from historical collection records. Pituophis ruthveni is primarily associated with sandy soils supporting pine forests within the historic range of longleaf pine (Pinus palustris). Telemetry data indicate a preference for sites with a

well-developed herbaceous vegetation generally maintained by frequent fire (Rudolph and Burgdorf, 1997). A close association with Baird's pocket gopher (Geomys breviceps) is evident at all sites (Rudolph and Burgdorf, 1997).

As part of a range-wide natural history study on P. ruthveni in Louisiana and Texas, we studied 30 naturally occurring (1 juvenile, 16 adult males, and 13 adult females) and 8 captive-bred (7 juveniles and 1 adult male) pine snakes in the field for up to 43 months. The objective of this study was to characterize the growth of this rare and poorly known species. We also compared growth rates of P. ruthveni with data from other studies of Pituophis.

Materials and Methods

Study Areas

Due to the extreme rarity of P. ruthveni, animals ($N = 38$) implanted with transmitters were located in several study areas: Bienville, Sabine, and Vernon Parishes in Louisiana, and in Angelina, Jasper, Newton, and Sabine Counties in Texas. All sites are within historic longleaf pine (Pinus palustris) habitat, although anthropogenic and silvicultural impacts have reduced the dominance of longleaf pine at most sites. The topography of all sites is gently rolling with intermittent and small permanent streams dissecting the sites. Soils vary considerably; however, extensive areas of deep sands occur at all sites. Pine forest consisting of P. palustris, shortleaf pine (P. echinata), loblolly pine (P. taeda), and the introduced slash pine (P. elliotii), with occasional hardwoods, dominates the uplands of all sites. Silvicultural treatments have increased the dominance of pine in most areas, and recent clearcuts and pine plantations occur at most sites. Various hardwood species (Quercus spp., Liquidambar styraciflua, Fagus grandifolia, Carya spp., Nyssa sylvatica, and many others) are more abundant and often dominant adjacent to the drainages.

The historic fire regime has been substantially altered at all sites. The effects of wildfires are limited due to fire suppression, and prescribed fires are less intense and are concentrated in the late winter and early spring at most sites. Consequently, hardwood encroachment is advanced and herbaceous vegetation is suppressed at most sites.

Survey Methods

Pine snakes were obtained by a combination of trapping and hand-capture between 1993 and 1997. Traps consisted of plywood and 6 mm hardware cloth boxes (1.3 x 1.3 x 0.3 m) with a funnel entrance on each side. Hardware cloth drift fences approximately 0.5 m in height extended 16 m from each funnel entrance to guide snakes into the traps. Traps were operated on a variable schedule at 10-15 sites during the months of March-October.

A total of 30 snakes was captured at or near a study site and all were implanted with radiotransmitters prior to their release in the field. In addition, eight of nine captive-bred snakes that were obtained from the Memphis Zoo and Aquarium were also implanted with transmitters and released at the Bienville Parish study site (one snake died in surgery). These snakes were the offspring of snakes from Bienville Parish that were used to establish a captive breeding program (Reichling, personal communication).

Fourteen snakes (of the 38 studied) were measured two times during the study, providing the data on growth reported here. Snakes were implanted with SI-2T transmitters (44 mm x 10 mm, 12 g; Holohil Systems LTD, Carp, ON). Each transmitter was equipped with a 20 cm whip antenna. A single small juvenile (no. 25; Table 1) was implanted with a smaller (2.5 g) transmitter constructed by Phillip Blackburn (Stephen F. Austin St. Univ.). Sex, total length, snout-vent length, and mass were recorded at the time of surgery (Table 1). Only one snake (no. 34; Table 1) had a transmitter mass that exceeded 5% of the body mass and it survived, without apparent harm, to the completion of the study.

Snakes were only handled during initial radio implantation and replacement (once every 14-15 months), and thus we could not determine reproductive status of the snakes. Therefore, we did not distinguish between gravid and non-gravid females. However, Pitch (1970), in an overview of reproduction in Pituophis (exclusive of P. ruthveni), concluded that sexual maturity in captive snakes is attained at three or four years of age. Therefore, we considered three of our captive snakes (nos. 34, 35, and 36; Table 1), which were one-year old at the time of their release, to be juveniles. One wild-

caught snake (no. 25; Table 1), which had a comparable initial total length and snout-vent length, but lower initial mass than all captive juveniles, was also considered to be a juvenile.

Transmitters were implanted following the general procedures of Reinert and Cundall (1982) and Weatherhead and Anderka (1984). Ketamine (Mallinckrodt Veterinary, Inc., Mundelein, IL) injected intramuscularly (80 mg/kg) or Halothane (Ayerst Labs, Inc., New York) as an inhalant was used as an anesthetic. Transmitters were implanted either subcutaneously or intraperitoneally. Transmitters had an approximate battery life of 6 (Blackburn) or 18 (Holohil) months and were replaced as necessary.

Snakes were allowed 2-14 days for recovery in the lab prior to release. Twenty-six of 30 wild-caught snakes were released at their point of capture. The remaining four wild-caught snakes were captured in areas not accessible for telemetry studies and were at risk because of adjacent highways; these snakes were released 5-40 km from their point of capture at safe sites where other snakes were under observation. The risks to the four repatriated snakes (all captured by local residents) and their receiving populations were considered to be less than the imminent danger posed by a busy highway and much human activity. This species is so rare that we decided to move these snakes to a safer habitat.

Following release, snakes were relocated on a variable schedule (1-7 times per week) depending on the particular research objectives of various studies in progress. At the time of transmitter replacement, most snakes were remeasured. Remains of snakes that died in the field, or their isolated transmitters, were examined for clues as to the possible cause of death.

Total lengths were used for calculating mean growth rates per month because sexual dimorphism in tail length was not apparent (Table 1), whereas the ratio of snout-vent length to mass was calculated as an indicator of the overall body condition and consequential health of snakes. Statistical analyses of the means of lengths and masses using t -tests were compared at the 0.05 level of significance (P).

RESULTS

The analysis of growth is based on 14 specimens for which two growth measurements were available (Table 1). However, estimates of mortality do not require two growth measurements; the analysis of mortality is therefore based on all 38 specimens that were studied in the field.

Growth

Total length.--Adult males reach larger sizes (mean initial SVL = 119.0, $N = 7$) than adult females (mean = 95.6, $N = 7$). Mean total length increase (cm) per month was 0.59 ± 0.39 (mean \pm 95% Confidence Interval, range = 0.02-2.14, $N = 14$; Table 1). Mean increase in total length per month of adult and juvenile snakes was 0.26 ± 0.25 (0.02-0.69, $N = 10$) and 1.40 ± 1.02 (0.59-2.14, $N = 4$), respectively. Mean increase in total length per month of adult males and females was 0.26 ± 0.24 (0.02-0.69, $N = 7$) and 0.30 ± 0.74 (0.11-0.65, $N = 3$), respectively. There was a negative relationship between increase in total length per month and total length of individual native ($N = 11$) and captive-bred ($N = 3$) snakes (Fig. 1; Table 1).

Mass.--Mean mass change (g) per month was 0.22 ± 6.81 (-30.04 to 18.25, $N = 14$). Mean change in mass per month of adult and juvenile snakes was -3.44 ± 8.31 (-30.04 to 0.57, $N = 10$) and $+9.38 \pm 10.14$ (4.09 to 18.25, $N = 4$), respectively. Mean change in mass per month of adult males and females was -4.46 ± 12.97 (-30.04 to 6.33), $N = 7$) and -1.08 ± 6.85 (-4.27 to 0.57, $N = 3$), respectively (Table 1).

Total length/mass ratios.--Growth rates of 14 individual snakes were calculated by comparing the changes in total length to mass ratios. Snakes with a negative slope (slopes down to right) had a mass gain relative to their increase in total length and snakes with a positive slope (slopes up to right) had a mass loss relative to their increase in total length.

Four (3 captive-bred and one wild-caught) juveniles (dashed lines; Fig. 2) increased in total length and mass at a greater rate than adults. However,

several adults decreased in total length/mass ratio during the study even though their length continued to increase. These adults began with a higher ratio and generally declined throughout the study (Fig. 2). Adult snakes have a lower ratio, which is probably characteristic of a mature body form, and the ratio for an individual might continue to decrease as the snake ages. This suggests an optimum diameter relative to mass that does not change at the same rate as the length (allometric growth). These data provide an important indication of growth rates of P. ruthveni.

The only juvenile snakes that survived to the end of the study were females (Fig. 2). These snakes increased in mean total length by 15.1% during the 8-13 month periods of observation, nearly identical to the 15.6% increase in length in females of P. c. deserticola in northern Utah during their second year of life (Parker and Brown, 1980). Three of the juvenile P. ruthveni that survived to the end of the study were observed in the field to contain a large midbody bulge that probably indicated recent feeding. Thus, we assumed that these snakes were able to obtain enough food to grow at a normal rate.

Of the 14 individuals of P. ruthveni for which two growth measurements were available, the health, condition, or recency of feeding/reproduction of the snakes can be indicated by the total length/mass ratio. The greater mass carried by a snake of a given length, is usually an indicator of better health of the animal (Plummer, 1997), but probably is also related to age because juveniles and adults may have different total length/mass ratios (allometric growth; Fig. 2). Accordingly, the smaller snakes had a higher total length/mass ratio and they gained mass at a greater rate throughout the study, whereas the larger snakes began the period of study with a lower total length/mass ratio and the rate of increase was much less (Fig. 2); five adults declined in mass during the study (Table 1).

Mortality

Of the 38 snakes released, all carrying transmitters, 13 survived to the end of the study and 25 were lost ($N = 6$) or died ($N = 19$), with an overall mortality rate of 50% and a monthly mortality rate of 8.33% ($= 19/228$ total months survived). Males made up 47.1% of the 17 snakes that survived at least

one year and comprised 24.2% of the total released ($N = 33$; excluding those implanted after September 1), while females made up 52.9% of the one-year survivors and 27.3% of the total. Two one-year surviving juveniles comprised 25% of all juveniles released, and 6.1% of the total released. Among adults only, one-year surviving males ($N = 8$) made up 47.1% of the 17 one-year survivors and 26.7% of the adults released.

Deleting individuals that were lost ($N = 6$), or died following late surgery (surgery after September 1; $N = 5$), a total of 27 snakes (19 adults and eight juveniles) is available for estimating mortality rates. These 27 individuals were present for a cumulative total of 437 months, during which 15 deaths occurred, resulting in a monthly mortality rate of 6.88%. Similar calculations for each sex give monthly mortality rates of 6.87% for males ($N = 9$; 131 mos) and 6.90% for females ($N = 6$; 87 mos). Similar data are available for five captive-bred juvenile snakes tracked for a total of 39 months. During this period, two deaths occurred, resulting in a monthly mortality rate of 5.13%. Data were insufficient to compare male and female juveniles.

Of the 15 adult mortalities, excluding those involving late surgery (Rudolph et al., 1998), vehicles were suspected as causes in three deaths; one snake was found as a carcass with a crushed transmitter adjacent to a major highway, and two snakes were found as carcasses adjacent to off-road vehicle trails with bruises or crushed vertebrae suggestive of vehicle damage. The remaining 10 documented mortalities are difficult to assign to a specific cause. Six of these individuals were observed in apparent healthy condition 7-10 days prior to death. Two of these six individuals were found as skeletal remains below ground and the only remains of another two were their isolated transmitters. Of the five carcasses located on the surface, four appeared to have been fed upon by vertebrates. However, it was impossible to determine whether predators or scavengers were responsible for the condition of the carcasses.

DISCUSSION

Any estimate of growth rate or a growth curve requires at least two measurements of size at known time intervals. In order to estimate age based

on the rate of growth, at least one known age is required. There is no published information available regarding growth rates of *P. ruthveni* based on wild individuals of known age. The only snakes ($N = 13$) for which both age and length are known are four hatchlings (Reichling, 1990) and nine snakes that were raised in captivity until eight were released in the field (one died in surgery). These 13 snakes provide the only available data on known ages and lengths from which an estimate of a growth curve can be obtained (Fig. 3). While the position of the curve at birth is probably accurate, the slope of the resulting regression line may be too steep because the nine post-hatchlings were raised in captivity (birth sizes were not recorded) for the first part of their lives and probably experienced a more rapid growth rate than would wild snakes because of the better food supply, constant environment, and lack of natural dormancy (Fig. 3).

Regardless of the potential inaccuracy of the regression line slope, the resulting individual growth curve estimates, based on captive individuals and four hatchlings (Fig. 3), suggest that one-year old and two-year old snakes are 80-100 cm and 100-120 cm in total length, respectively. Additional growth rates are known for snakes of known length, but unknown age. A female is known to have oviposited at a total length of 154 cm (Reichling, 1990). Thus, sexual maturity is probably reached by the time a snake has attained a total length of 120 cm and an age of about three years (Fig. 3). This estimate of age at sexual maturation is supported by Fitch (1970), who concluded that sexual maturity in other taxa of *Pituophis* (data on *P. ruthveni* were unavailable) is probably reached at three or four years of age.

The largest snake (no. 15; Table 1) experienced the greatest reduction in total length/mass ratio and also died during the study (Fig. 2; Table 1). This specimen was close to the maximum size (178 cm) known for the species (Conant and Collins, 1991). It is not surprising that juvenile and adult physiques are different. However, this relationship has not been documented in the literature for *P. ruthveni* and is possibly a very important predictor of when an individual reaches an adult physique and perhaps sexual maturity. Three of the four juveniles did not reach the adult ratio of approximately 0.30 or less (Fig. 2). The juvenile (at 0.268) that did reach the adult ratio

is not the largest of the four juveniles, but according to its total length/mass ratio, it might be the most mature.

In the only other extensive study of growth in Pituophis, Parker and Brown (1980) recorded length and weight changes in P. g. deserticola in northern Utah over a three-year period. Length increased by 24.2% in males and 15.6% in females during their second year of life. During the males' third year, length increased only by 9.9%. The length of females continued to increase by >10% per year during their third, fourth, and fifth years, but growth rates were significantly lower in both sexes in the third sampling year. Sexual dimorphism in size was apparent: of 35 females, only the largest exceeded 110 cm SVL and weighed 350 g, while 24 of 48 males exceeded 110 cm SVL and weighed 400-450 g.

In summary, this paper documents growth in length and mass of the Louisiana pine snake (Pituophis ruthveni). This species exhibits allometric growth in length to mass ratio, which indicates an optimum body size for adults. Annual increase in length might be similar to that observed for known-age gopher snakes (Pituophis catenifer) by Parker and Brown (1980). More robust snakes in this study gained mass more rapidly throughout their period of study. The observed allometric changes in robustness might be an important indicator for identifying the onset of sexual maturity, probably at a minimal total length of about 120 cm and an age of at least three years.

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Table 1. -- Growth in length and mass of specimens of *P. ruthveni* during specified intervals. F = female, M = male, SVL = snout-vent length, TL = total length. * denotes juveniles. Relative transmitter mass is for a 12 g transmitter implanted in all snakes, except no. 25, which carried a 2.5 g transmitter.

Snake Sex	Length		Change in		Mass		Change		Transmitter Interval	
	ID	(TL, SVL; cm)	TL, SVL (cm)	TL, SVL (%)	Mass (g)	Initial	in Mass (g, %)	Mass (g) / (months)	Initial	Mass (g)
No.		Initial	Final		Initial	Final				
36*	F	86.2, 75.9	103.3, 90.1	17.1, 14.2	0.198, 0.187	240.0	386.0	146.0, 60.8	0.050	7
34*	F	88.5, 78.0	106.1, 94.5	17.6, 16.5	0.199, 0.212	200.7	327.0	126.3, 62.9	0.060	13
25*	F	96.6, 85.9	108.9, 96.5	12.3, 10.6	0.127, 0.123	199.0	242.5	43.5, 21.9	0.013	7
35*	F	98.5, 86.0	106.2, 93.2	7.7, 7.2	0.078, 0.084	277.6	330.8	53.2, 19.2	0.043	13
16	F	124.0, 106.7	137.0, 120.5	13.0, 13.8	0.105, 0.129	563.0	574.4	11.4, 2.0	0.021	23
11	F	124.5, 109.0	129.5, 113.2	5.0, 4.2	0.040, 0.039	629.0	500.8	-128.2, -20.4	0.019	30
4	F	147.2, 127.6	151.5, 131.0	4.3, 3.4	0.029, 0.027	987.0	1005.0	18.0, 1.8	0.012	43
17	M	120.7, 105.0	123.5, 107.4	2.8, 2.4	0.023, 0.023	485.0	580.0	95.0, 9.6	0.025	16
18	M	127.5, 110.2	131.8, 113.9	4.3, 3.7	0.034, 0.034	588.0	543.6	-44.4, -7.6	0.020	29
29	M	131.0, 117.4	133.5, 119.2	2.5, 2.8	0.019, 0.015	447.1	559.0	111.9, 25.0	0.027	24

Table 1. -- Continued.

Snake Sex	Length (TL, SVL; cm)	Change in		Mass (g)	Change in Mass (g, %)	Transmitter Interval Mass (g) / (months)
		TL, SVL (cm)	TL, SVL (%)			
No.	Initial	Final		Initial	Final	Initial Mass (g)
33 M	132.5, 115.8	134.0, 117.0	1.5, 1.2	0.011, 0.010	528.4 479.4	0.023 3
10 M	134.9, 115.9	149.0, 130.0	14.1, 14.1	0.105, 0.122	822.0 770.0	0.015 31
3 M	148.5, 134.5	149.1, 134.6	0.6, 0.1	0.004, 0.001	728.3 850.0	0.016 36
15 M	156.9, 134.5	157.3, 135.8	0.4, 1.3	0.003, 0.010	996.9 606.4	0.012 16
Means F	109.4, 95.6	120.4, 105.6	11.0, 12.0	0.111, 0.114	442.3 480.9	0.031 19.4
Means M	136.0, 119.0	139.7, 122.6	3.7, 3.5	0.028, 0.031	656.2 626.9	0.020 22.1
Means F+M	122.7, 107.3	130.1, 114.1	7.4, 7.8	0.070, 0.073	549.3 553.9	0.025 20.8

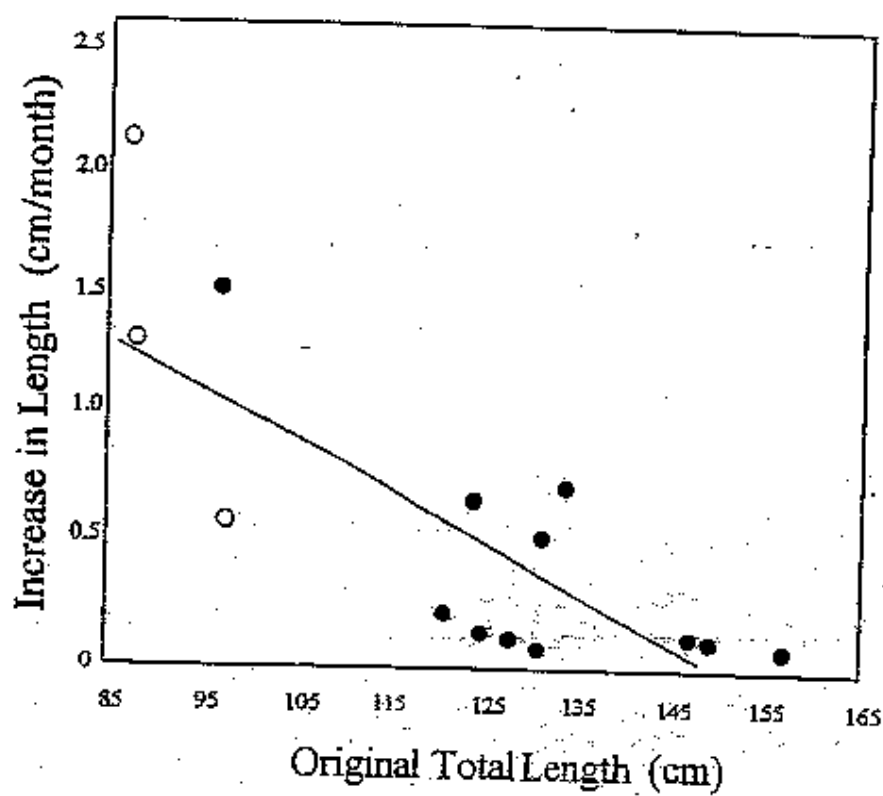
¹ Change is expressed as a percentage of initial TL and SVL, respectively.

² Change is expressed as a percentage of initial mass.

Legends to Figures

1. Length increases of native (closed circles) and captive-bred (open circles) P. ruthveni according to total length. Each symbol identifies the approximate growth rate of an individual snake. Regression line: $y = 3.51 - 0.0239x$.
2. Growth rates of P. ruthveni (N = 14). Lines represent individual adult snakes; dashed lines represent juveniles (all females).
3. Growth rates of nine individuals of P. ruthveni of known age. Closed circles are captive snakes released during this study. Lines join two measurements of three individuals. The triangles represent four hatchlings (Reichling, 1990). Regression line: $y = 57.39 + 0.078x$.

Fig. 1






Fig. 2

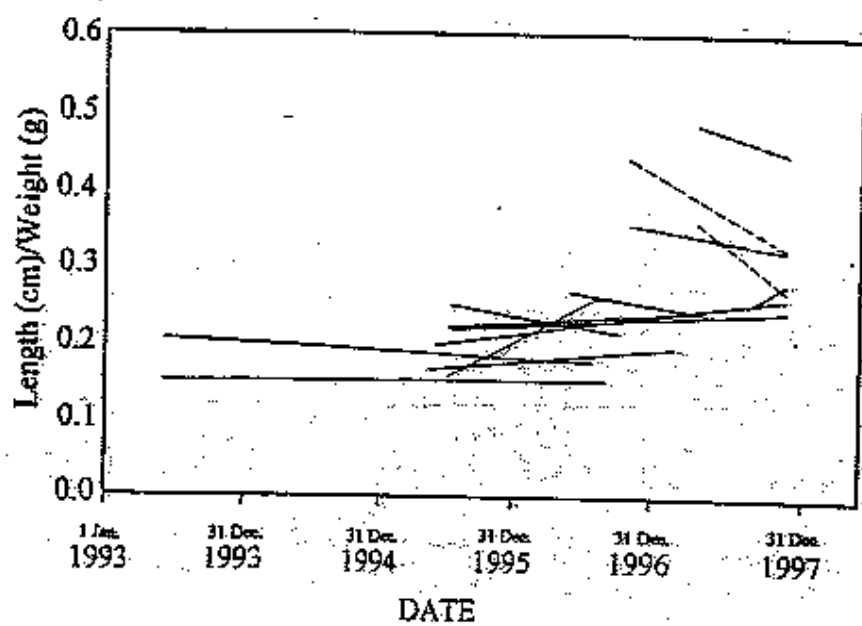
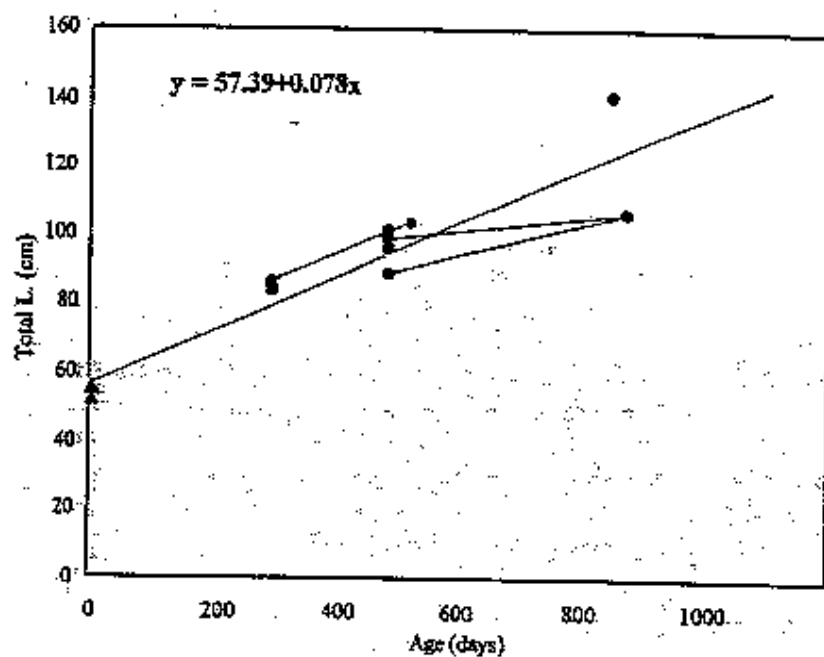


Fig. 3



Herpetological Natural History

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PREY HANDLING AND DIET OF LOUISIANA PINE SNAKES
(*PITUOPHIS RUTHVENI*) AND BLACK PINE SNAKES (*P. MELANOLEUCUS LODINGI*)
WITH COMPARISONS WITH OTHER SELECTED COLUBRID TAXA

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"Abstract. Diet and prey handling behavior were determined for Louisiana pine snakes (*Pituophis ruthveni*) and black pine snakes (*P. melanoleucus lodingi*). Louisiana pine snakes, which are sympatric with Baird's pocket gophers (*Geomys breviceps*), preyed heavily on pocket gophers and exhibited specialized behaviors that facilitated handling this prey species within the confines of burrow systems. Black pine snakes, which are not sympatric with pocket gophers, did not exhibit these specialized behaviors. For comparative purposes prey handling of *P. sayi sayi* and

Elaphe obsoleta lindheimeri were also examined."

"Key words. *Pituophis ruthveni*, Louisiana pine snake, *P. melanoleucus lodingi*, black pine snake, predation, *Geomys*."

INTRODUCTION

The Louisiana pine snake (*Pituophis ruthveni*) and the black pine snake (*P. melanoleucus lodingi*) are two taxa of conservation concern with limited distributions on the Gulf Coastal Plain (Sweet and Parker 1991). Both have fossorial adaptations, including thickened rostral scales and skeletal modifications of the head region (Knight 1986; Reichling 1995). *Pituophis ruthveni* is a rare species confined to eastern Texas and western Louisiana (Collins 1991; Conant 1956; Reichling 1995; Thomas et al. 1976). It is closely associated with longleaf pine (*Pinus palustris*) savannahs on sandy, well-drained soils (Rudolph and Burgdorf 1997; Young and Vandeventer 1988). These communities are maintained by frequent, low intensity ground fires (Komarek 1968; Platt et al. 1988, 1989). Data obtained in an ongoing radio-telemetry study of *P. ruthveni* (Rudolph and Burgdorf 1997; Rudolph et al. 1998) demonstrate a close association with burrow systems of Baird's pocket gophers (*Geomys breviceps*). *Pituophis m. lodingi* occupies a similarly restricted range on the lower Gulf Coastal Plain, from extreme eastern Louisiana to extreme western Florida (Sweet and Parker 1991). The ecology of *Pituophis m. lodingi* differs substantially

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from that of *P. ruthveni* in that its range is allopatric with that of pocket gophers, except for the extreme eastern portion of its range where it intergrades with *P. m. mugitus*. In this limited area, it is sympatric with the southeastern pocket gopher (*G. pinetis*).

The foraging behavior and diet of *P. ruthveni* and *P. m. lodingi* are unknown. In an effort to better understand the ecology of these rare taxa, we obtained data on diet and observed foraging and prey handling behavior both in the field and in the laboratory. We also observed prey handling behavior of *P. sayi sayi* and *Elaphe obsoleta* for comparative purposes.

MATERIALS AND METHODS

Data on diet in the wild were obtained from fecal samples obtained from wild caught *P. ruthveni* and *P. m. lodingi* specimens held in the laboratory for transmitter implantation or from dissection of dead animals. Hair, claw, bone, and eggshell were extracted from samples and identified by comparison with a reference collection. Two additional prey records for *P. ruthveni* and one for *P. m. lodingi* were obtained during field observations of radio-transmitted animals.

Given the importance of pocket gophers in their diet, we hypothesized that *P. ruthveni* may exhibit efficient behaviors for capturing subterranean prey. To test this hypothesis, we set up a large aquarium (130 X 30 cm) with two interior plexiglas inserts that defined a 6 cm wide space around the perimeter of the aquarium. This space was

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filled with slightly moist sandy loam soil to a depth of 40 cm. This soil provided a space within which Baird's pocket gophers could construct a burrow system. The 6 cm soil width resulted in the interior of the burrow being visible to an observer from outside the aquarium or by looking from above through the plexiglas insert.

For each trial a pocket gopher was introduced into the aquarium and given time to construct a burrow system 2-4 m in length. A snake was then introduced onto the soil surface adjacent to an open burrow entrance left unplugged by the gopher, or opened by the observer. The resulting behavior of the gopher and snake were observed. This procedure was repeated 20 times with 14 individual *P. rithveni* and 11 times with nine individual *P. m. lodingi*. Trials were also conducted six times with two bullsnakes (*P. sayi sayi*), and 12 times with seven Texas rat snakes (*Elaphe obsoleta lindheimeri*). All snakes, except for the *P. m. lodingi*, were from areas of sympatry with pocket gophers. These observations were compared with prey handling behaviors observed in cages (28 X 28 X 56 cm) that provided information on prey handling in conditions unrestrained by burrow walls.

A χ^2 test with Yates' correction was used to compare predation success among selected snake taxa. To avoid a violation of independence among samples due to repeated trials of individual snakes, we statistically analyzed the data using only the first trial for each snake.

RESULTS

Baird's pocket gophers were the major prey item (10 of 22) of *P. ruthveni* represented in the data set (Table 1). A minimum of 18 of the 22 prey items (pocket gophers, moles, and turtle eggs) were presumably obtained from subterranean sites. Small sample size precluded analysis of prey composition by snake size or sex. Only seven prey records were obtained for *P. m. lodingi*, predominately small mammals (Table 1).

All four taxa were efficient constrictors when handling small mammalian prey in open situations (cages). In a total of 35 (11 *P. ruthveni*, 11 *P. m. lodingi*, five *P. s. sayi*, and eight *E. obsoleta*) successful trials conducted in cages lacking obstructions, all taxa exhibited similar prey handling behavior (Table 2). All four taxa struck and grasped prey in their mouths, placed one or more full coils around the prey, and maintained their grasp with mouth and coils until the prey appeared dead. In a few instances, snakes released their mouth grasp before the prey was dead, but only after it was immobile. Small mammal prey used in these trials were an assortment of *G. breviceps*, *Peromyscus* spp., *Rattus norvegicus*, and *Sigmodon hispidus*. All prey were readily accepted with one notable exception. Three individual *P. m. lodingi* refused *Geomys* during 5 of 6 trials.

Prey handling behavior within burrow systems, however, varied markedly across taxa (Table 2). *Pituophis ruthveni* reacted to the occupied burrow systems immediately, presumably due to abundant prey-derived chemical cues. In all trials the snakes proceeded at a rapid

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rate through the burrow system until contact with the gopher. On only one of 20 trials was the gopher able to backfill the burrow sufficiently to prevent the snake's advance. *Pituophis ruthveni* confronted with a backfilled burrow initiated vigorous and powerful probing motions with its head and neck and was generally able to breach the barrier. Once contact was made with the gopher, three slightly different methods of prey handling occurred: (1) the snake rapidly proceeded past the gopher approximately $1/3$ to $1/2$ of the snake's total length and compressed the gopher by muscular kinking of its extended body (Fig. 1a); (2) the snake rapidly proceeded past the gopher, doubled back, and compressed the gopher using two lengths of its body (Fig. 1b); or (3) the snake briefly (< 2 sec.) grasped the gopher in its mouth until the snake positioned two lengths of its body in place as in (2) above. Only in method (3) was the snake's mouth used, and then only for one or two seconds. Otherwise, the snakes head was located several centimeters from the gopher until the gopher was dead, or nearly so. *Pituophis s. sayi* behaved similarly in all trials involving gophers in burrow systems (Table 2, c.f. Hisaw and Gloyd 1926).

Pituophis m. lodingi reacted differently (Table 2). In 9 of the 11 trials *P. m. lodingi* either refused to enter the burrow system, or entered but proceeded in a slow and deliberate manner. Individuals typically doubled back either before or after contact with the gopher, returning to the surface or to an unoccupied portion of the burrow system. Often, the gopher had detected the advancing snake and backfilled the burrow with soil, preventing actual contact by the time

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the slowly advancing snake arrived. In none of these trials did the snake initiate a predatory attack on the gopher or attempt to breach the backfill barriers. Two trials, both by the same snake that had previously eaten a *Geomys* in the cage trials, were successful. The first successful trial resembled that of an *E. obsoleta* (see below). However, the second successful trial resembled that of a *P. ruthveni*. The *P. m. lodingi* moved fairly rapidly through the burrow system, did not use its mouth to grasp the *Geomys*, and made no attempt to use coils to constrict the prey. This individual was less proficient than *P. ruthveni* throughout the prey handling sequence.

Elaphe o. lindheimeri behaved differently from all *Pituophis* (Table 2). *Elaphe o. lindheimeri* readily entered the burrow systems in apparent pursuit of the gopher. Movements were slow and deliberate, in marked contrast to those of *P. ruthveni* and *P. s. sayi*. The gophers had often detected the advancing snake prior to its arrival and initiated vigorous backfilling of the burrow. Backfilling was often successful (5 of 12 trials), and the snake was unable to penetrate the blockage and attack the gopher. If the snake arrived prior to backfilling, or was able to penetrate the blockage and attack the gopher (7 of 12 trials) the snake then grasped the gopher in its mouth and maintained this hold while attempting to constrict the gopher in the confines of the burrow system. These attempts, although always successful, appeared awkward. The snakes eventually succeeded in killing the gopher by obtaining a partial coil and/or compressing the gopher against the burrow wall, typically at the end of a burrow or at a sharp bend in the passage, with

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the anterior portion of its body.

Based on the first trial for each snake, *P. ruthveni* was more successful than either *P. m. lodingi* ($\chi^2 = 24.15$, $P < 0.001$) or *E. o. lindheimeri* ($\chi^2 = 6.38$, $P < 0.025$) in capturing *G. breviceps* within the confines of a burrow system. Sample size was too small to compare *P. s. sayi* success.

A field observation of *P. ruthveni* capturing a pocket gopher, although representing only a partial sequence, is consistent with the above trials. On 16 August 1996 a 1.4 m female *P. ruthveni* was located with 15 cm of its tail protruding from a pocket gopher burrow. Its tail was subsequently retracted into the burrow. Several minutes later a portion of the snake's body broke through the soil surface approximately 1.5 m from the burrow entrance. A struggling *G. breviceps* was held in a loop, not a full coil, of the snake's body. The surface breach was presumably a result of the pressure of the snake's kinked body breaking through the relatively thin (5 cm) overburden. The snake did not have a secure coil around the gopher and the snake's head was not visible. After approximately 5 min. the snake was able to retract its body and the gopher underground. Both anterior and posterior portions of the snake were intermittently observed for an additional 22 min. The gopher was not observed again.

DISCUSSION

The prey of *Pituophis* spp. consists primarily of small mammals

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(Sweet and Parker, 1991). The data reported here for *P. ruthveni* and *P. m. lodingi* are consistent with these reports. The prominence of pocket gophers in the diet of *P. ruthveni* is consistent with the close association of *P. ruthveni* with pocket gopher burrow systems. Telemetry studies (Rudolph and Burgdorf 1997; Rudolph et al. 1998) have demonstrated that *P. ruthveni* present on the surface are most frequently in the immediate vicinity of a pocket gopher burrow system. Pocket gopher burrow systems are the main type of site for shelter during the active season, hibernation, and escape from fire.

The importance of pocket gophers in the diet of *P. ruthveni* may be associated with the small clutch size ($X = 4$) and large hatchling size ($X = 54.4$ cm) of this species (Reichling 1990). Remarkably large hatchling size may be an adaptation to reduce the amount of time and growth necessary to reach a size sufficient to allow predation on pocket gophers. This strategy might have a selective benefit because of the paucity of small mammals in sandy upland sites in west Gulf Coastal Plain longleaf pine savannahs.

The reluctance of *P. m. lodingi* to prey on pocket gophers in this study is probably due to the lack of sympatry between these two taxa. The relative contribution of genetic and learned components to this behavior is unknown. Comparable data from *P. m. mugitus* from areas to the east of *P. m. lodingi*, where it is sympatric with *Geomys pinetis*, would be of interest.

The efficiency with which *P. ruthveni* and *P. s. sayi* handle pocket gophers in burrow systems has two critical components lacking in *P. m.*

Iodini and *E. o. lindheimeri*. First, the rapid searching through burrow systems reduces the probability of pocket gophers backfilling the burrow and precluding successful predation. In the loose soil of the experimental system, pocket gophers could backfill and pack the burrow, creating a burrow plug 4-8 cm in length in less than 1 min. *Pituophis ruthveni* and *P. s. sayi*, which possess substantial excavating abilities (Carpenter 1982; Reichling 1995), were delayed for a minute or more. In a natural situation this might allow critical time for pocket gopher escape. *Elaphe o. lindheimeri*, lacking specialized excavating abilities, were completely stopped by a completed burrow plug.

Second, the lack, or minimal, use of the mouth to grip the pocket gopher, combined with compression using a kink in the snake's extended body, reduces the risk of injury during prey handling in a confined space (Hisaw and Gloyd 1926). Efficient prey handling potentially reduces the time required to subdue dangerous prey species. In addition, the snake's vulnerable head and neck are a considerable distance from the prey, further reducing the probability of injury.

Our results support the previous hypothesis of a close association of *P. ruthveni* and *G. breviceps*, and the near restriction of *P. ruthveni* to longleaf pine savannahs (Rudolph and Burgdorf 1997). Our results are also consistent with the hypothesized cause of the apparent population declines and range contractions of *P. ruthveni* in recent decades (Rudolph and Burgdorf 1997). We suggest that alteration of the fire regime has resulted in successional loss of herbaceous vegetation and consequent declines in *G. breviceps* populations, the primary prey

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species of *P. ruthveni*.

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TABLE 1. Prey of *Pituophis ruthveni* and *P. melanoleucus lodingi* as determined from field observations, analyses of fecal samples and gastrointestinal tract contents.

Snake Taxon	Prey Taxon	Number Occurrences
<i>Pituophis ruthveni</i>	<i>Geomys breviceps</i>	10
	<i>Scalopus aquaticus</i>	4
	<i>Peromyscus</i> sp.	1
	<i>Sigmodon hispidus</i>	1
	Unid. mammal	2
	Turtle eggs*	4
<i>P. m. lodingi</i>	<i>Sigmodon hispidus</i>	2
	<i>Peromyscus</i> sp.	2
	<i>Silvalagus</i> sp.	1
	<i>Colinus virginianus</i> (eggs)	1
	Spider	1

* Probably *Trachemys scripta* based on size and habitat.

TABLE 2. Foraging behavior of selected snakes within burrows of Baird's pocket gophers and in open situations. *P. r.* = *Pituophis ruthveni*, *P. s.* = *P. sayi sayi*, *P. m.* = *P. melanoleucus lodingi*, *E. o.* = *Elaphe obsoleta lindheimeri*.

Taxon	# successful		Pursuit rate		Mouth used		Constriction*	
	1 st trial	all trials	slow	rapid	yes	no	coil	kink
Burrow trials								
<i>P. r.</i> (n = 14)	14 of 14	19 of 20	0	19	0	19**	0	19
<i>P. m.</i> (n = 9)	1 of 9	2 of 11	10	1	1	1	1	1
<i>P. s.</i> (n = 2)	2 of 2	6 of 6	0	6	0	6	0	6
<i>E. o.</i> (n = 7)	3 of 7	7 of 12	12	0	7	0	7	0
Open trials								
<i>P. r.</i> (n = 11)	11 of 11		NA		11	0	11	0
<i>P. m.</i> (n = 3)	2 of 3	6 of 11***	NA		6	0	6	0
<i>P. s.</i> (n = 2)	2 of 2	5 of 5	NA		5	0	5	0
<i>E. o.</i> (n = 7)	3 of 3	8 of 8	NA		8	0	8	0

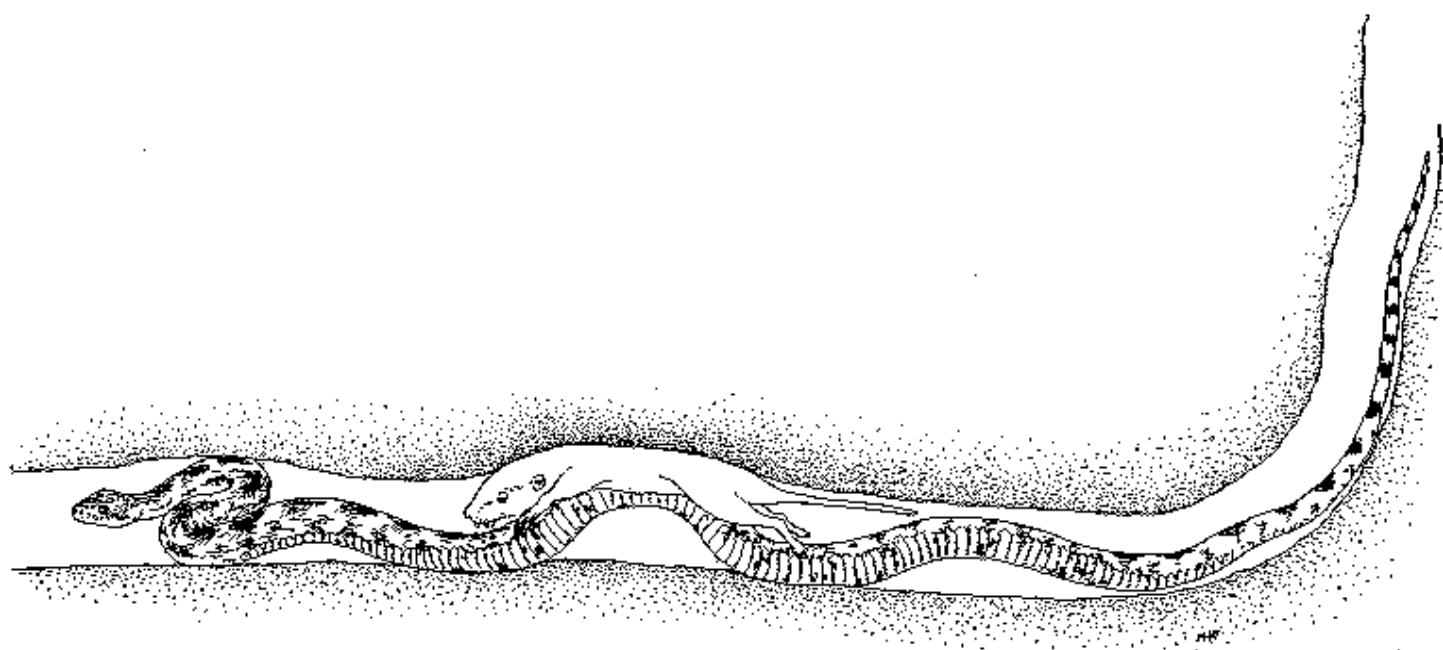
* See text for definition.

** Includes 2 trials in which mouth grasp was used for < 2 sec.

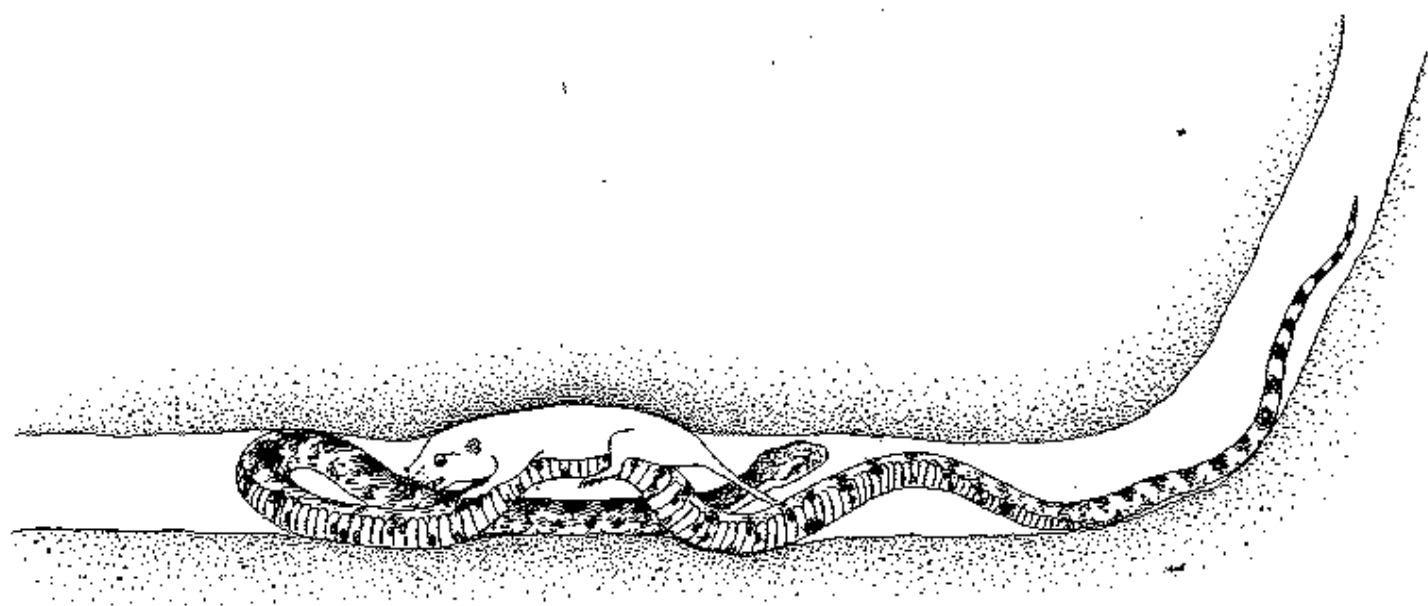
*** Three individual *P. m. lodingi* refused *G. breviceps* a total of 5 times.

Figure Caption

Fig. 1. Prey handling postures of Louisiana pine snake within a pocket gopher burrow.



A



B