Section 6 (Texas Traditional) Report Review

Attachment to letter dated: JAN 25 2006

Project Title: Determination of the Status of the Louisiana Pine Snake (*Pituophus ruthveni*)

Final or Interim Report? FINAL

Job #: WER 60 **Grant #:** E-14

Reviewer Station: East Texas Sub-office of the Arlington ESFO

Lead station was contacted and concurs with the following comments:
__Yes __No X Not applicable (reviewer is from lead station)

Interim Report (check one):

__ is acceptable as is

__ is acceptable as is, but comments below need to be addressed in the next report

__ needs revision (see comments below)

Final Report (check one):

__ is acceptable as is

x is acceptable, but needs minor revision (see comments below)

__ needs major revision (see comments below)

Comments:

We appreciate the considerable effort put into this project and we look forward to receiving the next draft of the Final Report with all final tables included. The only comment we have regards the reference on page 6 to six published manuscripts, a draft of an "in press" manuscript, and the USFWS CCA for the snake. None of these documents were attached, so we would appreciate receiving copies.

FINAL REPORT

As Required by

THE ENDANGERED SPECIES PROGRAM

TEXAS

Grant No. E - 14

Endangered and Threatened Species Conservation

Project WER60 -- Determination Of The Status Of The Louisiana Pine Snake (*Pituophis ruthveni*)

Prepared by:

D. Craig Rudolph, Richard N. Conner, Rickey Maxey

TEXAS PARKS & WILDLIFE

Robert Cook
Executive Director

Vacant
Program Director, Wildlife Diversity

Mike Berger
Division Director, Wildlife

28 October 2005

FINAL REPORT

STATE: Texas **GRANT NUMBER:** E - 14

GRANT TITLE: Endangered and Threatened Species Conservation

REPORTING PERIOD: 9/01/01 to 8/31/05

PROJECT NUMBER: WER60

PROJECT TITLE: Determination Of The Status Of The Louisiana Pine Snake (*Pituophis ruthveni*)

OBJECTIVE(S):

1. Intensively survey, using traps, a representative set of localities of varying habitat quality, within the historic range of the Louisiana pine snake in Texas.
2. Combine data from our previous telemetry studies with the proposed survey effort to formulate specific conclusions regarding the status of the Louisiana pine snake.
3. Assess the impact of roads and vehicular traffic on snake populations, including Louisiana pine snakes, to determine the need for, and type of management options.
4. Develop management guidelines for this species based on previous telemetry studies and proposed survey data.

Tasks:

1. Traps, of a design proven effective in capturing Louisiana pine snakes will be installed in arrays of 5 traps per site.
2. Localities will be chosen that are representative of the range of habitat conditions currently existing within the historic range of the species to provide data on the current distribution of the species within the historic range.
3. Traps will be operated during the snake activity season (Mar.- Oct.) for the duration of the study. These data will be combined with the extensive trapping data currently available from the best remaining habitat (over 25,000 trap days) to evaluate range wide status of the Louisiana pine snake.
4. Trap arrays will be arranged in a linear sequence of 5 traps per locality from 50m to 850m from existing roads and off-road vehicle trails to allow the concurrent investigation of the effects of vehicle mortality on snakes in general.

Summary Of Progress:

Please see Attachment A.

Location: Angelina, Newton, Sabine, and Tyler Counties, Texas.

Cost: Financial Status Report Unavailable at Time of Report

Prepared by: Craig Rudolph **Date:** 28 October 2005

Approved by: [signature] Neil (Nick) E. Carter **Date:** 11/15/2005

Craig Farquhar

From: Craig Rudolph [crudolph01@fs.fed.us]
Sent: Monday, October 24, 2005 7:55 AM
To: Craig Farquhar
Subject: Re: Final Report E-14

LPS Sec 6 rpt-05.doc (95 KB)

Craig:

Attached is the Final Report for Project WER60. Tables do not reflect the final trapping results that are just being collected. I suggest that once the final trapping results are in, I prepare final Tables, especially Tables 2 & 3 reflecting all trapping data for 2000-2005. There might also be minor revisions required in the text, but the general conclusions will not change.

Electronic copies of the Tables will be sent in a separate e-mail. I am having a problem attaching the Tables.

I also included additional copies of reprints. I will be glad to forward future reprints that are based on WER60 or concern Louisiana pine snakes as they become available.

Hard copies of this report are being mailed.

(See attached file: LPS Sec 6 rpt-05.doc)

Best,

D. Craig Rudolph
Research Ecologist
U. S. Forest Service
Southern Research Station
506 Hayter St.
Nacogdoches, TX, 75965

(936) 569-7981
crudolph01@fs.fed.us

ATTACHMENT A

Project WER60 – Determination of the status of the Louisiana pine snake (*Pituophis ruthveni*)

(New Study)

FINAL REPORT

10 October 2005

Reporting Period: October 1999 – August 2005

Contact Information: D. Craig Rudolph
USDA Forest Service
Southern Research Station
506 Hayter Street
Nacogdoches, Texas 75965

Ph.: (936) 569-7981
E-mail: crudolph01@fs.fed.us

Submitted by:
D. Craig Rudolph
Richard N. Conner
Ricky Maxey

ABSTRACT

Intensive trapping for Louisiana pine snakes was conducted during 2000-2005 at 14 localities in 12 counties within the historic range of the species in eastern Texas. A total of approximately 73,000 trap days resulted in the capture of 2 individuals, and did not verify extant populations at addition sites beyond those known in 1999. These results provide additional support for the conclusion that the Louisiana pine snake is rare and local (3 known localities) in Texas. Based on the precarious existence of the species at the three known sites, it is likely that the species is vulnerable to extirpation in Texas. Improved management, including habitat improvement and population increase, is required to increase the probability that the species survives in the state. Management guidelines are provided for the management of the habitat required by Louisiana pine snakes.

INTRODUCTION

This final report summarizes research accomplished on Project WER60 through September 2005. Work on this project began in late 1999 and has continued through 2005. The final (2005) trapping season is set to end in October 2005. A revised report will be submitted as soon as traps are closed for the 2005 season and tables prepared.

Prior to initiation of this project Louisiana pine snakes were known from three limited sites in Texas. During six years of additional trapping effort no additional sites have been located. The substantial effort expended to date on determining the status of Louisiana pine snakes in Texas underscores the precarious status of the species in the state.

OBJECTIVES

1. Intensively survey, using traps, a representative set of localities of varying habitat quality, within the historic range of the Louisiana pine snake in Texas.
2. Combine data from our previous telemetry studies with the proposed survey effort to formulate specific conclusions regarding the status of the Louisiana pine snake.
3. Assess the impact of roads and vehicular traffic on snake populations, including Louisiana pine snakes, to determine the need for, and type of management options.
4. Develop management guidelines for this species based on previous telemetry studies and proposed survey data.

METHODS

Traps were installed and monitored at 14 sites in 8 counties in eastern Texas. Survey sites were chosen to represent the best remaining habitat, based on insight gained from previous telemetry studies, that had not been previously surveyed. Since most high quality sites had been previously surveyed, several sites were in areas of lower habitat quality. All sites were within the broad historical range of the Louisiana pine snake. Trap construction and installation followed the methodology detailed in Rudolph et al. (1999). Where feasible, traps were installed at varying distances from roads to allow an assessment of road and vehicle impacts on snake populations. See Rudolph et al. (1999)

for a detailed explanation of this approach. The methods followed the guidelines established in the "Approach" stated in the Project Statement.

1. Traps, of a design proven effective in capturing Louisiana pine snakes will be installed in arrays of 5 traps per site.
2. Localities will be chosen that are representative of the range of habitat conditions currently existing within the historic range of the species to provide data on the current distribution of the species within the historic range.
3. Traps will be operated during the snake activity season (Mar. – Oct.) for the 5 year duration of the study. These data will be combined with the extensive trapping data currently available from the best remaining habitat (over 25,000 trap days) to evaluate range-wide status of the Louisiana pine snake.
4. Trap arrays will be arranged in a linear sequence of 5 traps per locality from 50m to 850m from existing roads and off-road vehicle trails to allow the concurrent investigation of the effects of vehicle mortality on snakes in general.

RESULTS AND DISCUSSION

During prior years of this Section 6 Project 65,110 trap days were accumulated at twelve localities in Anderson, Angelina, Jasper, Nacogdoches, Newton, Sabine, San Augustine, Tyler, and Wood Counties. During this, and previous trapping effort prior to 1999, the continued presence of *Pituophis ruthveni,* has only been documented on southern portions of the Angelina National Forest, a single site on the southern portion of the Sabine National Forest (Foxhunter's Hill), and on Temple-Inland Forest Products

Corporation land in northern Newton County (Scrappin' Valley). These three areas each consist of, at most, a few hundred hectares of occupied habitat.

During the 2005 trapping period (March – October) additional trapping was accomplished at seven of these sites in Angelina, Newton, Sabine, and Tyler Counties. A total of approximately 8000 trap days were accumulated at these seven sites during 2005. No additional *Pituophis ruthveni* records were obtained during this period. Table 1 lists the localities, ownership, and habitat type for the 14 sites where trapping occurred during the course of this project (2000-2005) and summarizes the total trapping effort. Tables 2 and 3 summarize the captures of snakes and other vertebrates during the 2005 trapping season.

This lack of success reflects the ongoing shift of trapping effort during recent years from known occupied sites to areas of suitable or marginal habitat that are not currently known to be occupied by Louisiana pine snakes. In particular, five of the sites investigated during 2005 are located on industrial forest lands that retain patches of apparently suitable habitat surrounded by intensive short rotation silviculture. These situations have not previously been found to support populations of *Pituophis ruthveni* in Texas, perhaps in part, due to lack of sufficient effort. However, recent detection of *Pituophis ruthveni* in similar habitat in Louisiana (Rudolph, unpubl. data) supported the importance of more intensive surveys of these situations in Texas. Louisiana pine snakes were not detected in these landscapes dominated by short-rotation silvicultural practices in Texas.

A manuscript detailing the current status of *Pituophis ruthveni*, incorporating the data from this project, is currently "in press" in the Southeastern Naturalist. A "draft" copy is appended to this report. The assessment of the status of the Louisiana pine snake contained in the manuscript concludes that the species is rare and currently confined to a total of six general areas in Texas and Louisiana. These areas consist of a few hundred to several thousand hectares of potential habitat, but in total represent a small fraction of the original range of the species. Recently obtained data from one of the larger areas of occupied habitat in Louisiana, based on capture rates in our traps, suggest that the population may be extremely low at that site. This information potentially raises concern for the continued survival of viable populations of this species.

During 2004 a "Candidate conservation agreement for the Louisiana pine snake, *Pituophis ruthveni*" was finalized. This document was signed by USF&WS, Dept. of Defense, U. S. Forest Service, Louisiana Dept. of Wildlife and Fisheries, and Texas Parks and Wildlife Department and details management objectives for the recovery of Louisiana pine snake populations. Results from Project WER60 were instrumental in providing data used in developing this agreement.

Six published manuscripts, a draft of an "in press" manuscript on the status of the Louisiana pine snake, and a copy of the USF&WS Candidate Conservation Agreement that use information developed using WER60 funding and/or funding from a previous Section 6 Agreement are appended to this report. In addition, two manuscripts are "in press" in Herpetological Natural History. A manuscript based primarily on data obtained in conjunction with the field work supported by this Project WER60 titled "Diet of crotalid snakes of the West Gulf Coastal Plain' is in review and additional manuscripts are anticipated.

In summary, investigations to date continue to suggest that the Louisiana pine snake is absent from much of its original range in Texas. It is apparently rare in the three limited areas in the state known to be currently occupied, and is presumably at high risk of extirpation in the state. Lack of success in locating additional occupied habitat despite massive trapping effort is cause for additional concern.

Four objectives were included in the Project Statement for Project WER60. These Objectives are addressed below.

Objective 1. Intensively survey, using traps, a representative set of localities of varying habitat quality, within the historic range of the Louisiana pine snake in Texas.

Surveys for Louisiana pine snakes were conducted under WER60 during the years 2000-2005 in a total of 14 sites in a total of seven counties within the historic range in eastern Texas (Table 1). Most of the high quality sites with a higher probability of supporting Louisiana pine snake populations had been surveyed between 1993 and 1999. Sites chosen for survey effort under WER60 were generally sites with a lower probability of supporting populations due to presence of lower quality habitat, based on results of previous telemetry studies, or distance from known occupied habitat.

Over 65,000 trap days were conducted in the 14 sites. Results were negative at 13 of these sites. Two Louisiana pine snakes were captured at the Angelina National Forest, County Line site which is immediately adjacent to habitat previously known to be occupied.

The generally negative results from extensive trapping effort suggest that the probability of the existence of additional populations in Texas is not great. See Objective 2 below.

Objective 2. Combine data from previous telemetry studies with survey effort to formulate specific conclusions regarding the status of the Louisiana pine snake.

During the course of this project approximately 73,000 trap days were conducted in potential Louisiana pine snake habitat in Texas (Table 1). Combined with previous trapping effort in Texas and additional trapping in Louisiana much is now known about the current status of the Louisiana pine snake. A manuscript incorporating results from this project has been prepared (Rudolph et al. In press). The major conclusions detailed in this manuscript are 1) The species is rare and local in occurrence, and may have declined in recent decades; 2) The Louisiana pine snake is currently known to occur is six general areas within its historic range (3 in Texas); 3) Habitat alteration and loss has been extensive throughout the historic range of the Louisiana pine snake; 4) intensive short-rotation silvicultural practices and alteration of the fire regime are the primary factors resulting in habitat degradation and fragmentation of populations; and 5) Improved management is necessary to recover Louisiana pine snake populations and avert extirpation of existing populations.

The extensive trapping at 14 additional localities in Texas supported by WER60 through 2005 support and extend the conclusions listed above. The primary emphasis during the surveys conducted under WER60 was to target sites influenced by intensive silvicultural practices, fragmentation, and isolation from known occupied habitat. During six years a total of more than 73,000 trap days at 14 sites failed to locate additional occupied habitat. Combined with previous trapping effort in Texas and ongoing trapping in Louisiana, the Louisiana pine snake is currently known to exist in three areas of limited extent in Texas, and three larger areas in Louisiana.

In Texas, Louisiana pine snake populations have been documented, since the mid-1990s, in three remnant areas of apparently high quality habitat. These areas are 1) Angelina National Forest, north and east of Boykin Springs and southwest of State Highway 63 in Angelina and Jasper Counties; 2) Sabine National Forest, Foxhunter's Hill area in extreme southern Sabine County; and 3) Temple-Inland, Inc. property (Scrappin' Valley) in northern Newton County. Each of these areas consists of only a few hundred hectares of known occupied habitat. These three areas contain the highest quality longleaf pine savannah habitat remaining in Texas. Previous telemetry studies in each of these three areas (Rudolph et al 1997, unpubl. data) demonstrate that Louisiana pine snakes make extensive use of the remnant savannah habitat.

The extensive trapping at sites in 10 counties in Texas (Rudolph et al. In press, this report) have failed to confirm existing populations in additional areas. These sites, all within the general historic range of the species, include most of the remaining high quality pine savannah sites in Texas, and otherwise suitable areas subject to intensive, short rotation silviculture and/or fire suppression. These results support the possibility that the Louisiana pine snake, historically recorded in 15 counties in Texas, may persist in only 3 small areas of remnant habitat in portions of four counties.

Four factors should be considered in relation to the above conclusion. First, not all potential sites in Texas have been surveyed for Louisiana pine snakes. Second, even at sites known to be occupied, trap success is low, sometimes as low a one capture per several thousand trap days. Thus the possibility exists that surveys can fail to detect Louisiana pine snakes, even after considerable trapping effort. Third, single Louisiana pine snakes were collected in Tyler and Montgomery Counties in the early 1990s

(Rudolph et al In press) suggesting that addition populations could occur. However, habitat in these areas is highly degraded and may not be able to support viable populations. Finally, recent surveys in Bienville Parish, Louisiana recorded two Louisiana pine snakes from landscapes heavily dominated by intensive, sort rotation silviclufure. However, land use change has been relatively recent in this area, and these individuals may represent surviving individuals rather than a viable population.

In conclusion, available data suggest that Louisiana pine snakes persist in Texas at a few, perhaps as few as three, small and isolated sites. The probability of substantial numbers of additional occupied sites, and any sites consisting of more than a few hundred hectares is low. This represents an apparent decline from a historic range that occupied portions of 15 counties in the eastern portion of the state. The remaining populations remain highly vulnerable to the factors presumably responsible for past declines; in particular fragmentation, road and vehicle impacts, and an inappropriate fire regime resulting in habitat degradation (Rudolph et al, 1997, in press).

Objective 3. Assess the impact of roads and vehicular traffic on snake populations, including Louisiana pine snakes, to determine the need for, and type of management options.

Previous research on Louisiana pine snakes and other snake species identified roads, associated vehicular traffic, and off-road vehicles as a factor impacting snake populations (Rudolph et al. 1998, 1999). Trap results suggested that populations of larger snake species were depressed adjacent to roads, and that this effect extended at least 800 m from the roads. Trap success was depressed by nearly 50% at distances up to 450 m from roads, compared to trap success at 850 m. (Rudolph et al. 1999). Using a different approach, it was concluded that timber rattlesnake (*Crotalus horridus*) populations in eastern Texas persisted primarily in areas of lower road densities (Rudolph et al. 1998). In addition, several Louisiana pine snakes both live and dead, were noted on roads during the course of this work.

Captures of Louisiana pine snakes are too few to directly assess impacts of roads on populations. However, during previous telemetry studies 4 of 15 (27%) of mortalities of snakes in the field were associated with vehicles, including off-road vehicles, and roads (Himes et al. 2002). Substantial additional trap data are available from the trapping conducted under WER60 (Table 4). These data do not show a clear relationship between trap success and distance from the primary roads involved. An assessment of road impacts on snake populations was not the primary objective considered in choosing locations for surveys. Consequently, additional roads in many of the survey locations are a confounding factor. Rather than contradicting the earlier results, the surveys conducted under WER60 emphasize the prevalence of roads on the landscape available to Louisiana pine snakes. Taken together, the above data suggest that roads and vehicles have the potential to depress Louisiana pine snake populations throughout most of the historical range. Roads and substantial vehicle traffic fragment all three of the known populations still extant in Texas.

Available data on vehicle related mortality, reduction of snake populations adjacent to roads, and the presence of numerous roads in Louisiana pine snake habitat suggest that road related mortality of Louisiana pine snakes is a management issue. However, the magnitude of the potential impact on populations is unknown. State highways 63 and 87 and a large number of minor roads pass through occupied habitat, thus the possibilities for effective mitigation are limited. Four general categories for mitigating road and vehicle related mortality exist (Bennett 1991, Jackson and Griffin 1999); crossing structures, fences or barriers, road closures, and altering driver behavior.

Louisiana pine snake activity is dispersed across the landscape. Lack of intensive use areas, i.e. communal hibernacula, preclude the efficient use of crossing structures and fencing of roads to mitigate vehicle impacts. The cost/benefit ratio is simply too great to make these approaches practical. Road closures are a feasible management action. It is probably not feasible to close major highways and roads, however smaller management roads and off-road vehicle use areas could be closed in occupied habitat. National Forests and Grasslands in Texas have closed areas to off-road vehicle use, in part due to Louisiana pine snake considerations, and some road closures are under consideration.

Appendix I outlines management guidelines, including those relevant to road and vehicle issues, that could be implemented to improve the viability and begin restoration of Louisiana pine snakes in Texas.

Objective 4. Develop management guidelines for Louisiana pine snakes based on previous telemetry studies and survey data.

Previous research indicated that Louisiana pine snakes are inhabitants of pine and pine oak savannahs, primarily on sandy, well drained soils (Reichling 1995, Rudolph et al. 2002, Ealy et al. 2004). The presence of a well-developed herbaceous layer is also critical. A frequent fire return interval reduces the development of a dense midstory layer and allows a well-developed herbaceous layer to be maintained. These habitat characteristics are those necessary to support Baird's pocket gopher populations.

The available data demonstrates that the prey of Louisiana pine snakes consists primarily of Baird's pocket gophers (Rudolph et al. 2002). Habitat alteration that reduces the herbaceous vegetation can eventually result in depressed pocket gopher populations. It is hypothesized that at some point pocket gopher populations decline to a level that can no longer support viable Louisiana pine snake populations (Rudolph and Burgdorf 1997).

Based on available data the management of Louisiana pine snake populations would seem to require management for a fire-maintained savannah community on well-drained sandy uplands. These communities should be monitored to insure that an adequate herbaceous layer, supporting a healthy pocket gopher population, is present. Most potential habitat is within the historic longleaf pine belt, as are currently known extant populations Louisiana pine snake populations (Rudolph et al. in press). Longleaf pine, due to its many adaptations to survival in a frequent fire regime, is generally the most appropriate species to manage for in existing Louisiana pine snake habitat in Texas.

Louisiana pine snake habitat is generally similar to that required by Red-cockaded Woodpeckers (*Picoides borealis*), Bachman's Sparrows (*Aimophila bachmani*), and many additional plant and animal species of conservation concern on the West Gulf Coastal Plain. Habitat management for these species is often similar to that required for Louisiana pine snake and provides multiple opportunities that should not be overlooked.

Vehicle related mortality is occurring in Louisiana pine snake populations (Himes et al. 2002). The presence of roads and vehicle traffic within, and adjacent to, existing Louisiana pine snake populations in Texas should be addressed. Limited mitigation measures are available to reduce the levels of vehicle related mortality. Given the apparent critical status of the species in Texas, it would be prudent to address the issue of vehicle related mortality. Closing of occupied habitat to off-road vehicle use and closing roads, where feasible, would improve the probability of population survival and recovery.

In the long-term management should attempt to increase and expand populations of Louisiana pine snakes to reduce the probability of further declines. The existence of unoccupied blocks of apparently suitable habitat, within the historic range of the species, suggests that extant populations, currently existing in similar size blocks, are vulnerable to extirpation. It is critical that low quality habitat adjacent to currently occupied habitat be restored to allow population expansion. In the absence of population expansion, it is likely that the currently existing populations lack long-term viability.

A long-term management plan should also address the potential for establishing, or locating, additional populations. This would involve additional surveys for existing populations, possible establishment of a captive breeding program based on genetic stock from Texas, and reintroduction of the species to suitable unoccupied habitat. Any reintroduction program should only be undertaken after careful consideration by a diverse panel of experts.

SUMMARY

As a result of intensive survey efforts since 1993, the current status of the Louisiana pine snake in Texas is much improved. The Louisiana pine snake is rare and local in isolated small patches of suitable habitat, and is presumably extirpated from much of its historic range in the state. Habitat loss due to land use changes and alteration of the original fire regime are the primary causes of these declines. Intensive management of the remaining populations and their habitat is crucial to prevent final extirpation. In the long-term, management to restore habitat and expand populations is necessary to insure that viable populations are present.

ACKNOWLEDGMENTS

Partial support for this research was provided by the U. S. Fish and Wildlife Service, Texas Parks and Wildlife Department and Louisiana Department of Wildlife and Fisheries through Section 6 funding. Temple-Inland Inc, Champion International, International Paper Company, The Nature Conservancy, and Mill Creek Ranch provided access to study areas and other assistance. We also thank David Baggett, Ross Carrie, Jim Cathy, Chris Collins, Mike Duran, Marc Ealy, Robert Fleet, Mac Hardy, Jason Helvey, John Himes, Rich Johnson, Trish Johnson, Ellis Jones, Eric Keith Wendy Ledbetter, Theron Majors, Chris Melder, Ken Moore, Kevin Mundorf, John Neiderhofer, Scott Riddle, Steve Shively, Preston Taylor, Toni Trees, John Tull and others for field assistance. Texas Parks and Wildlife Department and Louisiana Department of Wildlife and Fisheries provided the necessary scientific collecting permits.

LITERATURE CITED

Anonymous. 2005. Candidate Conservation Agreement for the Louisiana Pine Snake (*Pituophis ruthveni*). U. S. Fish and Wildlife Service, Region 4, Atlanta, Georgia.

Bennett, A. F. 1991. Roads, roadsides and wildlife conservation, a review. Pp. 99-118 *in* D. A. Saunders and R. J. Hobbs (eds), Nature Conservation II: The Role of Corridors. Surrey Beatty & Sons, Heidelberg, Victoria, Australia.

Ealy, M. J., R. R. Fleet, and D. C. Rudolph. 2004. Diel activity patterns of the Louisiana pine snake (*Pituophis ruthveni*) in eastern Texas. Texas Journal of Science 56:383-394.

Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2002. Growth rates and mortality of the Louisiana pine snake (*Pituophis ruthveni*). Journal of Herpetology 36:683-687.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake and its relevance to the evolutionary species concept. Journal of Herpetology 29:186-198.

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 49:111-122.

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. 2002. Prey handling and diet of Louisiana pine snakes (*Pituophis ruthveni*) and black pine snakes (*P. melanoleucus lodingi*), with comparisons to other selected colubrid taxa. Herpetological Natural History 9:57-62.

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. Pp. 129-136 *in* G. L. Evink, P. Garrett, and D. Zeigler (eds.), Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99, Florida Department of Transportation, Tallahassee, Florida.

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 29:146-148.

Jackson, S. D. and C. R. Griffin. 1999. Toward a practical strategy for mitigating highway impacts on wildlife. Pp. 17-22 *in* G. L. Evink, P. Garrett, and D. Zeigler (eds.), Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99, Florida Department of Transportation, Tallahassee, Florida.

Table 1. List of TX Sec VI sites included in this report.

Locality	County	Owner	Habitat	Trap Days	Years Open	*P.r.* captures
Angelina NF (County Line) - south side of SH 65, 2 km SE of intersection with FS road 347	Jasper	USDAFS	Longleaf pine savannah	8745	2000-2003	Yes
Angelina NF (Owl) - South side of FS rd 306, 4 km E of intersection with FS rd 333	Jasper	USDAFS	Longleaf pine savannah	4090	2002-2005	No
Beef Creek - 3.2 km west of intersection SH 96 & R255	Jasper	Temple-Inland	Loblolly plantations with longleaf inclusions	3090	2003-2005	No
Garlington - 4.5 km west of intersection SH 96 & R255	Jasper	Temple-Inland	Loblolly plantations with longleaf inclusions	3090	2003-2005	No
Gus Engeling Wildlife Management Area - 3 km NE of Bethel	Anderson	State of Texas	Oak crosstimbers	5825	2000-2002	No
Little Rocky Preserve - CR 1007, 5 km SW of Browndell	Jasper	The Nature Conservancy	Mixed pine savannah	2275	2000-2001	No
Mill Creek Ranch - east of FM 2869, 2-3 km south of SH 154	Wood	Private	Oak crosstimbers	10765	2000-2003	No
Sabine NF (Comp. 135) - compartment 135, south of FS rd 117	Sabine	USDAFS	Longleaf pine savannah	*To be updated*		No
Sabine NF (Pineland) - 5 km east of Pineland, east side of FS rd 119 in FS compartment 91	Sabine	USDAFS	Longleaf pine savannah	4280	2000-2003	No
Sabine NF (San Augustine Sandhills) - compartments 51 & 52 near intersection SH 147 & FM 1279	San Augustine	USDAFS	Longleaf pine savannah	1970	2002-2003	No

Table 1. List of TX Sec VI sites included in this report.

Sabine NF (Stark tract) - south of FS rd 196 in FS compartments 141 & 142	Sabine & Newton	USDAFS	Longleaf pine savannah	2310	2000-2001	No
Scrappin' Valley - 9 km NE of Mayflower	Newton	Temple-Inland	Loblolly plantations	6500	2000-2005	No
Tonkawa - north of FM 1087, 9 km west of Garrison	Nacogdoches	Temple-Inland	Loblolly plantations with pine-oak savannah	9435	2000-2002	No
Woodpecker Hill - 6.5 km east of Hillister	Tyler	Louisiana Pacific	Loblolly plantations with longleaf inclusions	3090	2003-2005	No

Table 2. Snake Captures by Species - 2005

Trap Number

Species	BC-1	BC-2	BC-3	BC-4	BC-5
Agkistrodon contortrix	1	1			5
Agkistrodon piscivorus					
Cemophora coccinea					
Coluber constrictor					
Elaphe guttata					
Elaphe obsoleta			1	2	1
Farancia abacura					
Heterodon platirhinos					
Masticophis flagellum	6	1	3	8	7
Micrurus fulvius					
Thamnophis proximus					
Unidentified					
Total 36	7	2	4	10	13

SV-1	SV-2	SV-3	SV-4	SV-5	Species
1	2			4	*Agkistrodon contortrix*
				1	*Agkistrodon piscivorus*
					Cemophora coccinea
1		1			*Coluber constrictor*
1		2			*Elaphe guttata*
3	3	2			*Elaphe obsoleta*
					Farancia abacura
					Heterodon platirhinos
10	4	8		1	*Masticophis flagellum*
1			1		*Micrurus fulvius*
					Thamnophis proximus
					Unidentified
17	9	13	1	6	**Total 46**

Species	GA-1	GA-2	GA-3	GA-4	GA-5
Agkistrodon contortrix	2	3	1	3	3
Agkistrodon piscivorus					
Cemophora coccinea					
Coluber constrictor		1			
Elaphe guttata	3	4	1	4	2
Elaphe obsoleta		3			
Farancia abacura					
Heterodon platirhinos					1
Masticophis flagellum	5	3	10	9	4
Micrurus fulvius				1	1
Thamnophis proximus					
Unidentified			1		
Total 65	10	14	13	17	11

WH-1	WH-2	WH-3	WH-4	WH-5	Species
2	2	1			*Agkistrodon contortrix*
					Agkistrodon piscivorus
					Cemophora coccinea
		4			*Coluber constrictor*
	1	1		1	*Elaphe guttata*
2	2				*Elaphe obsoleta*
					Farancia abacura
					Heterodon platirhinos
5	5	8		8	*Masticophis flagellum*
6	1		1		*Micrurus fulvius*
1					*Thamnophis proximus*
					Unidentified
16	11	14	1	9	**Total 51**

Species	Owl-1	Owl-2	Owl-3	Owl-4	Owl-5
Agkistrodon contortrix	3				2
Agkistrodon piscivorus					
Cemophora coccinea		1			
Coluber constrictor	2	1			1
Elaphe guttata	1	1		2	1
Elapho obsoleta					1
Farancia abacura					1
Heterodon platirhinos			1		
Masticophis flagellum	2				5
Micrurus fulvius					
Thamnophis proximus					1
Unidentified					
Total 26	8	3	1	2	12

Grand total = 224

Legend

BC = Beef Creek
GA = Garlington
Owl = ANFOwl Cluster
SV = Scrappin' Valley
WH = Woodpecker Hill

Table 3. Other Vertebrate Captures by Species - 2005

Species	Trap Number											Species
	BC-1	BC-2	BC-3	BC-4	BC-5		SV-1	SV-2	SV-3	SV-4	SV-5	
Unidentifiable anuran												Unidentifiable anuran
Bufo. sp.												*Bufo* sp.
Bufo valliceps		3		1			1			1		*Bufo valliceps*
Bufo woodhousii							1					*Bufo woodhousii*
Rana sp.												*Rana* sp.
Rana catesbeiana												*Rana catesbeiana*
Rana clamitans												*Rana clamitans*
Rana sphenocephala				1								*Rana sphenocephala*
Anolis carolinensis	1		5	1			2					*Anolis carolinensis*
Cnemidophorus sexlineatus			1	1					1	1	2	*Cnemidophorus sexlineatus*
Eumeces fasciatus									1			*Eumeces fasciatus*
Ophisaurus attentuatus												*Ophisaurus attentuatus*
Sceloporus undulatus		1	3	2	1							*Sceloporus undulatus*
Scincella lateralis												*Scincella lateralis*
Terrapene ornata												*Terrapene ornata*
Unidentifiable bird										1		Unidentifiable bird
Aimophilus aestivalis		1										*Aimophilus aestivalis*
Thryothorus ludovicianus		1					1		5			*Thryothorus ludovicianus*
Blarina carolinensis												*Blarina carolinensis*
Chaetodipus hispidus			1									*Chaetodipus hispidus*
Cryptotis parva												*Cryptotis parva*
Didelphis virginiana												*Didelphis virginiana*
Geomys breviceps										1		*Geomys breviceps*
Mustela frenata												*Mustela frenata*
Neotoma floridana												*Neotoma floridana*
Ochrotomys nuttallii												*Ochrotomys nuttallii*
Peromyscus sp.	1		1		3							*Peromyscus* sp.
Reithrodontomys fulvescens									1			*Reithrodontomys fulvescens*
Sciurus sp.												*Sciurus* sp.
Sigmodon hispidus					2		1				3	*Sigmodon hispidus*
Sylvilagus floridanus				3						1	2	*Sylvilagus floridanus*
Unidentifiable small mammal												Unidentifiable small mammal
Total 34	2	6	11	9	6		6	0	8	5	7	**Total 26**

Table 3. Other Vertebrate Captures by Species - 2005

Species	Trap Number: GA-1	GA-2	GA-3	GA-4	GA-5	WH-1	WH-2	WH-3	WH-4	WH-5	Species
Unidentifiable anuran							1		1		Unidentifiable anuran
Bufo sp.											*Bufo* sp.
Bufo valliceps					1						*Bufo valliceps*
Bufo woodhousii		1									*Bufo woodhousii*
Rana sp.							1				*Rana* sp.
Rana catesbeiana											*Rana catesbeiana*
Rana clamitans											*Rana clamitans*
Rana sphenocephala		2	1			2		1	1	1	*Rana sphenocephala*
Anolis carolinensis	1		1	7	1	1	1			2	*Anolis carolinensis*
Cnemidophorus sexlineatus	2	1	3							2	*Cnemidophorus sexlineatus*
Eumeces fasciatus											*Eumeces fasciatus*
Ophisaurus attentuatus									1		*Ophisaurus attentuatus*
Sceloporus undulatus				1							*Sceloporus undulatus*
Scincella lateralis											*Scincella lateralis*
Terrapene ornata							1				*Terrapene ornata*
Unidentifiable bird											Unidentifiable bird
Aimophilus aestivalis									2		*Aimophilus aestivalis*
Thryothorus ludovicianus	1										*Thryothorus ludovicianus*
Blarina carolinensis						1					*Blarina carolinensis*
Chaetodipus hispidus											*Chaetodipus hispidus*
Cryptotis parva				1							*Cryptotis parva*
Didelphis virginiana											*Didelphis virginiana*
Geomys breviceps											*Geomys breviceps*
Mustela frenata											*Mustela frenata*
Neotoma floridana								1			*Neotoma floridana*
Ochrotomys nuttallii										2	*Ochrotomys nuttallii*
Peromyscus sp.	1				1		1	5		5	*Peromyscus* sp.
Reithrodontomys fulvescens											*Reithrodontomys fulvescens*
Sciurus sp.			1				1				*Sciurus* sp.
Sigmodon hispidus	2						3		1	1	*Sigmodon hispidus*
Sylvilagus floridanus	1	1								1	*Sylvilagus floridanus*
Unidentifiable small mammal				1	1				1		Unidentifiable small mammal
Total 33	8	5	6	10	4	4	9	7	7	14	**Total 41**

Table 3. Other Vertebrate Captures by Species - 2005

	Trap Number				
Species	**Owl-1**	**Owl-2**	**Owl-3**	**Owl-4**	**Owl-5**
Unidentifiable anuran					
Bufo sp.			1		
Bufo valliceps		1	1		1
Bufo woodhousii			4	9	
Rana sp.					
Rana catesbeiana			1		1
Rana clamitans	1				
Rana sphenocephala					
Anolis carolinensis	1	5		1	1
Cnemidophorus sexlineatus	4	7	11	4	
Eumeces fasciatus					1
Ophisaurus attentuatus		2			
Sceloporus undulatus	1	1		2	
Scincella lateralis				1	
Terrapene ornata					
Unidentifiable bird					
Aimophilus aestivalis					
Thryothorus ludovicianus					1
Blarina carolinensis	1				
Chaetodipus hispidus					
Cryptotis parva					
Didelphis virginiana				1	1
Geomys breviceps					1
Mustela frenata					1
Neotoma floridana					
Ochrotomys nuttallii					1
Peromyscus sp.	1	1		2	
Reithrodontomys fulvescens					
Sciurus sp.					
Sigmodon hispidus			1	2	
Sylvilagus floridanus	1			1	1
Unidentifiable small mammal					
Total 79	10	17	19	23	10

Totals by Species

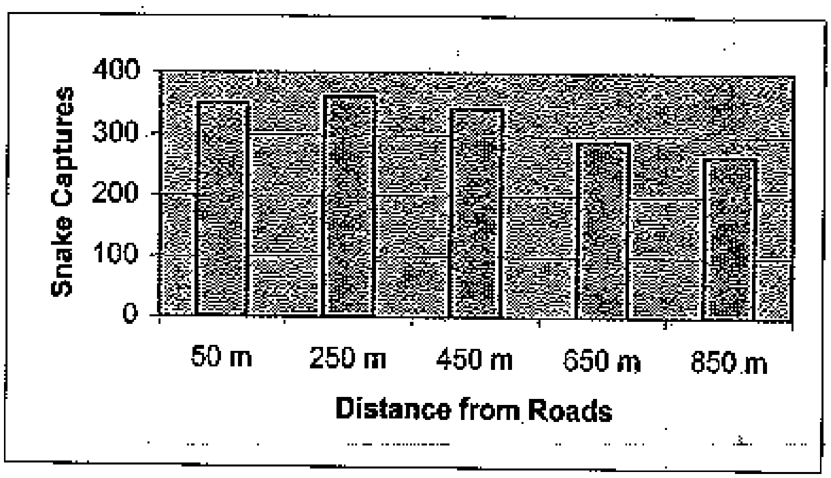
2	Unidentifiable anuran
1	*Bufo* sp.
10	*Bufo valliceps*
15	*Bufo woodhousii*
1	*Rana* sp.
2	*Rana catesbeiana*
1	*Rana clamitans*
9	*Rana sphenocephala*
31	*Anolis carolinensis*
40	*Cnemidophorus sexlineatus*
2	*Eumeces fasciatus*
3	*Ophisaurus attentuatus*
12	*Sceloporus undulatus*
1	*Scincella lateralis*
1	*Terrapene ornata*
1	Unidentifiable bird
3	*Aimophilus aestivalis*
9	*Thryothorus ludovicianus*
2	*Blarina carolinensis*
1	*Chaetodipus hispidus*
1	*Cryptotis parva*
2	*Didelphis virginiana*
2	*Geomys breviceps*
1	*Mustela frenata*
1	*Neotoma floridana*
3	*Ochrotomys nuttallii*
22	*Peromyscus sp.*
1	*Reithrodontomys fulvescens*
2	*Sciurus* sp.
16	*Sigmodon hispidus*
12	*Sylvilagus floridanus*
3	Unidentifiable small mammal
213	

Legend

BC = Beef Creek
GA = Garlington
Owl = ANF Owl Cluster
SV = Scrappin' Valley
WH = Woodpecker Hill

Table 4. Snake captures at varying distances from roads.

Locality	Number of years trapped	Distance from Road 50 m	250 m	450 m	650 m	850 m	Totals
Angelina NF (County Line)	4	21	42	28	49	51	191
Angelina NF (Owl)	4	35	43	29	25	30	162
Gus Engeling Wildlife Management Area	3	64	76	66	36	17	259
Mill Creek Ranch	4	64	83	59	53	51	310
Sabine NF (Pineland)	4	18	24	23	20	18	103
Scrappin' Valley	5	95	52	104	69	57	377
Tonkawa	3	53	41	33	38	42	207
	Totals	350	361	342	290	266	



DRAFT

Status of the Louisiana Pine Snake, *Pituophis ruthveni*

D. Craig Rudolph[a,*], Shirley J. Burgdorf[a,§], Richard R. Schaefer[a], Richard N. Conner[a], Ricky W. Maxey[b]

[a]Wildlife Habitat and Silviculture Laboratory (maintained in cooperation with the College of Forestry, Stephen F. Austin State Univ.), U.S.D.A. Forest Service, Southern Research Station, 506 Hayter Street, Nacogdoches, TX 75962, U. S. A.

[b]Texas Parks and Wildlife Department, P. O. Box 4655, SFASU, Nacogdoches, TX 75962, U. S. A.

[§]Current address: U. S. Fish and Wildlife Service, 510 Desmond Drive, Suite 102, Lacey, WA 98503-1263, U. S. A.

* Corresponding Author. Tel.: 936-569-7981; *E-mail address:* *crudolph01@fs.fed.us*

ABSTRACT

Extensive trapping surveys across the historic range of the Louisiana pine snake (*Pituophis ruthveni* Stull) suggest that extant populations are extremely small and limited to remnant patches of suitable habitat in a highly fragmented landscape. Evaluation of habitat at all known historic localities of *P. ruthveni* documents the widespread degradation of the fire-maintained pine ecosystem throughout the historic range of the species. The primary factors leading to degradation of *P. ruthveni* habitat are intensive pine silviculture and alteration of the pre-European fire regime. Habitat restoration on public lands is feasible and could potentially restore populations of this critically rare species.

INTRODUCTION

The Louisiana pine snake, *Pituophis ruthveni*, has long been considered one of the rarest snakes in the United States (Conant 1956, Young and Vandeventer 1988). *Pituophis ruthveni* is restricted to eastern Texas and west-central Louisiana, a range that coincides with that of *Pinus palustris* Mill. (longleaf pine) on the west Gulf Coastal Plain (Conant 1956, Thomas et al. 1976, Reichling, 1995). Prior to recent fieldwork, fewer than 60 records of *P. ruthveni* were represented in the literature or museum collections.

Until recently, very little was known concerning the ecology of *P. ruthveni*. Available information consisted primarily of distribution and habitat data based on collection records (Conant, 1956, Thomas et al., 1976, Young and Vandeventer 1988) and reproductive biology in captivity (Reichling 1990). This paucity of information stimulated recent investigations into the ecology of *P. ruthveni* (Rudolph and Burgdorf 1997; Rudolph et al. 1998, 2002; Himes et al. 2002, 2003a, 2003b). This work suggests that alteration of the fire regime has led to habitat alteration resulting in declines of *Geomys breviceps* Baird (Baird's pocket gopher), a primary prey of *P. ruthveni* (Rudolph et al. 2002). These changes are thought to have led to population declines of *P. ruthveni*.

The limited range of *P. ruthveni*, combined with its apparent rarity, have led to recent concerns about the conservation status of the species (Young and Vandeventer 1988; Reichling 1990, 1995). Recent authors have suggested that range restrictions and population declines have been substantial (Young and Vandeventer 1988, Reichling 1995). Past and ongoing habitat alterations, due to loss of forest habitat, intensive silviculture, and alteration of fire regimes, have been severe throughout the range of the species, further heightening concern about the status of *P. ruthveni* (Reichling 1995, Rudolph and Burgdorf 1997, Rudolph et al. 1998). In response to these developments the U. S. Fish and Wildlife Service has recently initiated an evaluation of the status of the species.

During the course of our investigations of the ecology of *P. ruthveni*, we have conducted extensive trapping for the species throughout its historic range, visited all known localities, and obtained data on habitat, diet, and behavior (Himes et al. 2002, 2003a, 2003b; Rudolph and Burgdorf 1997; Rudolph et al. 1998, 2002). A substantial number of recent distributional records resulted from this field work, and it is appropriate to assess the current status and distribution of *P. ruthveni*.

MATERIALS AND METHODS

Beginning in March 1993, traps were installed in Texas and Louisiana within the general limits of the historic range of *P. ruthveni*. Trap sites were initially chosen based on recent records and suitability of habitat to maximize the probability of capturing individuals. Subsequent sites were chosen from localities within the historic range of the species representing a range of habitat conditions.

Traps consisted of treated plywood tops and bottoms (1.2 X 1.2 m) supported by wooden uprights 0.45 m in height. The sides were screened with hardware cloth (3.2 or 1.5 mm mesh). A hinged door in the top allowed access by investigators. Snakes could enter the traps through 4 funnel entrances constructed of hardware cloth and placed in the midpoint of each side of the trap. Drift fences extended approximately 15 m from each funnel entrance. These were constructed of hardware cloth approximately 60 cm in width and buried approximately 10 cm in the soil. A water source was placed in each trap.

Traps were operational from early March to late October inclusive, the approximate activity period of *P. ruthveni* (unpubl. data). Captured *P. ruthveni* were returned to the Laboratory. Snakes were sexed, measured (SVL, TL, mass), and implanted with a PIT tag or radio-transmitter depending on current research needs. Snakes were returned to the point of capture within 2-14 days of implanting procedures.

Habitat was assessed at each trap site. In addition, all historical localities of *P. ruthveni* were visited and habitat assessed. For purposes of this research, habitats were ranked, on a four-category scale, from excellent to poor based on the following criteria:

Excellent - forested habitat; sandy, well-drained soils predominate; at least 50% herbaceous cover; pocket gophers widespread and common.

Good - forested habitat; sandy, well-drained soils present; at least 25% herbaceous cover; pocket gophers present.

Marginal - forested habitat; sandy, well-drained soils present; at least 10% herbaceous cover; pocket gophers present (at least along highway and utility rights-of-way).

Poor - failure to meet any one of the above minimum criteria.

These general criteria were based on information in the literature and obtained during our radio-telemetry studies (Rudolph and Burgdorf 1997).

RESULTS

Traps were placed at 14 sites in 10 counties in Texas and at 9 sites in 5 parishes in Louisiana between 1993 and 2001. A total of 98,143 trap days were accumulated during this nine-year period resulting in the capture of 2372 snakes of 23 species. Twenty-six *P. ruthveni* were captured (Table 1). Overall, trap success was one *P. ruthveni* per 3775 trap days. However, for sites where at least one *P. ruthveni* was captured (n = 6), the success rate was one snake per 733 trap days (range one snake per 355 to 1888 trap days). Eleven of the 23 sites were within 15 km of a historic locality for *P. ruthveni*, and the species was captured at five of these sites. Nine of these eleven sites had good or excellent habitat. The twelve remaining sites were within the general area of the historic range, but > 15 km from known locality records; *P. ruthveni* was not captured at any of these sites. Eleven of these 12 sites had some good or excellent habitat remaining. Habitat that qualified as good or excellent is currently rare in eastern Texas and west-central Louisiana due to habitat alteration. Most sites are small, a few hundred hectares, and isolated.

The 137 records of *P. ruthveni* available through 2001 are from 15 counties in Texas and nine parishes in Louisiana (Fig. 1). Since 1990, a total of 37 records of *P. ruthveni* are available. All but two of these records are from six limited areas in four counties (Angelina, Jasper, Newton, Sabine) in Texas and four parishes

(Bienville, Nachitoches, Vernon, Winn) in Louisiana (Fig. 2). The two additional records are single individuals from Tyler and Montgomery Cos. in Texas.

The recent habitat condition (1999-2000) at all known *P. ruthveni* localities in Texas and Louisiana is summarized in Table 2. A total of 118 localities were evaluated and 53 (45%) of the localities retain some habitat in excellent or good condition. On public lands, 26 of 37 localities (70%) fall into the excellent or good categories, and on privately owned lands only 27 of 81 (33%) of the localities retain some habitat in excellent or good condition. The situation on private lands is changing rapidly. Of the 27 localities assessed as excellent or good, 10, all in Bienville Parish, LA, are currently being altered due to changes in silvicultural practices, primarily through intensified management of short-rotation pine plantations.

DISCUSSION

Pituophis ruthveni has always been considered rare (Stull 1940, Conant 1956). Recent studies have expressed concern about the current status of the species (Young and Vandeventer 1988; Reichling 1990, 1995). The results of our trapping surveys and our assessment of habitat condition at all known *P. ruthveni* localities support the concern that *P. ruthveni* may have declined in occurrence and possibly in local abundance. Detailed locality information is not provided due to the intense collecting effort to supply the commercial pet trade, especially in Louisiana.

Trap success was low at all sites where *P. ruthveni* is known to occur. We are, however, confident that our traps were effective in capturing snakes. Large numbers of snakes were captured, including all of the larger species regularly occurring in upland habitats in the region. Although our trap surveys were not designed to provide estimates of population size, occasional recaptures suggest that the currently existing populations are not large. How the current population densities compare to those prior to extensive habitat alteration is unknown.

Currently *P. ruthveni* populations are known to exist, based on multiple records since 1990, in six general areas. In Texas, populations exist on the southern portion of the Angelina National Forest in Angelina and Jasper Counties, on the southern portion of the Sabine National Forest in Sabine County, and on private land immediately south of the Sabine National Forest in Newton County. In Louisiana, *P. ruthveni* populations currently exist on Fort Polk Military Reservation and the adjacent unit of the Kisatchie National Forest in Vernon Parish, and on Peason Ridge Military Reservation in Vernon and Nachitoches Parishes. Another population exists in an extensive area on primarily private lands, mostly industrial timber lands, in Bienville and extreme northern Nachitoches Parishes.

Much of the remaining suitable habitat in Bienville Parish is currently undergoing a major increase in the intensity of the silvicultural management of pine plantations, and the future of this population is unclear. In Sabine and Newton Counties in Texas currently occupied habitat is limited to a few hundred hectares. Only three areas, Fort Polk Military Reservation and the adjacent unit of the Kisatchie National Forest, and Peason Ridge Military Reservation in Louisiana and the southern portion of the Angelina National Forest in Texas have extensive areas of suitable, frequently burned longleaf pine habitat remaining that is not currently subject to extensive change in management intensity.

Our extensive trapping and collecting at 17 additional sites since 1993 failed to document the existence of other extant populations. Most of these sites are at or near historical *P. ruthveni* localities. We suggest that the combined effects of habitat alteration and fragmentation have eliminated *P. ruthveni* from significant portions of its historic range. However, the single individuals recorded from Tyler and Montgomery Counties in Texas during the 1990s suggest that remnant populations may still persist in these fragmented and degraded habitats. In addition, substantial amounts of suitable habitat still exist on the Kisatchie District of the Kisatchie National Forest in southern Nachitoches Parish, Louisiana. Historical records are known from the Kisatchie District and our trapping in this area did not, in retrospect, sample the best remaining habitat. This area probably has the highest potential for finding additional extant populations of *P. ruthveni,* and we recommend that surveys be conducted in this area.

Pituophis ruthveni is closely associated with longleaf pine growing on sandy, well-drained soils (Conant 1956 Young and Vandeventer 1988, Reichling 1995, Himes et al. 2003b). The once extensive longleaf pine ecosystem of the southeastern United States is one of the most threatened ecosystems in the United States (Bridges and Orzell 1989, Frost, 1993, Conner et al. 2001). Less than 5% of the original extent of the longleaf pine ecosystem survives, and much that remains is extensively altered by changes in fire regimes, silviculture, and land use changes (Frost 1993). *Pituophis ruthveni* is also closely associated with a well-developed herbaceous ground cover of grasses and forbs, and with *Geomys breviceps* that are dependent on herbaceous vegetation (Rudolph and Burgdorf 1997, Rudolph et al. 2002, Himes et al. 2003b). *Pituophis ruthveni* use pocket gopher burrow systems for subsurface retreats, including hibernacula and escape from fire, and prey heavily on pocket gophers (Young and Vandeventer 1988; Rudolph and Burgdorf 1997; Rudolph et al. 1998, 2002).

Most of the longleaf pine ecosystem that occurred on the West Gulf Coastal Plain has been converted to other land uses including urbanization, agriculture, and intensive silviculture. These land uses appear to be incompatible with the survival of *P. ruthveni*. The less intensive silvicultural practices of the past, specifically longer rotations and use of prescribed fire, were often compatible with the existence of *P. ruthveni* populations. The substantial *P. ruthveni* population in Bienville Parish, for example, existed primarily on industrial forest land managed using fairly long rotations and prescribed fire for control of competing vegetation. However, the development and increasing implementation of more intensive silvicultural practices is eliminating much of the remaining suitable habitat on private lands. These practices include clear-cutting, intensive mechanical site preparation, planting of pine species other that longleaf, short rotations, fertilization, and use of herbicides instead of prescribed fire for control of competition. The substitution of herbicides for prescribed fire likely has an important impact on *P. ruthveni*. Silvicultural managers use herbicides to control herbaceous as well as woody vegetation, both of which compete with the pine crop. The absence of fire allows the continuous buildup of a thick duff layer further suppressing the herbaceous layer. The ultimate result is a highly altered forest with a minimal herbaceous component, conditions apparently unsuitable for pocket gophers or *P. ruthveni* (Reichling 1995, Rudolph and Burgdorf 1997).

The known existing populations of *P. ruthveni* are concentrated on public lands (national forests and military installations) and private lands managed for a diversity of wildlife values. Compared to most private lands, management of public lands tends to include less intensive site preparation, longer timber rotations, retention of longleaf pine, and use of prescribed fire both for control of competing vegetation and management of a fire-maintained ecosystem. However, even on public lands, the current fire regime on most sites is insufficient to maintain a sparse midstory and diverse herbaceous understory (Conner and Rudolph 1989). Consequently, most pine habitat has a well-developed hardwood midstory and only a sparse herbaceous component due to competition from woody species in the mid- and understory. Recent records of *P. ruthveni* are primarily from the isolated patches of habitat where the influence of fire has been most effective in well-developed herbaceous understory conditions.

The situation on most private lands is different. Industrial forest lands and significant portions of smaller private ownerships are intensively managed for fiber production. The practices used, especially the short rotations and substitution of herbicides for prescribed fire, preclude the existence of a well-developed herbaceous community. These lands, based on recent records and trapping surveys, do not support viable populations of *P. ruthveni*.

Populations of *P. ruthveni* are also subject to impact by the increasing density of roads and associated vehicular traffic, including off-road vehicles. Although the absolute numbers were small, 25 % (3 of 12) of mortalities of radio-tracked *P. ruthveni* were caused by vehicles (unpubl. data). In addition, research conducted in association with surveys for *P. ruthveni* suggests that populations of large snake species may be reduced by 50% within 500 m of roads with moderate traffic levels (Rudolph et al. 1999). Most existing *P. ruthveni* habitat is within 500 m of currently existing roads.

Pituophis ruthveni is currently rare in the relict patches of fire-maintained pine habitat that remain, primarily on public lands. These areas are reasonably well dispersed throughout the historic range of the species. Intervening habitats that once supported populations of *P. ruthveni* are increasingly altered, primarily by intensive silviculture, and the species is, or may soon be, extirpated. The existing populations on national forests, military installations, and private lands are presumably small and increasingly fragmented due to habitat alteration. The long-term survival of these populations depends on sufficient management to reverse the decline of the fire-maintained pine ecosystem, primarily in the longleaf pine habitats.

Most critical is the restoration of a prescribed fire regime sufficient to prevent the encroachment of a dense hardwood midstory and recovery of a vigorous herbaceous community. Economic considerations may preclude improvement on private lands, with the limited exception of small areas specifically managed for *P. ruthveni* and other species adapted to fire-maintained pine ecosystems. However, numerous obstacles exist, especially in implementing an adequate prescribed fire regime. Managers need to resolve issues relating to liability, smoke management, air quality standards, and agency regulations to effectively use fire as a management tool to support viable populations of *P. ruthveni* and overall biodiversity in the long term. In addition, environmental groups have obtained rulings in federal courts limiting the use of prescribed fire on National Forests and Grasslands in Texas.

The potential for restoration on public lands is considerably greater than on private lands. Management of national forest lands and military installations within the range of *P. ruthveni* currently include prescribed fire as a management tool. Increased use of prescribed fire is planned, driven primarily by the management needs of *Picoides borealis* (Vieillot), the Red-cockaded Woodpecker, a federally listed endangered species. Habitat management appropriate for the *Picoides borealis* is also appropriate for *P. ruthveni*, and numerous additional species adapted to fire-maintained pine ecosystems, many of which are of conservation concern (Bridges and Orzell 1989; Conner et al. 2001).

The current status of *P. ruthveni* is a result of habitat alteration due primarily to widespread intensive silviculture and alteration of the pre-European fire regime. Extant populations appear to be extremely small, and inhabit limited patches of suitable habitat that are highly fragmented and isolated. Without improved management of fire-maintained pine habitats, recovery and possibly survival of *P. ruthveni* is unlikely.

ACKNOWLEDGMENTS

We thank Steve Reichling, Lee Fitzgerald, and two anonymous reviewers for comments on an early draft of this manuscript. Partial support for this research was provided by the U. S. Fish and Wildlife Service, Texas Parks and Wildlife Department, the Louisiana Department of Game and Fisheries, and Temple-Inland, Inc. Temple-Inland, Inc., Champion International, International Paper Company, The Nature Conservancy, and Mill Creek Ranch provided access to study areas. We also thank David Baggett, Ross Carrie, Jim Cathy, Chris Collins, Mike Duran, Marc Ealy, Robert Fleet, Mac Hardy, Jason Helvey, John Himes, Rich Johnson, Trish Johnson, Ellis Jones, Eric Keith, Wendy Ledbetter, Theron Magers, Chris Melder, Ken Moore, Kevin Mundorf, John Neiderhofer, Scott Riddle, Steve Shively, Preston Taylor, Tony Trees, John Tull and others for field assistance. Texas Parks and Wildlife Department and the Louisiana Department of Wildlife and Fisheries provided the necessary scientific collecting permits.

LITERATURE CITED

Bridges, E. L. and S. L. Orzell. 1989. Longleaf pine communities of the west Gulf Coastal Plain. Natural Areas Journal 9:246-263.

Conant, R. 1956. A review of two rare pine snakes from the gulf coastal plain. American Museum Novitates 1781:1-31.

Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded Woodpecker colony status and trends on the Angelina, Davy Crockett and Sabine National Forests. U.S. Department of Agriculture, Forest Service Research Paper SO-250, New Orleans, LA.

Conner, R. N., D. C. Rudolph, and J. R. Walters. 2001. The Red-cockaded Woodpecker: surviving in a fire-maintained ecosystem. University of Texas Press, Austin, TX. 363 pp.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proceedings of Tall Timbers Fire Ecology Conference 18:17-43.

Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2002. Growth rates and mortality of the Louisiana pine snake (*Pituophis ruthveni*). Journal of Herpetology 36:683-687.

Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2003a. Body temperature variations of the Louisiana pine snake (*Pituophis ruthveni*) in a longleaf pine ecosystem. Herpetological Natural History 9:117-126.

Himes, J. G., L. M. Hardy, D. C. Rudolph, and S. J. Burgdorf. 2003b. Movement patterns and habitat selection by native and repatriated Louisiana pine snakes (*Pituophis ruthveni*): implications for conservation. Herpetological Natural History 9:103-116.

Reichling, S. B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). Southwestern Naturalist 35:221-222

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. Journal of Herpetology 29:186-198.

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 (supplement): 111-122.

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., Garrett, P., Seigler, D. (Eds.), Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99. Florida Department of Transportation, Tallahassee, FL, pp. 129-136.

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 29:146-148.

Rudolph, D. C., S. J. Burgdorf, R. N. Conner, C. S. Collins, D. Saenz, R. R. Schaefer, and T. Trees. 2002. Prey handling and diet of the Louisiana pine snakes (*Pituophis ruthveni*) and black pine snakes (*P. melanoleucus lodingi*), with comparisons to other selected colubrid taxa. Herpetological Natural History 9:57-62.

Stull, O. G. 1940. Variations and relationships in snakes of the genus *Pituophis*. Bulletin of the United States National Museum 175:1-225.

Thomas, R. A., B. J. Davis, and M. R. Culbertson. 1976. Notes on variation and range of the Louisiana pine snake, *Pituophis melanoleucus ruthveni* Stull (Reptilia, Serpentes, Colubridae). Journal of Herpetology 10:252-254.

Young, R. A. and T. L. Vandeventer. 1988. Recent observations on the Louisiana pine snake, *Pituophis melanoleucus ruthveni* (Stull). Bulletin of the Chicago Herpetological Society 23:203-207.

Table 1. Trap results for Louisiana pine snakes in Louisiana and Texas (1993-2001)

LOCATION	COUNTY/PARISH	# TRAP DAYS	# SNAKE CAPTURES	MEAN NUMBER DAYS/CAPTURE
Kepler Lake Area	Bienville Par., LA	3900	11	355
Kisatchie NF*, Winn District	Nachitoches /Winn Par., LA	5664	3	1888
Kisatchie NF, Kisatchie District	Nachitoches Par., LA	8575	0	-
Kisatchie NF, Vernon District	Vernon Par., LA	260	0	-
Cravens	Vernon Par., LA	2550	0	-
Hoy	Beauregard Par., LA	3675	0	-
Singer	Beauregard Par., LA	3675	0	-
Dido	Vernon Par., LA	735	0	-
Anacoco	Vernon Par., LA	2252	0	-
Sabine NF, Foxhunter's Hill	Sabine Co., TX	5226	6	871

Sabine NF, Stark Tract	Newton Co., TX	2425	0	-
Sabine NF, San Augustine Sandhills	San Augustine Co., TX	1235	0	-
Sabine NF, Pineland	San Augustine Co., TX	2425	0	-
Scrappin' Valley, North	Newton Co., TX	1260	3	420
Scrappin' Valley, South	Newton Co., TX	2425	0	-
Little Rocky	Jasper Co., TX	2208	0	-
Angelina NF, Southern Portion	Angelina/Jasper Cos., TX	3018	3	1006
Angelina NF, western Portion**	Angelina Co., TX	0	0	-
Mill Creek Ranch	Wood Co., TX	0	0	-
Roy E. Larsen Sandylands Preserve	Hardin Co., TX	0	0	-

Brushy Creek	Trinity Co., TX	0	0	-
Gus Engling WMA***	Anderson Co., TX	0	0	-
Tonkawa	Nacogdoches Co., TX	0	0	-
Total All Areas		98,143	26	733****

* National Forest

** Four closely associated sites

***Wildlife Management Area

****Locations with 0 captures deleted

Table 2. Habitat quality assessments of historic Louisiana pine snake localities on public and private lands in eastern Texas and eastern Louisiana. Entries are number of localities (%) for all known records.

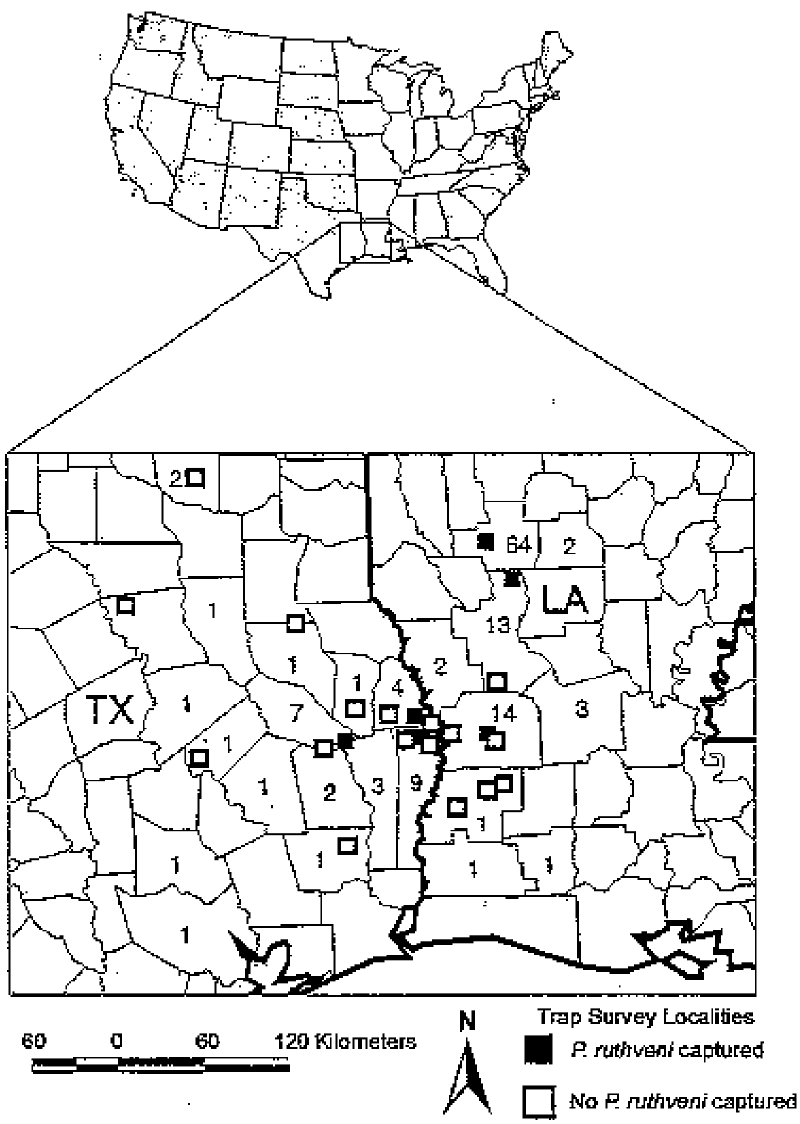
OWNERSHIP	EXCELLENT	GOOD	MARGINAL	POOR
Public	16 (43)	10 (27)	3 (8)	8 (22)
Private	14 (17)	13 (16)	16 (20)	38 (47)
Total	30 (25)	23 (19)	19 (16)	46 (39)

Figure Legends

Figure 1. Louisiana pine snake records by county and parish, and localities of trapping surveys conducted during this study. Numbers indicate total records of Louisiana pine snakes, historical and this study, for each county or parish. Open squares indicate approximate location of trapping localities where pine snakes were not captured; solid squares indicate approximate location of trapping localities where snakes were captured or known to occur since 1990.

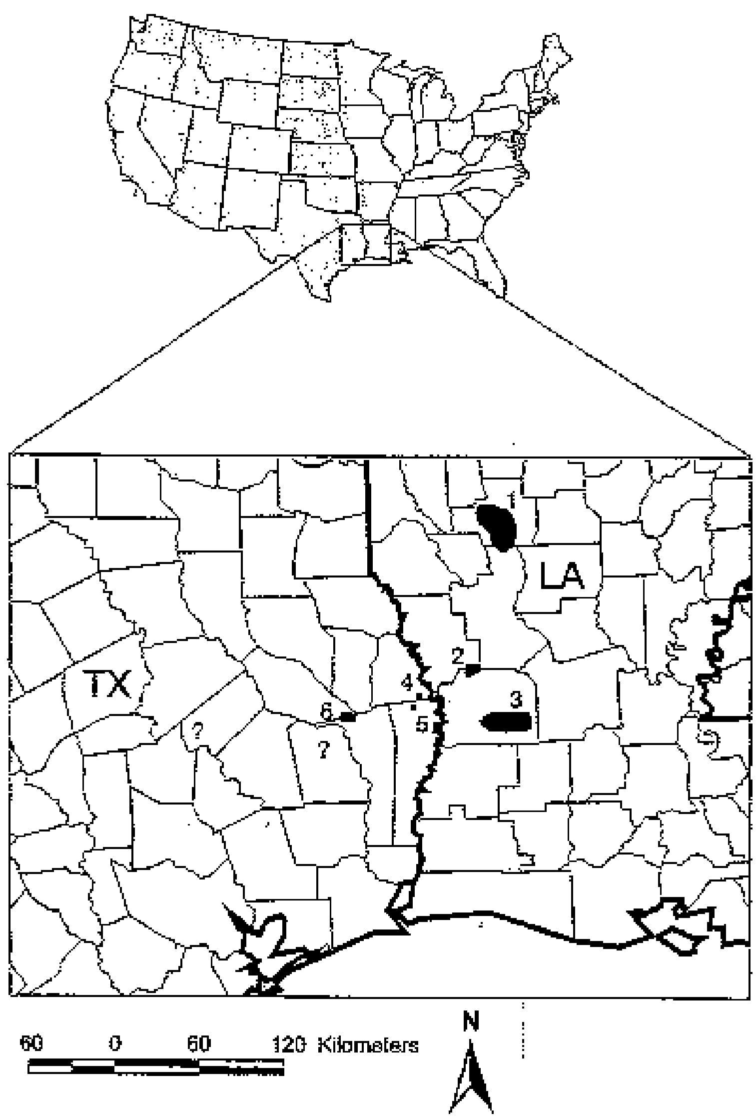
Figure 2. Approximate location (black) of extant populations of Louisiana pine snakes (multiple records since 1990). Questionmarks indicate single records in areas lacking significant amounts of suitable habitat.

Fig. 1



TX
LA
2
1
1
1
7
1
4
2
13
64
2
14
3
1
1
2
3
9
1
1
1
1
1
1
60 0 60 120 Kilometers
N
Trap Survey Localities
P. ruthveni captured
No P. ruthveni captured

Fig. 2



CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

BETWEEN

U. S. Fish and Wildlife Service

U.S. Forest Service

Fort Polk, U. S. Department of Defense

Texas Parks and Wildlife Department

Louisiana Department of Wildlife and Fisheries

September 2003

SUMMARY

This Candidate Conservation Agreement (CCA) is intended to identify and establish management protection for the Louisiana pine snake (*Pituophis ruthveni*), a candidate for Federal listing, on National Forest lands in Texas and Louisiana, and on Fort Polk Military Reservation in Louisiana. Longleaf and shortleaf-pine communities throughout the historic range of the Louisiana pine snake have been dramatically reduced by changes in land use. Remaining habitat has been degraded by fire suppression; the predominant use of dormant season fire; and the implementation of intensive, short-rotation silviculture on non-federal lands. A secondary threat may be mortality associated with vehicle traffic. As a result, populations of the Louisiana pine snake appear to have declined alarmingly, both in numbers and in range.

PURPOSE OF THE CANDIDATE CONSERVATION AGREEMENT

This CCA has been initiated in order to conserve the Louisiana pine snake on Federal lands by protecting known populations and habitat, reducing threats to its survival, maintaining its ecosystem, and restoring degraded habitat. This agreement is intended to establish a framework for cooperation and participation in the Louisiana pine snake's protection, conservation, and management within the boundaries of certain lands in Texas and Louisiana. While implementation of this CCA may not preclude the eventual need to list the Louisiana pine snake, it addresses pressing needs of the species. It is through such cooperation in implementing and refining conservation measures that certain candidates and species of concern may be recovered without the necessity of listing. In furtherance of these efforts, this

CCA is implemented by the U.S. Fish and Wildlife Service (USFWS), U.S. Forest Service's (USFS) Southern Research Station (SRS), USFS National Forests in Texas, USFS Kisatchie National Forest in Louisiana, Department of Defense's Fort Polk Military Installation, Texas Parks and Wildlife Department (TPWD), and Louisiana Department of Wildlife and Fisheries (LDWF), collectively referred to as the Cooperators.

Management commitments made through this agreement should benefit not only the Louisiana pine snake, but also the Navasota ladies's-tresses (*Spiranthes parksii*), Texas trailing phlox (*Phlox nivalis* var. *texensis*), and red-cockaded woodpecker (*Picoides borealis*), all federally listed as endangered. Plant and animal species of concern that should benefit include the white firewheel (*Gaillardia aestivalis* var. *winkleri*), slender gay-feather (*Liatrus teuis*), scarlet catchfly (*Silene subciliata*), Texas trillium (*Trillium pusillum* var. *texanum*), Bachman's sparrow (*Aimophila aestivalis*), Henslow's sparrow (*Ammodramus henslowii*), Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), and the northern scarlet snake (*Cemophora coccinea*). Additionally, other important species such as the eastern wild turkey (*Meleagris gallopavo sylvestris*), and northern bobwhite (*Colinus virginanus*) will benefit. Management actions are anticipated to result in the restoration and protection of the longleaf pine ecosystem of east Texas and western Louisiana, a habitat that has experienced substantial decline, and continues to disappear from the landscape of the southeastern United States.

I. COOPERATORS AND IMMEDIATE POINTS OF CONTACT

A. U.S. Fish and Wildlife Service
East Texas Suboffice of the Arlington Ecological Services Field Office
701 North First Street
Lufkin, Texas 75901
Fish and Wildlife Biologist **Jeffrey A. Reid** (936-639-8546)

B. U.S. Fish and Wildlife Service
Louisiana Ecological Services Field Office
646 Cajundome Blvd., Suite 400
Lafayette, LA 70506
Fish and Wildlife Biologist **Troy Mallach** (337-291-3123)

C. National Forests in Texas
701 North First Street
Lufkin, TX 75901
Forest Biologist **Eddie Taylor** (936-639-8565)

D. Kisatchie National Forest in Louisiana
2500 Shreveport Highway
Pineville, LA 71360-2009
Wildlife Biologist **Steve Shively** (318-793-9427)

E. Fort Polk Military Installation
AFZX-DPW-ENRMD
1823 23rd Street, Building 2505
Fort Polk, LA 71459-5509

Stephanie Stephens (337-531-7078)

F. Texas Parks and Wildlife Department
P.O. Box 7600, SFA Station
Nacogdoches, TX 75962
Wildlife Diversity Biologist **Ricky Maxey** (936-564-0234)

G. Louisiana Department of Wildlife and Fisheries Heritage Program
P.O. Box 98000
Baton Rouge, LA 70898-9000
Gary Lester (225-765-2820)

H. U.S. Forest Service, Southern Research Station
P.O. Box 7600, SFA Station
Nacogdoches, TX 75962
Research Scientist **Craig Rudolph** (936-569-7981)

II. AUTHORITY

The authority for the respective parties to enter into this voluntary CCA derives from the Endangered Species Act (ESA) of 1973, as amended (16 U.S.C. 1531-1544); the Fish and Wildlife Act of 1956, as amended [16 U.S.C. 742(a)-754]; and the Fish and Wildlife Coordination Act, as amended [16 U.S.C. 661-667(e)]. In 1973, the ESA was enacted with the purpose of conserving threatened and endangered species and preventing their extinction. All federal agencies were called upon to utilize their authorities in furtherance of the purposes of the ESA by carrying out conservation programs for these species.

The USFWS is a Federal land-management and regulatory agency responsible for implementation of the ESA and coordination with Federal and State agencies in their efforts to prevent the extinction of species and loss of their habitats. The USFWS is responsible for monitoring candidates and species of concern, and facilitating conservation programs through inter-agency agreements. These CCA are intended to direct specific conservation efforts to species of concern, to outline management practices that will prevent further decline of their habitat, and to ensure regular, periodic review of their status.

The USFS is a land management agency responsible for 192 million acres of national forests and grasslands within 44 states. This area serves as habitat for many native plant and animal species, including rare and endangered species. As a result, the USFS has implemented a national policy to specifically manage much of this area for the benefit of sensitive plant and animal species in order to prevent their need for federal listing (USFS Manual 2670).

On January 25, 1994, the USFWS and several other agencies entered into a Memorandum of Understanding (MOU), initiated by the USFS, in order to facilitate the conservation of candidate and other sensitive species. The purpose of the MOU was to establish a framework for cooperation in the conservation of species that are tending toward federal listing as threatened or endangered. The MOU calls for the development of Conservation Agreements that are intended to address site-specific and species-specific threats. This Conservation Agreement, dealing with a species that lies within USFS boundaries in east Texas and western Louisiana, is developed under authority of the 1994 MOU. Furthermore, the 1996 Revised Land and Resource Management Plan for the National Forests and Grasslands in Texas, and the 1999 Revised Land and Resource Management Plan for the Kisatchie National Forest, include the following goals: manage for the long-term sustainability of diverse ecological systems; manage for ecosystems which are unique and recognized as declining within Louisiana and Texas; and enhance threatened, endangered, and sensitive species through restoration of the processes and habitats these populations require.

III. SPECIES INVOLVED

The species addressed by this CCA is the Louisiana pine snake, a non-venomous constrictor of the Colubridae family. Formerly described as a pine snake subspecies (*Pituophis melanoleucus ruthveni*) based on two specimens taken in Louisiana (Stull 1929), its taxonomic status has been reassessed and determined to be a valid evolutionary species, both geographically isolated and genetically distinct (Reichling 1995). The Louisiana pine snake has subsequently been accepted as a full species (Collins 1997).

The Louisiana pine snake is a large snake, usually 120 to150 cm (4 to 5 feet) long (Tennant 1998; Young and Vandeventer 1988). The largest reported specimen was 178 cm (5.8 feet) long (Conant and Collins 1991, Davis 1971). A recent study by Himes *et al.* (2002) suggests that one-year-old and two-year-old snakes reach 80 to100 cm (2 to 3 feet) and 100 to 120 cm (3 to 4 feet) in total length, respectively. Juvenile females increased in mean total length by 15.1% during the 8 to 13-month period of study. The species also exhibited allometric growth in length to mass ratio, indicating an optimum body shape for adults. Although more robust snakes gained mass more rapidly throughout the period of study, their largest snake (157.1 cm [5.2 feet]) experienced the greatest reduction in mass (from 996.9 to 606.4 grams) and died during the study.

Sexual maturity may be attained at a minimal total length of 120 cm (4 feet) and an age of at least three years (Himes *et al.* 2002). A female is known to have oviposited at a total length of 154 cm (5.1 feet) (Reichling 1990). The species is oviparous, with a gestation period of about 21days (Reichling 1988), followed by 60 days of incubation. This species exhibits a remarkably low reproductive rate, with the smallest clutch size (3 to 5) of any North American colubrid snake and the largest eggs of any U.S. snake (Reichling 1990), generally 12 cm (5 in.) long and 5 cm (2 in.) wide. It also produces the largest hatchlings reported for any North American snake, ranging 45 to 55 cm (18 to 22 in.) in length, and up to 107 grams in weight. This low fecundity magnifies other threats to the Louisiana pine snake; species with such low reproductive rates are typically incapable of quickly recovering from events that affect population size, increasing their potential for local extirpations.

Pocket gophers appear to be the primary food source of Louisiana pine snakes (Rudolph *et al.* 2002), although other reported food items include other rodents, cottontails, amphibians, and ground-nesting birds and eggs (Dundee and Rossman 1989; Tennant 1998). In captivity, they refused day-old chicks but fed readily on small rats (Reichling 1988).

Louisiana pine snakes appeared to be most active March-May and fall (especially November) and least active December-February and summer (especially August) (Himes 1998). Even during the active season, Louisiana pine snakes spend the majority of their time below-ground in mammal burrows, specifically pocket gopher burrow systems (Ealy 1998; Himes 1998; Rudolph *et al.* 1998). Although diurnal, snakes remained underground and inactive (short-range movements of only 3 to 8 m) nearly 60% of their day. Above-ground Louisiana snakes usually moved underground at least once during the day, possibly for foraging, body cooling, or predator avoidance. Louisiana pine snakes were most active between 1000 to1800 hours, especially late-morning and mid-afternoon (Ealy 1998, Himes 1998). Snakes generally emerged from below-ground burrows before noon, except in October when they did not appear until 1400 to1600 hours (Ealy 1998). Hibernation sites were always within pocket gopher burrow systems.

During May-October, body temperatures of seven underground snakes ranged 15 to 33 degrees C, while active snakes above-ground ranged 20 to 36.7 degrees C. Above-ground snakes tended to move to underground burrows or to above-ground shade as their body temperatures approached 34 degrees C (Ealy 1998).

The annual home range of Louisiana pine snakes varied 5 to 78 hectares (ha) (12 to195 acres) in size, and averaged 27.7 ha (69 ac) (Rudolph and Burgdorf 1997). Himes (1998) found that adult males had larger home ranges (58 ha [145 ac]) than females (14 ha [25 ac]) and juveniles (5 ha [12 ac]). Ealy (1998) reported that Louisiana pine snakes in east Texas usually moved less than 10 m (33 feet) daily. However, when snakes did move longer distances, usually from one pocket gopher burrow system to a new one, the average daily distance moved was 163 m (538 feet): 204 m (673 feet) for females and 173 m (571 feet) for males (Ealy 1998). Adult males in Louisiana moved an average of 150 m (495 feet) daily, adult females 105 m (346 feet), and juveniles 34 m (112 feet) (Himes 1998). Males tended to make moves of more than 150 m (495 feet) in May-July, while females moved long distances primarily in July-September (Ealy 1998). Movement frequency (moving more than 10m/day) of individual pine snakes ranged 14 to 86% and averaged 46% of sample days. There was no indication of seasonal migration.

IV. HABITAT OF THE LOUISIANA PINE SNAKE

The Louisiana pine snake is generally associated with sandy, well-drained soils; open pine forests, especially longleaf pine savannah; moderate to sparse midstory; and a well-developed herbaceous understory dominated by grasses. Its activity appears to be heavily concentrated on low, broad ridges overlain with sandy soils (Rudolph and Burgdorf 1997).

Using radiotelemetry, Himes (1998) studied the habitat preferences of 9 native adults and one juvenile Louisiana pine snake in Louisiana's Bienville Parish, along with one adult and 7 juvenile captive-bred snakes released into the area, during 1995 to 1997. Native Louisiana pine snakes were recorded most frequently in pine forests (56%), followed by pine plantation (23%) and clear-cuts (9%). They were found minimally, or not at all, in grasslands, pine-hardwood, hardwood, and hardwood-pine sites. The captive-released snakes were found more frequently in pine plantations (38%) and pine forests (29%), followed by minimal use in other habitat types (Himes 1998).

Baird's pocket gophers (*Geomys breviceps*) appear to be an essential component of Louisiana pine snake habitat. They create the burrow systems in which Louisiana pine snakes are most frequently found, and serve as a major source of food for the species (Rudolph and Burgdorf 1997; Rudolph and Conner 1996; Rudolph *et al.* 1998b; Rudolph *et al.* 2002). Up to 90% of radio-tagged snake relocations have been underground in pocket gopher burrow systems, and movement patterns are typically from one pocket gopher burrow system to another. In Louisiana, habitat selection by Louisiana pine snakes seemed to be determined by the abundance and distribution of pocket gophers and their burrow systems (Himes 1998). Although active snakes did utilize debris and logs as temporary shelters, they were most often found adjacent to pocket gopher burrows. Snakes disturbed on the surface retreated to nearby burrows, and hibernation sites were always within burrows. Both native and captive-released snakes were found most frequently in areas containing an ample number of pocket gopher mounds (Himes 1998), and snakes stayed active longer and moved greater distances where pocket gopher burrows were abundant (Ealy 1998).

Pocket gopher abundance is dependent upon an abundance of herbaceous ground-cover and loose, sandy soils. The amount of herbaceous vegetation is related to canopy cover. Generally, a rich ground layer requires a high degree of solar penetration onto the forest floor. Himes (1998) found that pocket gopher abundance was associated with a low density of trees and an open canopy, which allowed greater sunlight, more understory growth, and better forage for pocket gophers. Pocket gopher mounds were commonly found in pine forests and open pine plantations. However, they were not commonly found in clear-cuts and other forest types.

V. STATUS AND DISTRIBUTION OF THE LOUISIANA PINE SNAKE

The Louisiana pine snake historically occurred in portions of northwest Louisiana and central-east Texas, its range roughly coinciding with a disjunct portion of the longleaf pine ecosystem situated west of the Mississippi River. A total of 61 historical records confirmed an original range of 7 Louisiana parishes and 12 Texas counties (Jennings and Fritts 1983). Analysis conducted by the USFS SRS expanded the historic range to 9 parishes and 14 counties. However, only three Texas records were post-1980, and all post-1980 Louisiana records involved only one parish.

Records collected in Texas since 1993 by the USFS SRS have confirmed the presence of the Louisiana pine snake in Angelina, Jasper, Newton, Sabine, and Tyler counties, generally the southern portion of Sabine National Forest (NF) (Sabine County); and the southern portion of Angelina NF (Angelina, Jasper, and Tyler counties) (Rudolph *et al.* 1999). However, nearly all recent records are from two separate areas, each measuring less than 7 km (4 miles) in radius, within a larger area approximately 70x20 km (42x12 miles) in extent. A third population occurs in Scrappin' Valley, land managed by Temple-Inland Forest Products Corporation in northern Newton County.

Louisiana records since 1993 document the presence of Louisiana pine snakes in at least 4 parishes: Bienville, Vernon, Sabine, and Natchitoches. The majority (12) of these records have been from Bienville Parish on forestland owned by International Paper (Rudolph *et al.* 1999). Federal lands in Vernon Parish, managed by USFS and used by the U. S. Army for military training, also provide habitat. Seven pine snakes have been found in south Vernon Parish on Fort Polk and USFS's Vernon Unit. Fort Polk is currently funding a study to determine pine snake distribution and habitat on its lands. Three more snakes, and possible evidence of a third population area, have been found near the juncture of Vernon, Sabine and Natchitoches parishes on Peason Ridge and the Kisatchie Ranger District.

Most of the recent pine snake records are based on captures (19) made during extensive trapping (20,000 trap-days) by the USFS SRS for radio-telemetry studies (Rudolph and Burgdorf 1997, Rudolph *et al.* 1999). Louisiana pine snakes have not been documented in over a decade in some of the best remaining habitat within the historical range, suggesting that the species is no longer present, or has become extremely rare in these areas.

Surveys documenting the current condition of fire climax longleaf pine forests, and the results of pine snake radio telemetry, suggest that extensive population declines and local extirpations of the Louisiana pine snake have occurred during the last 50 to 80 years. Rudolph (2000) conducted a habitat assessment of all known historical localities of the Louisiana pine snake and categorized each location as excellent, good, marginal or poor based on habitat characteristics of occupied sites. Of the 77 sites assessed, only 34% (26) were considered capable of supporting a viable population of pine snakes.

Although once considered fairly common, the Louisiana pine snake is now recognized as one of the rarest snakes in North America, and one of the rarest vertebrate species in the United States (Young and Vandeventer 1988). As a candidate, the Louisiana pine snake receives no formal Federal protection under the Endangered Species Act. It is State listed as threatened in Texas and protected from direct harm and unauthorized collection. It is classified as imperiled to vulnerable in Louisiana.

VI. PROBLEMS FACING THE LOUISIANA PINE SNAKE

Possible threats to the Louisiana pine snake may include direct human predation and collection for the pet trade. Urban development, conversion to agriculture, intensive short-rotation silvicultural practices, road construction, and mining have all contributed to loss and fragmentation of Louisiana pine snake habitat. Remaining habitat occurs in isolated blocks and is often degraded by fire suppression. The primary threats to the pine snake continue to be habitat loss and alteration of the fire regime, apparently restricting the pine snake to only portions of its previous range (Rudolph and Burgdorf 1997). In addition, vehicle mortality may be increasing in importance.

HABITAT LOSS AND FRAGMENTATION

Virtually all remaining timber in the South was cut during intensive commercial logging from 1870 to 1920, followed by conversion to pine plantations (Frost 1993). In 1935, possibly only 1.2 million ha (3 million ac) of longleaf pine forests remained in Louisiana and Texas, and only 3% of this existed as uncut, mature pine stands. Published data from the 1980's indicated that only 15% in Louisiana and 7% in Texas of the 1935 levels of natural longleaf-pine forest still remained (Bridges and Orzell 1989).

The majority of historic longleaf and shortleaf pine savannah forests have been replaced with dense plantations of fast growing loblolly and slash pine. Slash pine is not native to this area, and loblolly was historically restricted to downslope areas with moist soils, or on higher areas along riparian terraces and bottomlands.

Commercial pine plantations (non-Federal land) are typically grown in very dense, closed canopy stands that are harvested on very short rotations of less than 40 years. These forests have sparse and poorly structured understory plant communities, an early successional trait that is present at the time of harvest and throughout the rotation, rendering them generally unsuitable for pocket gophers.

Most of the recent pine snake records in Louisiana have occurred on industrial forest land owned by International Paper in Bienville Parish, indicating that this site may currently support the densest known pine snake population. However, timber stands here are now being harvested, altering current habitat conditions with unknown results to the pine snake. The corporation is replanting the site to reduce impacts, but the potential for success has not be determined.

FIRE SUPPRESSION

The suppression of natural fire events from the upland landscape may represent the greatest threat to the Louisiana pine snake in recent years, decreasing both the quantity and quality of habitat available for pine snakes (Rudolph and Burgdorf 1997). The longleaf pine savannah forest occupied by the pine snake had evolved as a fire climax community, adapted to the occurrence of frequent, but low-intensity, ground fires. These natural fire events on sandy, well drained soils typically maintained an overstory dominated by longleaf pine, with minimal midstory cover but a well developed understory of native bunch grasses and herbaceous plants. These "park-like" forests supported ideal habitat for pocket gophers and, subsequently, Louisiana pine snakes.

In the absence of frequent and effective fires, these upland pine savannah ecosystems rapidly develop a mid-story of hardwoods and off-site species (that would have normally occurred on more moist, downslope soils) which suppresses or eliminates any herbaceous understory. Since the presence of pocket gophers is directly related to the extent of herbaceous vegetation available to them, their population numbers and distribution declines as such vegetation declines.

Ealy (1998) studied the activity of seven (7) pine snakes at two sites in east Texas, one which received prescribed burns, and one which did not. The frequently burned area maintained a rich herbaceous groundcover that supported more pocket gophers, allowing snakes in this area to make use of both pocket gopher burrows and rotten stumps/root systems that had burned out. As a result, snakes at this site were able to stay active longer and move greater distances than snakes at the unburned site. No pine snakes have been captured in areas substantially degraded by fire suppression (Rudolph and Burgdorf 1997).

These problems are further compounded by a current trend to replace prescribed burning with applications of herbicides to reduce vegetative competition. However, this practice also eliminates herbaceous growth. Further research on the long-term implications of this practice, particularly impacts on understory plant communities, is necessary.

The largest and densest existing population of Louisiana pine snakes occurs on industrial forestland owned by International Paper in Louisiana's Bienville Parish, where burning has historically been used to reduce and manage undergrowth. Sawtimber stands are now being harvested from this site, but the corporation is designing management actions for the pine snake that include prescribed burning.

Observations by Rudolph *et al.* (1998b) suggest that Louisiana pine snakes are adapted to the periodic occurrence of fire. Nine Louisiana pine snakes residing in areas subjected to prescribed burns during 1994 to1997 all survived with no apparent damage. Three snakes observed during the fires all moved into pocket gopher burrows as flames neared. Active (above-ground) snakes are usually found within a few meters of pocket gopher burrows, and can quickly retreat underground as a fire approaches. Louisiana pine snakes above ground but away from known burrows could be at greater risk (Rudolph et.al. 1998b).

VEHICLE MORTALITY

Louisiana pine snakes are also impacted by vehicle-caused mortality, both on state roads and on off road trails by off road vehicles, but the full extent of the impact is still unknown. The USFS SRS documented the loss of 3 snakes (25%) from its radio telemetry study to vehicle traffic, including off road vehicles (Rudolph *et al.* 1999). Further research by the USFS SRS indicates that roads with moderate to high traffic levels can reduce adjacent populations of large snakes by 50 to75%. Moreover, measurable impacts to population numbers and community structure may extend up to 850 meters (2,805 feet) away from road corridors (Rudolph *et al.* 1999). Rudolph *et al.* (1998a) found that distribution of timber rattlesnakes (*Crotalus horridus*) was significantly associated with low road density. Populations in east Texas may be restricted to riparian habitats due to a greater road density and mortality in the adjacent uplands.

Fort Polk is currently funding a study of the Louisiana pine snake on its reservation lands and on USFS's Vernon Unit to identify possible impacts from roads on Federal lands. Although initial results have found no evidence of road mortality for the Louisiana pine snake (C. Rudolph pers. comm., 2003), this may be a function of both low capture rates (and possibly few pine snakes) and low traffic volume in the study area. Additional research is necessary, but other data suggest that motorized vehicles on certain roads and trails have the potential to impact Louisiana pine snake abundance and community structure.

Known conflicts between Louisiana pine snakes and motorized vehicles currently exist in the Longleaf Ridge Area of south Angelina NF. Compartments with the greatest potential for pine snake loss include 74 thru 77, 79 thru 92, and south portions of 73 and 78. Motorized vehicles have eliminated a large part of the Millstead Branch bog community and the Catahoula Barrens community in Compartment 84. The southern portion of the Upland Wilderness Area may also provide important habitat. In Sabine NF, pine snake habitat is at similar risk of vehicle conflict in Compartments 139 (Foxhunter's Hill), 141 and 142 (Stark Tract).

VI. CONSERVATION ACTIONS TO BE CARRIED OUT

All Cooperators agree to support educational programs involving the Louisiana pine snake. All Cooperators will seek funding for carrying out the Conservation Actions identified below, and will collaborate on cost-sharing opportunities as they become available. It is understood that all funding commitments made pursuant to this CCA are subject to budget authorizations and approval by the appropriate agency. Cooperators will plan to meet on an annual basis to evaluate the activities identified below and determine their effectiveness in conserving the Louisiana pine snake.

For all parties, the areas discussed herein will be treated as special management areas for the pine snake, and protected as such to the maximum extent possible. Adverse impacts to the species will be avoided, and beneficial management activities will be continued or implemented. In consideration of the premises of this document, the respective responsibilities and provisions of each party are as follows:

A. U.S. Fish and Wildlife Service agrees to the following conditions for the designated period of time:

1. Continue to record and report the status of the Louisiana pine snake, as required

by Congress and current policy.

2. Review and comment on any management plans, proposed strategies, reports, and other documents that may impact the Louisiana pine snake.

3. Work with cooperators on ways to reduce adverse impacts associated with any proposed project or activity that could adversely affect the Louisiana pine snake or habitat areas covered by this CCA.

4. Seek funding to support Louisiana pine snake research and habitat restoration and management.

B. The National Forests in Texas agree to the following conditions for the designated period of time:

1. Compartments 73 thru 81 and 84 thru 92 of the Angelina National Forest, and Compartments 90 thru 92, 114 thru 124 (Moore Plantation), 126 thru 129, 132, 135, and 139 (Foxhunters Hill), and 140-142 (Stark Tract) of Sabine National Forest, are specifically identified for the following conservation measures. Within these areas, management actions such as prescribed burning, thinning, and longleaf pine restoration will be prioritized to maintain or establish herbaceous-dominated vegetative understory conditions on appropriate sites. Upland Island Wilderness area actions are limited to prescribed burning only.

a. Conduct an aggressive prescribed burning program that is <u>specifically designed</u> to reduce or eliminate existing shrub encroachment, restore herbaceous dominated conditions, and prevent future woody shrub encroachment, within existing and potential longleaf pine woodlands.

b. Target burning for optimum, or potentially optimum, longleaf pine habitat areas, and ensure that prescribed burns in the Longleaf Ridge area receive priority.

c. Ensure that burns are carried out during the most effective season and on a periodic and regular basis, preferably every 2 to 3 years in longleaf pine habitat, in order to ensure sufficient and timely restoration of herbaceous communities.

d. Initiate detailed monitoring to measure the success of burns at reducing understory and restoring herbaceous conditions. Modify burn program, if needed, as new information on fire management is developed.

2. Within historical longleaf pine habitat, where practicable, continue aggressive thinning and early conversion of existing slash pine and loblolly pine stands to longleaf pine forest. Retain all residual longleaf pines within these stands.

3. Inventory and evaluate off road vehicle use and trails within sensitive pine snake habitat to determine if and where motorized vehicular use is adversely affecting pine snake populations. Take appropriate management action (including closure), in order to minimize damage to resources and ensure their integrity and

sustainability.

a. Maintain existing area closures south of Hwy. 63 (current closure order expires 12/15/04) to motorized off road vehicles within sensitive pine snake habitat. Close roads to public vehicle use south of Hwy. 63 to the extent reasonably possible, from February through October, unless the road is required for administrative use, access to private land, school bus route, or permitted special use.

b. Roads in Compartments 73 thru 81 and 84 thru 92 of the Angelina NF, and in Compartments 139 thru 142 of the Sabine NF, including FDR 113 and FDR 196, will be considered for closure.

4. Continue to support research involving trapping and other techniques to better determine the population numbers, range, habitat, behavior, and specific management requirements of the pine snake.

5. Support research, as funding and personnel are available, to establish and maintain herpetofaunal monitoring stations throughout longleaf pine woodland habitat to document the seasonal presence/absence of terrestrial reptiles and amphibians in the forest.

6. As funding and personnel are available, support studies to determine pocket gopher dynamics within USFS boundaries, including population numbers, distribution, suitable habitat, and the effects of fire.

7. Develop an information and education program that encourages forest users to refrain from harassing or harming snakes.

8. Provide for review to the Cooperators any management plans or other documents that may affect pine snake recovery.

9. Seek funding and staffing necessary to carry out the above management actions through all available channels.

10. Participate in an annual Louisiana pine snake meeting to discuss the results of implementing this CCA.

C. Kisatchie National Forest agrees to the following conditions for the designated period of time: KNF has map!

1. Continue a prescribed burning program that is specifically designed to reduce or eliminate existing shrub encroachment, restore herbaceous-dominated conditions, and prevent future woody shrub encroachment within the existing and potential longleaf-pine ecosystem.

a. Target burning for the best longleaf pine and restorable longleaf pine habitats. 13K growing 10K winter

b. Visually ensure that the burning program enhances maintenance or restoration of herbaceous communities.

2. Continue thinning and conversion of existing slash pine, loblolly, and shortleaf pine stands to longleaf pine habitat on suitable sites, consistent with the Kisatchie NF Forest Plan.

3. Determine if and where motorized vehicular use is adversely affecting pine snake populations, and take appropriate management action to reduce these threats. E-Dist Mov-t to close w/ trail system *

4. Cooperate with studies involving trapping and other techniques to better determine the population numbers, range, habitat, behavior, and specific management requirements of the pine snake.

5. Provide for review to the Cooperators any management plans or other documents that may affect pine snake recovery.

6. Develop an information and education program that encourages forest users to refrain from harassing or harming snakes.

7. Support Louisiana pine snake studies, as funding and personnel are available, to determine pocket gopher dynamics within USFS boundaries, including population numbers, distribution, suitable habitat, and the effects of fire.

8. Participate in an annual Louisiana pine snake meeting to discuss the results of implementing this CCA.

D. The U.S. Forest Service's Southern Research Station, agrees to the following conditions for the designated period of time:

Diel status

1. Continue, as funding permits, surveys for the Louisiana pine snake throughout its historic range to better determine its current status and distribution. 24k/100 traps

2. Continue, as funding permits, to assess the impacts of vehicular traffic on snake populations.

3. Consult with cooperators.on the status and management of Louisiana pine snakes.

E. The Fort Polk Military Installation agrees to the following conditions for their lands for the designated period of time:

1. Within guidance of the Fort Polk Management Plan and the Integrated Natural Resources Management Plan, continue a prescribed burning program that is <u>specifically designed</u> to reduce or eliminate existing shrub encroachment, restore herbaceous dominated ground cover conditions, and prevent future woody shrub encroachment within longleaf pine woodlands.

a. Target burning for the best longleaf pine and restorable longleaf pine habitats.

b. Initiate monitoring to measure the success of burns at reducing understory and restoring herbaceous conditions. Modify burn program, if needed, as new information on fire management is developed.

2. Continue thinning and early conversion of existing slash pine and loblolly pine stands to longleaf pine woodland habitat on suitable sites, where practical.

3. Continue to educate soldiers and civilians on Fort Polk about the Louisiana pine snake.

a. Provide information on the Louisiana pine snake at the 40-hour Environmental Compliance Officer's Course.

b. Continue distribution of flyers with photos of the Louisiana pine snake and information on its habitat and status.

4. Cooperate with research involving trapping and other techniques to better determine population numbers, range, habitat, behavior, and specific management requirements of the Louisiana pine snake.

5. Cooperate in establishing and maintaining herpetofaunal monitoring stations throughout longleaf pine woodland habitat to document the seasonal presence/absence of terrestrial reptiles and amphibians.

6. Provide for review to the Cooperators any management plans or other documents that may affect Louisiana pine snake recovery.

F. Texas Parks and Wildlife Department agrees to the following conditions for the designated period of time:

1. Review and comment on plans or proposed strategies that may impact the pine snake within Texas.

2. Work with other cooperators on proposed projects or activities within Texas that could adversely affect the pine snake.

3. Work cooperatively to support specific projects that will create or maintain suitable habitat for the Louisiana pine snake.

4. Work cooperatively to support projects that will educate the public concerning the plight of the Louisiana pine snake and the management requirements that will produce suitable habitat.

5. Work with private landowners who may have or could create suitable habitat for Louisiana pine snakes, using incentive programs such as the Landowner Incentive Program, subject to the availability of funds.

G. Louisiana Department of Wildlife and Fisheries agrees to the following conditions for the designated period of time:

1. As time and staff allows, review and comment on plans or proposed strategies that may impact the pine snake within Louisiana.

2. Work with other cooperators on any proposed project or activity within Louisiana that could adversely affect the pine snake.

3. Work cooperatively to support specific projects that will create or maintain suitable habitat for the Louisiana pine snake.

4. Work cooperatively with cooperators whenever possible to support projects that will educate the public concerning the plight of the Louisiana pine snake and the management requirements that will produce suitable habitat.

5. Work with private landowners who may have or could create suitable habitat for pine snakes, using incentive programs such as the Landowner Incentive Program, as funding is available.

VIII. ADAPTIVE MANAGEMENT

This CCA is conceptually based on adaptive management principles. All Cooperators agree and recognize that implementation of the conservation actions included in this CCA will be considered experimental, consistent with the concepts of adaptive management. The experimental approach to habitat manipulations and desired forest conditions will provide managers with the most effective and efficient method to restore, enhance, maintain and/or create Louisiana pine snake habitat through the adaptive management process. The effectiveness of all conservation measures and monitoring methods will be reviewed by the Cooperators at an annual meeting. Based upon such evaluation, appropriate modifications to the management scheme will be incorporated, to the best ability of the Cooperator, to further enhance the goals of this CCA.

IX. DURATION OF AGREEMENT

A. The duration of this CCA is five (5) years following the date of the last signature below, and will automatically be extended for another five-year term, unless terminated within 90 days before the date of renewal by written notice from any party.

B. The parties involved will annually review the CCA and its effectiveness to determine whether revision is necessary. During the last month in which it is valid, the CCA must be reviewed and either modified, renewed, or terminated. If some portion of this CCA cannot continue to be carried out or if cancellation is desired, the party requesting such action will notify the parties within one month of the changed circumstances.

C. No obligation shall be in effect after expiration of this CCA, with the exception of normal provisions of the Endangered Species Act, although this CCA will be considered for renewal. If it becomes known that there are threats to the survival of the subject species that cannot be resolved through this and other Conservation Agreements, the species will be retained in candidate status and considered for listing.

X. DUPLICATE ORIGINALS

This Agreement may be executed in any number of duplicate originals. A complete original of this Agreement shall be maintained in the official records of each of the Parties hereto.

XI. SIGNATURES

The parties identified herein have caused this Louisiana Pine Snake Candidate Conservation Agreement to be executed as of the date of the last signatures shown on the following pages;

National Forests in Texas
Kisatchie National Forest
Southern Research Station
Fort Polk Military Installation
U.S. Fish and Wildlife Service, Region 2
U.S. Fish and Wildlife Service, Region 4
Texas Parks and Wildlife Department
Louisiana Department of Wildlife and Fisheries

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

National Forests in Texas Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake

Pituophis ruthveni

Kisatchie National Forest Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

Southern Research Station Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

Fort Polk Military Installation Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

U.S. Fish and Wildlife Service, Region 2 Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

U.S. Fish and Wildlife Service, Region 4 Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

Texas Parks and Wildlife Department Date

CANDIDATE CONSERVATION AGREEMENT

for the

Louisiana pine snake
Pituophis ruthveni

Louisiana Department of Wildlife and Fisheries Date

LITERATURE CITED

Bridges, E.L. and S.L. Orzell. 1989. Longleaf pine communities of the West Gulf coastal Plain. Natural Areas Journal 9:246-253.

Collins, J.T. 1997. Standard common and current scientific names for North American amphibians and reptiles. Fourth Edition. Society of the Study of Amphibians and Reptiles Herpetological Circular 25:1-40.

Conant, R. and J.T. Collins. 1991. A field guide to reptiles and amphibians of eastern and central North America. 3rd ed. Houghton Mifflin Co., Boston, MA.

Davis, B.J. 1971. A new size record for the Louisiana pine snake, *Pituophis melanoleucus ruthveni.* Texas Journal of Science 23:145.

Dundee, H.A. and D.A. Rossman. 1993. The amphibians and reptiles of Louisiana. Louisiana State University Press, Baton Rouge, LA. 300 pp.

Ealy, M.J. 1998. Activity patterns of the Louisiana pine snake in eastern Texas. Master's thesis, Stephen F. Austin State University, Nacogdoches, TX. 74pp.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Pgs. 17-43 *In*: S.M. Hermann (ed.). Proceedings of the Tall Timbers Fire Ecology Conference, No. 18, The longleaf pine ecosystem: ecology, restoration and management. Tall Timbers Research Station, Tallahassee, FL.

Himes, J.G. 1998. Activity patterns, habitat selection, excavation behavior, growth rates, and conservation of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*). Master's thesis, Louisiana State University, Shreveport, LA. 58 pp.

Himes, J.G., L.M. Hardy, D.C. Rudolph, and S.J. Burgdorf. 2002. Growth rates and mortality of the Louisiana pine snake (*Pituophis ruthveni*). Journal of Herpetology 36(4):683-687.

Jennings, R.D. and T.H. Fritts. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni.* U.S. Fish and Wildlife Service and University of New Mexico Museum of Southwestern Biology, Albuquerque, NM. 32pp.

Reichling, S.B. 1988. Reproduction in captive Louisiana pine snakes, *Pituophis melanoleucus ruthveni.* Herpetological Review 19(4):77-78.

Reichling, S.B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes:Colubridae). Southwestern Naturalist 35(2):221-222.

Reichling, S.B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. Journal of Herpetology 29(2):186-198.

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 49:111-122.

Rudolph, D.C., and R.N. Conner. 1996. Radio-telemetry study of Louisiana pine snakes in eastern Texas and western Louisiana. Unpublished report to Texas Parks and Wildlife and Louisiana Department of Wildlife and Fisheries, Baton Rouge, LA. 7 pp.

Rudolph, D.C., S.J. Burgdorf, R.N. Conner, C.S. Collins, D.Saenz, R.R. Schaefer, C.M. Duran, M. Ealy, and J.G. Himes. 2002. Prey handling and diet of Louisiana pine snakes (*Pituophis melanoleucus*) and black pine snakes (*P. melanoleucus lodingi*) with comparisons to other selected colubrid snakes. Herpetological Natural History 9:57-62.

Rudolph, D.C., S.J. Burgdorf, R.N. Conner, and J.G. Dickson. 1998a. The impact of roads on the timber rattlesnake (*Crotalus horridus*) in eastern Texas. Proceedings of the International Conference on Wildlife Ecology and Transportation (Fort Myers, FL). G.L. Evink, P. Garrett, D. Zeigler, and J. Berry (eds.). Florida Department of Transportation, Tallahassee, FL.

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. Proceedings of the Third International Conference on Wildlife Ecology and Transportation (Missoula, MT). G.L. Evink, P. Garrett, and D. Zeigler (eds.). Florida Department of Transportation, Tallahassee, FL. FL-ER-73-99.

Rudolph, D.C., S.J. Burgdorf, J.C. Tull, M. Ealy, R.N. Conner, R.R. Schaefer, and R.R. Fleet. 1998b. Avoidance of fire by Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. Herpetological Review 29(3):146-148.

Stull, O.G. 1929. The description of a new subspecies of *Pituophis melanoleucus* from Louisiana. Occasional Papers of Museum of Zoology, University of Michigan 205:1-3.

Tennant, A. 1998. A field guide to Texas Snakes, second edition. Gulf Publishing field guide series. Gulf Publishing Company, Houston, TX. 291 pp.

Young, R.A., and T.L. Vandeventer. 1988. Recent observations of the Louisiana pine snake, *Pituophis melanoleucus ruthveni* Stull. Bulletin of the Chicago Herpetological Society 23 (12):203-207.

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 presumably 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.
All Points			
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	$t = -2.68$ $P < 0.0088$
Points w/in 3 km of Permanent Streams			
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; Sulentich 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 (Vandeventer & Young 1989).

Causes of mortality and population decline.—Louisiana pine snake populations are thought to have declined in recent decades (Jennings & Fritz 1983; Young & Vandeventer 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 & Vandeventer 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; Sulentich 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-

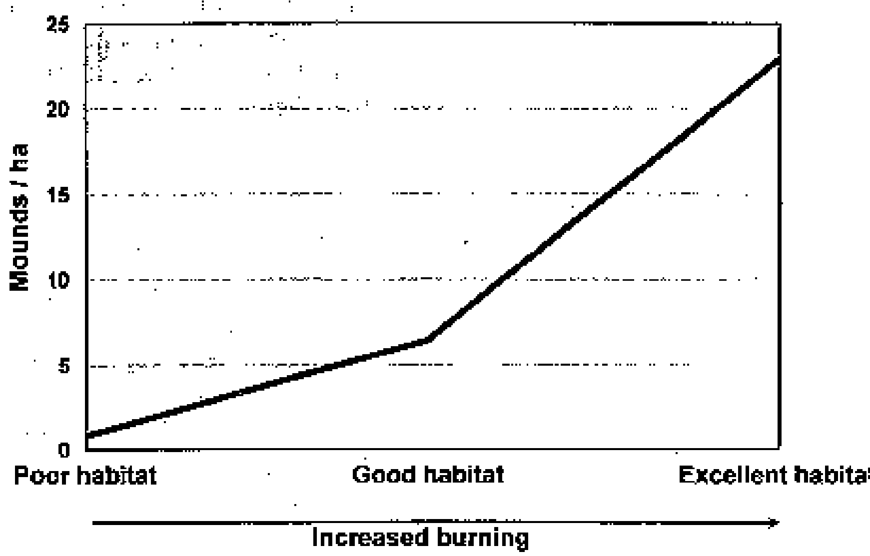


Figure 1. Hypothesized relationship between effectiveness of burning and pocket gopher (*Geomys breviceps*) density based on preliminary data on mound density.

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

The authors wish to thank Robert R. Fleet, James A. Neal, Ronald E. Thill, Daniel Saenz and two anonymous reviewers for commenting on earlier drafts of this manuscript. The U.S. Fish and Wildlife Service, Texas Parks and Wildlife Department and the Louisiana Department of Game and Fisheries provided funding for the research on *Pituophis* under Section 6 of the U.S. Endangered Species Act. Texas Parks and Wildlife Department issued the necessary scientific collecting permits.

LITERATURE CITED

Andersen, D. C. 1987. *Geomys bursarius* burrowing patterns: influence of season and food patch structure. Ecology, 68:1306-1388.

Adams, C. E., J. K. Thomas, K. J. Strnadel & S. L. Jester. 1994. Texas rattlesnake roundups: implications of unregulated commercial use of wildlife. Wildl. Soc. Bull., 22:234-330.

Andersen, D. C. 1987. *Geomys bursarius* burrowing patterns: influence of season and foodpatch structure. Ecology, 68:1306-1318.

Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pp. 99-118 *in* Nature Conservation II: The role of Corridors (D. A. Saunders & R. J. Hobbs, eds.). Surrey Beatty & Sons, Heidelberg, Victoria, Australia, 442 pp.

Bridges, E. L. & S. L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Natural Areas Journal, 9:246-253.

Brown, W. S. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47:101-115.

Brown, W. S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. Society for the Study of Amphibians and Reptiles. Herpetological Circular No. 22.

Brown, W. S. & D. B. Greenberg. 1992. Vertical-tree ambush posture in *Crotalus horridus*. Herpetol. Rev., 23:67.

Conant, R. 1956. A review of two rare pine snakes from the Gulf coastal plain. Amer. Mus. Novitates, 1781:1-31.

Davis, W. B., R. R. Ramsey & J. M. Arendale, Jr. 1938. Distribution of pocket gophers (*Geomys breviceps*) in relation to soils. J. Mammology, 19:412-418.

Dundee, H. A. & D. A. Rossman. 1989. The amphibians and reptiles of Louisiana. Louisiana State Univ. Press, Baton Rouge, Louisiana, 300 pp.

Ehmann, H. & H. Cogger. 1985. Australia's endangered herpetofauna: a review of criteria and policies. Pp. 435-437 *in* Biology of Australian Frogs and Reptiles (G. Gregg, R. Shine, & H. Ehmann, eds.). Surrey Beatty & Sons, Sydney, New South Wales, Australia, 527 pp.

English, P. F. 1932. Some habits of the pocket gopher, *Geomys breviceps breviceps*. J. Mammalogy, 12:253-256.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. of the Tall Timbers Fire Ecology Conf. 18:17-43.

Frost, C. C., J. Walker & R. K. Peet. 1986. Fire dependent savannas and prairies of the Southeast: original extent, preservation status and management problems. Pp. 348-357 *in* Wilderness and Natural Areas in the Eastern United States: a Management Challenge (D. L. Kulhavy & R. N. Conner, eds.). Center for Applied Studies, School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas, 416 pp.

Galligan, J. H. & W. A. Dunson. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biol. Conserv., 15:34-28.

Jennings, R. D. & T. H. Fritz. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni*. U. S. Fish and Wildl. Serv. and the Univ. of New Mexico Mus. of Southwestern Biol. pp 1-32.

Klauber, L. M. 1956. Rattlesnakes: their habits, life histories, and influence on mankind. University of California Press, Berkeley, California, 1533 pp.

Komarek, E. V. 1964. The natural history of lightning. Proc. of the Tall Timbers Fire Ecology Conf., 3:139-183.

Lalo, J. 1987. The problem of roadkill. American Forests 50:50-52.

Martin, W. H. 1992. The timber rattlesnake: Its distribution and natural history. Pp. 13-22 *in* Conservation of the timber rattlesnake in the northeast (T. F. Tyning, ed.). Massachusetts Audubon Society, Lincoln, Massachusetts, 40 pp.

Mount, R. H. 1975. The reptiles and amphibians of Alabama. Auburn Univ. Agri. Exp. Sta., Auburn, Alabama.

Outcalt, K. W. & P. A. Outcalt. 1994. The longleaf pine ecosystem: an assessment of current conditions. Unpubl. report on USDA Forest Service Forest Inventory and Analysis Data. 23 pp.

Platt, W. J., G. W. Evans, & S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Naturalist 131:491-525.

Reichling, S. B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). SW Naturalist, 35:221-222.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. J. Herpetology, 29:186-198.

Reinert, H. K., D. Cundall & L. M. Bushar. 1984. Foraging benhavior of the timber rattlesnake, *Crotalus horridus*. Copeia 1984:976-981.

Saenz, D., S. J. Burgdorf, D. C. Rudolph & C. M. Duran. 1996. *Crotalus horridus* (timber rattlesnake). Climbing. Herpetol. Rev., 27:145.

Sulentich, J. M., L. R. Williams & G. N. Cameron. 1991. *Geomys breviceps*. Mammalian Species, 383:1-4.

Sweet, S. S. & W. S. Parker. 1991. *Pituophis melanoleucus*. Catalogue of American Amphibians and Reptiles, 474:1-8.

TPWD. 1992. Texas threatened and endangered species. Texas Parks and Wildlife Department, Austin, Texas, 4 pp.

Young, R. A. & T. L. Vandeventer. 1988. Recent observations on the Louisiana pine snake, *Pituophis melanoleucus ruthveni*, Stull. Bull Chicago Herp. Soc., 23:203207.

Journal of Herpetology, Vol. 36, No. 4, pp. 683–687, 2002

Growth Rates and Mortality of the Louisiana Pine Snake (*Pituophis ruthveni*)

John C. Himes,[1,2,3] Laurence M. Hardy,[1] D. Craig Rudolph,[4] and Shirley J. Burgdorf[4,5]

[1]*Museum of Life Sciences, Louisiana State University in Shreveport, One University Place, Shreveport, Louisiana 71115-2399, USA*
[4]*Wildlife Habitat and Silviculture Laboratory, Southern Research Station, USDA Forest Service, Nacogdoches, Texas 75962-7600, USA*

The genus *Pituophis* (Serpentes: Colubridae) contains three species of snakes in the United States (Collins, 1997): *Pituophis catenifer*, *Pituophis melanoleucus*, and *Pituophis ruthveni*. 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) agreed with the recognition of specific status for *P. ruthveni*, but 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 because of the snake's limited distribution (Reichling, 1995; Thomas et al., 1976), low population density (Jennings and Fritts, 1983; Reichling, 1989), and secretive nature (Reichling, 1988).

A radiotelemetry study initiated in 1993 (Rudolph and Burgdorf, 1997; Rudolph et al., 1998) confirms the basic conclusions about the ecology of *P. ruthveni* obtained from collection records. *Pituophis ruthveni* is primarily associated with pine forests in sandy soils within the historic range of longleaf pine (*Pinus palustris*). Telemetry data indicate a preference for well-developed herbaceous vegetation generally maintained by 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 rangewide natural history study on *P. ruthveni* in Louisiana and Texas, we studied 30 naturally occurring (one juvenile, 16 adult males, and 13 adult females) and eight captive-bred (seven juveniles and one adult male) pine snakes in the field for up to 43 months. The objective of this paper is to characterize the growth of this rare and poorly known species. We also compare growth rates of *P. ruthveni* with data from other studies of *Pituophis*.

Because of 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 (*P. 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 hills 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 (*Pituophis echinata*), loblolly pine (*Pituophis taeda*), and the introduced slash pine (*Pituophis elliottii*), 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 because of 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.

Pine snakes were obtained by trapping and hand-capture between 1993 and 1997. Traps consisted of plywood and 6-mm hardware cloth boxes (1.3 × 1.3 × 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. Traps were operated on a variable schedule at 10–15 sites during the months of March to 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 (S. B. Reichling, pers. comm.).

Fourteen snakes (of the 38 studied) were measured two times during the study, providing the data on growth reported here. Estimates of mortality do not require two growth measurements and are therefore based on all 38 specimens that were studied in the field. Snakes were implanted with SI-2T transmitters (44 × 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. 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 nongravid females. However, Fitch (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

[2] Present address: Department of Biological Sciences, Box 5018, University of Southern Mississippi, Hattiesburg, Mississippi 39406-5018, USA.
[3] Corresponding Author. E-mail: john.himes@usm.edu
[5] Present address: United States Fish and Wildlife Service, 510 Desmond Drive, Suite 102, Lacey, Washington 98503-1263, USA.

TABLE 1. Growth in length and mass of specimens of *Pituophis 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 ID no.	Sex	Length (TL, SVL; cm)		Change in TL, SVL (cm)	Change in TL, SVL (%)[a]	Mass (g)		Change in Mass (g, %[b])	Transmitter mass (g)/initial mass (g)	Interval (months[c])
		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 (Dec)
34*	F	88.5, 78.0	106.4, 94.5	17.6, 16.5	0.199, 0.212	200.7	327.0	126.3, 62.9	0.060	13 (Dec)
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 (Dec)
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 (Dec)
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 (Jun)
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 (Dec)
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 (Jan)
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 (Nov)
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 (Dec)
29	M	131.0, 117.4	133.5, 119.2	2.5, 1.8	0.019, 0.015	447.1	559.0	111.9, 25.0	0.027	24 (May)
33	M	132.5, 115.8	134.0, 117.0	1.5, 1.2	0.011, 0.010	528.4	479.4	−49.0, −9.3	0.023	3 (Dec)
10	M	134.9, 115.9	149.0, 130.0	14.1, 14.1	0.105, 0.122	822.0	770.0	−52.0, −6.3	0.015	31 (Dec)
3	M	148.5, 134.5	149.1, 134.6	0.6, 0.1	0.004, 0.001	728.3	850.0	121.7, 16.7	0.016	36 (Mar)
15	M	156.9, 134.5	157.3, 135.8	0.4, 1.3	0.003, 0.010	996.9	606.4	−390.5, −39.2	0.012	16 (Nov)
Means	F	109.4, 95.6	120.4, 105.6	11.2, 12.0	0.111, 0.114	442.3	480.9	38.6, 21.2	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	−29.6, −1.6	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	4.5, 9.8	0.025	20.8

[a] Change is expressed as a percentage of initial TL and SVL, respectively.
[b] Change is expressed as a percentage of initial mass.
[c] Month of final capture is in parentheses.

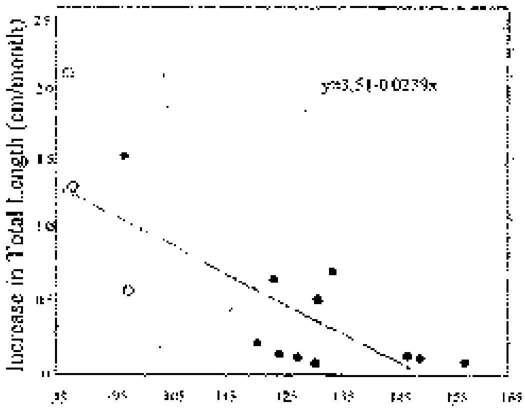


FIG. 1. Length increases of native (closed circles) and captive-bred (open circles) *Pituophis ruthveni* according to total length. Each symbol identifies the approximate growth rate of an individual snake. Regression line: y = 3.51 − 0.0239x.

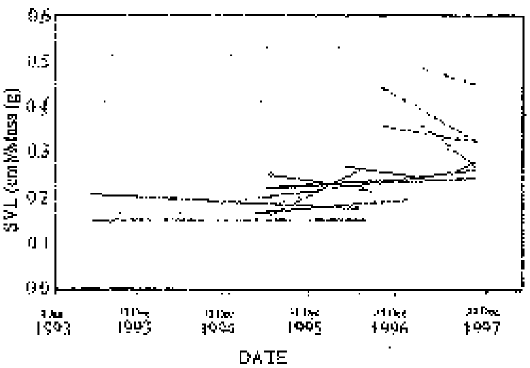


FIG. 2. Growth rates of *Pituophis ruthveni* (N = 14). Lines represent individual adult snakes; dashed lines represent juveniles (all females).

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) was used as an inhalant. Transmitters were implanted either subcutaneously or intraperitoneally. All transmitters (except the single Blackburn transmitter) had an approximate battery life of 18 months and were replaced as necessary. The Blackburn transmitter had an expected battery life of six months.

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 by local residents 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 and their receiving populations were considered to be less than the imminent danger posed by a busy highway and much human activity.

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: Total Length.—Adult males reached larger sizes than adult females (Table 1). Mean total length increase (cm) per month was 0.59 ± 0.39 (mean ± 95% Confidence Interval, range = 0.02–2.14, *N* = 14). Mean increase in total length per month for juvenile snakes was 1.40 ± 1.02 (0.59–2.14, *N* = 4). 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 (0.11–0.63, *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 juvenile snakes was 9.35 ± 10.14 (4.09 to 18.25, *N* = 4). 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.

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 gained mass relative to their increase in total length and snakes with a positive slope lost mass relative to their increase in total length.

Four (three 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 individual growth dynamics 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 *Pituophis 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 8.3% (= 19/228 total months survived). Males made up 47.1% and females made up 52.9% of the 17 snakes that survived at least one year. Two one-year surviving juveniles comprised 25% of all juveniles.

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) were 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 6.9%. Similar calculations give monthly mortality rates of 6.9% for both sexes (males $N = 9$; 131 months; females $N = 6$; 87 months). Five captive-bred juvenile snakes were tracked for 39 months. During this period, two deaths occurred, resulting in a monthly mortality rate of 5.13%.

Of the 15 adult mortalities, excluding two 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 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 and two of these six individuals were found as skeletal remains below ground. The only remains of another two were their isolated transmitters. Of 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.

Any estimate of growth rate or a growth curve requires at least two measurements of size at known time intervals. To estimate age based on the rate of growth, at least one known age is also required. There

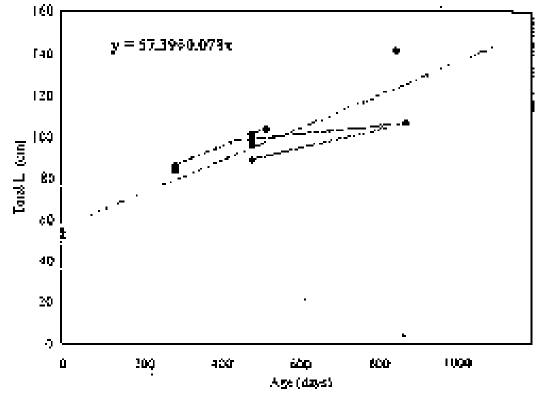


FIG. 3. Growth rates of nine individuals of *Pituophis ruthveni* of known age. Closed circles are captive snakes released during this study. Lines join two measurements of three individuals. The triangles represent four hatchlings (Reichling, 1990). Regression line: $y = 57.39 + 0.078x$.

is no published information 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). Although the position of the curve at birth is probably accurate, the slope of the resulting regression line may be too steep because the nine posthatchlings were raised in captivity for the first part of their lives (birth sizes were not recorded). They probably experienced a more rapid growth rate than would wild snakes because of the food supply, constant environment, and lack of natural dormancy (Fig. 3).

Regardless of the possible 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 (consistent with the trend) 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 juveniles and adults differ in shape. 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 shape 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 was not the largest of the four juveniles, but according to its total length/mass ratio, it might have been the most mature.

In the only other extensive study of growth in *Pituophis*, Parker and Brown (1980) recorded length and weight changes in *P. c. 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, whereas 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 (*P. ruthveni*). This species exhibits allometric growth in length to mass ratio, which indicates an optimum body shape for adults. Annual increase in length might be similar to that observed for known-age gopher snakes (*P. 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.

Acknowledgments.—S. B. Reichling of the Memphis zoo and Aquarium provided nine study snakes. The Louisiana Department of Wildlife and Fisheries and the Texas Parks and Wildlife Department provided partial funding. We thank the International Paper company and Temple-Inland for permission to conduct portions of this study on their land and the Magnolia Road Hunt Club for providing lodging. For critical reviews of the manuscript, we thank S. J. Beaupre, C. J. Cole, R. N. Conner, D. L. Cundall, L. Fitzgerald, and D. P. Reagan. We also thank J. Jordan, J. Jordan Jr., K. Moore, R. Carrie, M. Ealy, R. Schaefer, C. Collins, J. Tull, and M. Duran for field assistance.

Literature Cited

Collins, J. T. 1997. Standard common and current scientific names for North American Amphibians and Reptiles. 4th ed. Society for the Study of Amphibians and Reptiles, Herpetology Circular 19:1–40.

Conant, R., and J. T. Collins. 1991. A field Guide to Reptiles and Amphibians of Eastern and Central North America. 3rd ed. Houghton Mifflin Co., Boston, MA.

Fitch, H. S. 1970. Reproductive cycles of lizards and snakes. Miscellaneous Publications of the Museum of Natural History, University of Kansas 52:1–247.

Jennings, R. D., and T. H. Fritts. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni*. U.S. Fish and Wildlife Service and the University of New Mexico Museum of Southwestern Biology, Albuquerque.

Parker, W. S., and W. S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee Public Museum, Publications in Biology and Geology 7:1–104.

Plummer, M. V. 1997. Population ecology of green snakes (*Opheodrys aestivus*) revisited. Herpetological Monographs 11:102–123.

Reichling, S. B. 1988. Louisiana's rare and elusive snakes. Louisiana Conservationist 40:12–14.

———. 1989. Reproductive biology and current status of the Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. *In* C. J. Uricheck (ed.), Proceedings of the 13th Annual International Herpetological Symposium, pp. 95–98. International Herpetological Symposium, Inc., Danbury, CT.

———. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). Southwestern Naturalist 35:221–222.

———. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni* and its relevance to the evolutionary species concept. Journal of Herpetology 29:186–198.

Reinert, R. K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705.

Rodríguez-Robles, J. A., and José M. De Jesús-Escobar. 2000. Molecular systematics of New World gopher, bull, and pinesnakes (*Pituophis*: Colubridae), a transcontinental species complex. Molecular Phylogenetics and Evolution 14:35–50.

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 49:111–122.

Rudolph, D. C., S. J. Burgdorf, R. R. Schaefer, R. N. Conner, and R. T. Zappalorti. 1998. Snake mortality associated with late season radio-transmitter implantation. Herpetological Review 29:155.

Stull, O. G. 1929. The description of a new subspecies of *Pituophis melanoleucus* from Louisiana. Occasional Papers of the Museum of Zoology, University of Michigan 205:1–3.

Thomas, R. A., B. J. Davis, and C. R. Culbertson. 1976. Notes on variation and range of the Louisiana pine snake, *Pituophis melanoleucus ruthveni* Stull (Reptilia, Serpentes, Colubridae). Journal of Herpetology 10:252–254.

Weatherhead, P. J., and F. W. Anderka. 1984. An improved radio transmitter and implantation technique for snakes. Journal of Herpetology 18:264–269.

Accepted: 8 January 2002.

TEXAS J. SCI. 56(4):383-394 NOVEMBER, 2004

DIEL ACTIVITY PATTERNS OF THE LOUISIANA PINE SNAKE (*PITUOPHIS RUTHVENI*) IN EASTERN TEXAS

Marc J. Ealy, Robert R. Fleet and D. Craig Rudolph

Texas Parks and Wildlife Department, 1700 7th St., Rm. 101
Bay City, Texas 77414;
Department of Mathematics and Statistics, Stephen F. Austin State University
Nacogdoches, Texas 75962 and
USDA Forest Service, Southern Research Station, 506 Hayter St.
Nacogdoches, Texas 75965

Abstract.—This study examined the diel activity patterns of six Louisiana pine snakes in eastern Texas using radio-telemetry. Snakes were monitored for 44 days on two study areas from May to October 1996. Louisiana pine snakes were primarily diurnal with moderate crepuscular activity, spending the night within pocket gopher burrows or inactive on the surface. During daylight hours, snakes spent approximately 59% of their time underground within gopher burrows, burned out/rotten stumps, or nine-banded armadillo (*Dasypus novemcinctus*) burrows. Remaining time was spent on the surface either close to subterranean refuge, or in long distance movements that generally terminated at another pocket gopher burrow system. Long distance movements occurred on 45% of the days snakes were monitored and averaged 163 m/movement. When snakes were active, movements related to ambientair temperature; 82% of these movements occurred between 1000 and 1800 hours. These results confirm that Louisiana pine snakes are diurnal and closely associated with Baird's pocket gophers and their burrow systems, and have provided new insight on the ecology of this rare snake.

The Louisiana pine snake (*Pituophis ruthveni*), first described by Stull (1929), is a large-bodied constrictor of the family Colubridae and until recently was considered one of 15 subspecies of *Pituophis melanoleucus* (see Sweet & Parker 1990; Collins 1991; Crother et al. 2003). The Louisiana pine snake is allopatric to other *Pituophis* and its distribution is primarily restricted to the longleaf pine (*Pinus palustris*) ecosystem of west-central Louisiana and eastern Texas (Conant 1956; Reichling 1995). The longleaf pine ecosystem is perpetuated by frequent fire (Platt et al. 1988; Frost 1993). Louisiana pine snakes are semi-fossorial and are closely associated with Baird's pocket gopher (*Geomys breviceps*) burrow systems (Rudolph & Burgdorf 1997). Baird's pocket gophers are the predominant prey of Louisiana pine snakes and their burrow systems are used for foraging, shelter, escape from frequent fires, and hibernation (Rudolph et al. 1998; 2003).

Many have reported on the apparent rarity of *P. ruthveni*; this can be partly attributed to its semi-fossorial habits and secretive nature (Conant 1956; Young & Vandeventer 1988; Rudolph & Burgdorf 1997). Only 57 records of *P. ruthveni* were available through 1990 (Conant 1956; Jennings & Fritts 1983; Young & Vandeventer 1988; Reichling 1989). As a result, this species is considered to be one of the rarest snakes in North America (Thomas et al. 1991). Extreme rarity has prevented researchers from collecting substantial ecological and natural history data on the species and accounts for the paucity of available literature.

In 1993, the USDA Forest Service Southern Research Station initiated a long term study of home range and habitat use of free ranging Louisiana pine snakes in eastern Texas and west-central Louisiana through the use of radio-telemetry. This portion of the study was conducted from May through October 1996 to elucidate diel activity patterns of this snake in eastern Texas.

Study Areas

Two areas were used to monitor Louisiana pine snakes in eastern Texas. Foxhunter's Hill is a 500 ha longleaf pine savanna located on the Sabine National Forest approximately 25.5 km south of Hemphill, Texas, in Sabine County. The second area, Scrappin' Valley, owned by Temple-Inland Forest Products Corporation, is approximately 29 km south of Hemphill, Texas, in Newton County. The portion of Scrappin' Valley used as the study area is a 450 ha longleaf pine savanna. Characteristics common to both sites are: soils with high sand content; diverse herbaceous flora dominated by little bluestem (*Schizachyrium scoparium*) and bracken fern (*Pteridium aquilinum*); over story dominated by longleaf pine (*Pinus palustris*), sparsely distributed blackjack oak (*Quercus marilandica*) and blue jack oak (*Quercus incana*); and areas of encroachment by sweet gum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), and yaupon (*Ilex vomitoria*) as a result of past fire suppression. Foxhunter's Hill possesses moderate topographic relief, average basal area of 9 m^2/ha, and heavy leaf litter accumulation and was burned by prescription in late winter of 1993. Scrappin' Valley has lower topographic relief than Foxhunter's Hill, average basal area of 6 m^2/ha, moderate leaf litter accumulation, and was burned in late winter of 1995. Generally, Scrappin' Valley was burned annually while Foxhunter's Hill was burned every 3-5 years, resulting in differential leaf litter accumulation in the two areas.

MATERIALS AND METHODS

Transmitter implantation.—Louisiana pine snakes were captured on the study areas by hand or in drift fence/funnel traps. Temperature sensitive transmitters (Holohil Systems Ltd., SI-2T) 29mm long and 10 mm in diameter with 28 cm whip antennae were implanted subcutaneously following the general procedure of Weatherhead & Anderka (1984). Transmitter life-span was approximately 18 months and maximum transmission range was approximately 1200 m.

Radio-telemetry/data collection.—Snakes were located early in the morning before they became active and emerged from subterranean shelter. A Trimble GPS Professional unit and data logger was used to record each snake's location. Air temperature at the snake's location was measured with a mercury thermometer 0.5 m above the ground in the shade. Substrate temperature was recorded in one of two ways: if the snake was aboveground, the thermometer was placed on the substrate as close as possible to the snake without disturbing it; if below ground, the thermometer was inserted approximately 5 cm into the soil. Snake body temperature was determined by comparison of transmitter pulse rate with a calibration curve for each transmitter.

Throughout the day until sunset, transmitter pulse counts and air temperatures were recorded at 30-45 minute intervals. When the pulse count of a transmitter changed by becoming much slower or faster, indicating a temperature change of the implanted transmitter, the snake was relocated to determine if snake activity had occurred. Six snakes, three on Foxhunter's Hill, and three on Scrappin' Valley were monitored from dawn to dusk for a total of 44 snake days. Movements were recorded and calculated only if an individual moved more than 10 m from its previous location on a given day (Slip & Shine 1988). Movements on six additional days were recorded during the course of other data collection and were also available. Movement distances were calculated through the use of Trimble GPS Pathfinder Office software (Trimble Mapping and GIS Systems Division, Sunnyvale, CA).

Periodic night checks were conducted by locating snakes at sunset and again at midnight and before sunrise to determine if the snakes were active nocturnally. Additional data regarding movement and choice of underground refugia were collected from these and other snakes in addition to the 44 snake monitoring days.

Habitat measurements were taken at each snake relocation point as required for various aspects of research on *P. ruthveni*. Additional habitat measurements were taken at 100 stratified random points determined by overlaying a grid on the overall study site and using the intersections of the grid lines as the random points. The only habitat measurement relevant to this study was the number of burrows counted within an 11.2 m radius (0.04 ha) of each habitat point. *Geomys breviceps* "burrows" were counted as the number of visible push-up mounds and all other burrows were enumerated by the number of actual openings at or near the soil surface.

Data analysis.—Distance moved per snake each day was tested by a Mann-Whitney U-test. Chi-square contingency tests were used to evaluate the time each snake utilized above ground and below ground environments, movement frequency, and refuge/shelter types used. Frequency of movements during 12 two-hour time periods were evaluated by Chi-square contingency tests and all statistical analyses were performed at an alpha level of 0.05.

RESULTS

Six *P. ruthveni* (5 F, 1 M) were monitored during all or most of a total of 44 snake days between July and October, 1996. During the 44 snake days of monitoring, individual snakes were located at the surface between sunrise and sunset for 145 hrs of a total of 354 hrs (41%). The remainder of their time was spent underground in *G. breviceps* burrows, nine-banded armadillo burrows, and decayed or burned stump holes and associated root channels.

In order to determine nocturnal behavior, the six *P. ruthveni* were monitored at approximately sunset, midnight, and sunrise for a total of 20 snake days during July and August. With one exception, all snakes were located below ground in *G. breviceps* burrows each night (n = 17). The exception, a female, was located on the surface beneath dense herbaceous vegetation at sunset on three separate days and remained in that location until the next morning. One of these instances was during pre-ecdysis. For the 44 snake days when extensive monitoring occurred, snakes were assumed to have spent the previous night in *G. breviceps* burrows, based on early morning detections, a total of 29 times. These same snakes were assumed to have spent the succeeding night in subterranean retreats in 38 instances (35 in *G. breviceps* burrows, three in *D. novemcintus* burrows) based on detections at dusk. Data are not available for the remaining 21 nights.

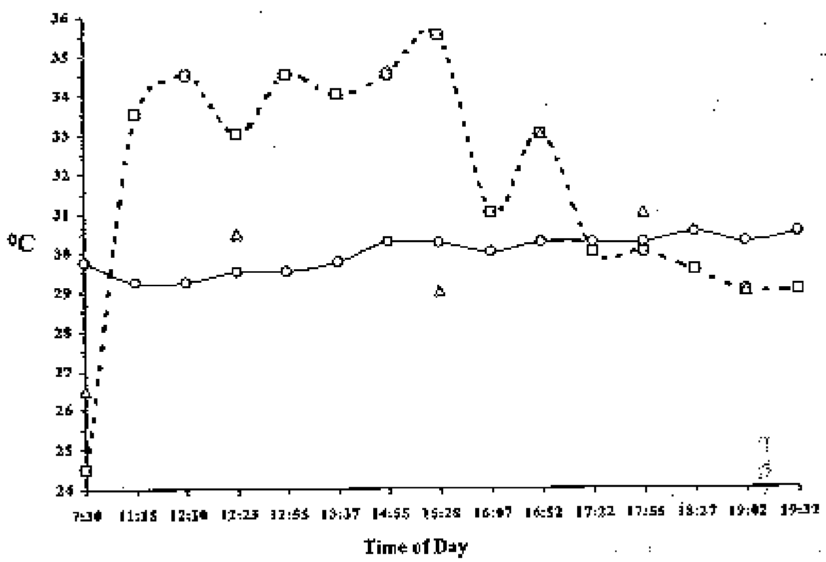


Figure 1. Body temperature (open circles), air temperature (open squares), and substrate temperature (open triangles) for a Louisiana pine snake (*Pituophis ruthveni*) spending daylight hours underground in a Baird's pocket gopher (*Geomys breviceps*) burrow. Adult female 143 on 14 July 1996.

Pituophis ruthveni monitored for daily activity during this study evinced three general daily activity patterns. In 17 cases, snakes remained in *G. breviceps* burrow systems for the entire daily tracking period (Fig. 1). All six snakes except one female from Scrappin' Valley spent at least one entire day in a *G. breviceps* burrow. Conversely, three individuals spent an entire day on the surface. Two of these individuals moved significant distances (225 m and 59 m), and the third was in pre-ecdysis condition with clouded eyes.

In 24 cases various combinations of time were spent on the surface and below ground. These cases were usually associated with substantial surface movement (19 of 24), usually culminating with entrance into another underground refuge (22 of 24) (Fig. 2). Of these 24 snake days, 12 involved snakes that were on the surface when first located in the morning and 12 were in *G. breviceps* burrow systems from which they subsequently emerged. It is unclear if the snakes initially located on the surface had emerged from underground refugia early or had spent the night on the surface, although sampling for nocturnal activity suggests the former in most instances.

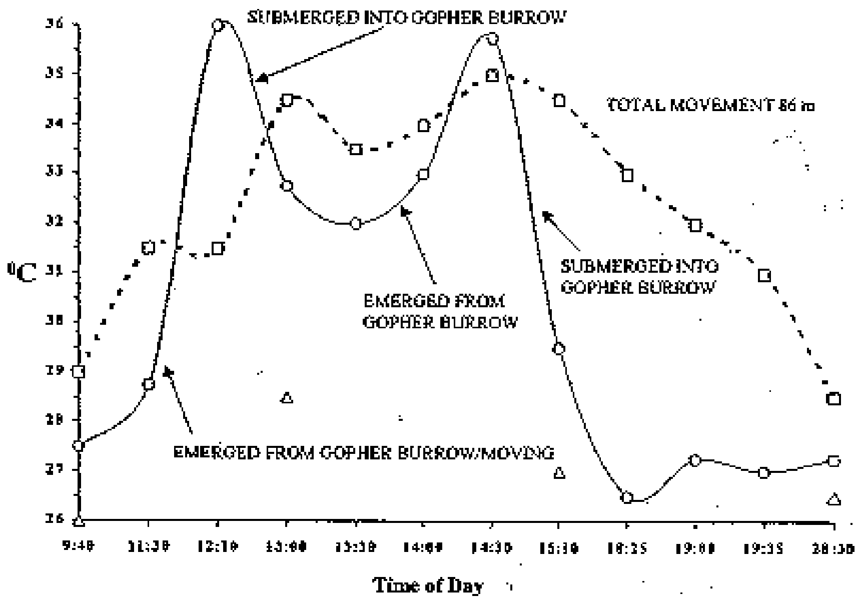


Figure 2. Body temperature (open circles), air temperature (open squares), and substrate temperature (open triangles) for a Louisiana pine snake (*Pituophis ruthveni*) spending portions of a day underground in a Baird's pocket gopher (*Geomys breviceps*) burrow and portions above ground. Adult female 118 on 03 August 1996.

On the 27 snake days in which at least a portion of the day was spent on the surface plus six additional snake days for which movement distances are available, seven snakes remained in the same location, exhibiting only minor movements of < 10 m throughout the day. One individual moved 72 m from its initial location, but returned to its initial location by dusk. In 25 instances snakes moved substantial distances (> 10 m) during the day and were located an average of 163 m (range 11-625 m) from their initial location. Movements occurred from shortly after sunrise until dusk with the majority (82%) between 10:00 and 18:00 hours (Fig. 3). Overall, snakes moved a substantial distance on 20 of 44 days monitored (45.5%). There was a significant difference in frequency of movement between Scrappin' Valley and Foxhunter's Hill snakes ($\chi 2 = 9.99$, $df = 1$, $P < 0.005$) with the Scrappin' Valley snakes moving more frequently (Table 1). Daily movement distances were calculated by summing straight line measurements between consecutive locations and should be interpreted as an underestimation since snakes rarely travel in a straight line (Secor 1994). On days when movement occurred, snakes at Scrappin' Valley (Table 1) moved greater distances, ($\bar{x} = 189$ m, $n = 19$) than did those on Foxhunter's Hill ($\bar{x}$

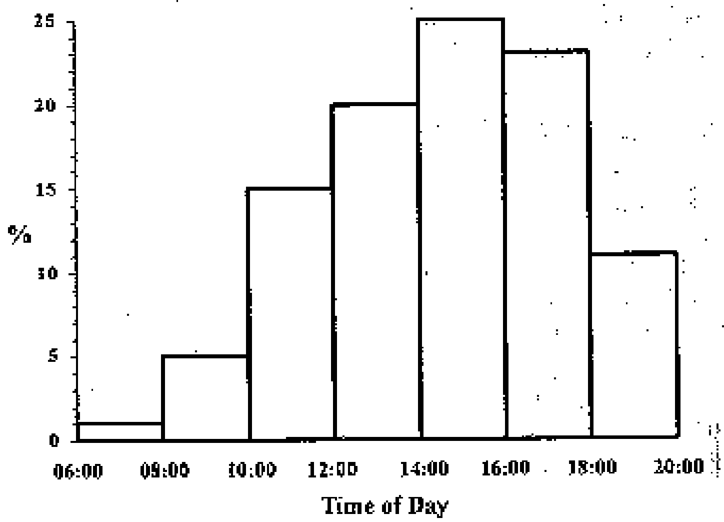


Figure 3. Frequency distribution (%) of movements by six Louisiana pine snakes (*Pituophis ruthveni*) relative to time of day. Data for 12 May - 27 October 1996.

= 91 m, n = 7); this difference was significant (U = 40.5, df = 26, $P < 0.05$).

Pine snake use of underground refugia was recorded on 44 days during which daily activity patterns were monitored and on other days when snakes were located for home range computation. Snakes used *G. breviceps* burrows (80.9%), decayed or burned stumps (15.4%), or *D. novemcintus* burrows (3.7%) as underground refugia. Based on habitat data collected at random points (Table 2), Scrappin' Valley had significantly higher densities of *G. breviceps* burrows (χ^2 = 193.9, df = 1, $P < 0.005$) and other types of retreats (χ^2 = 10.2, df = 1, $P < 0.005$) than Foxhunter's Hill. Compared to snakes at Foxhunter's Hill, snakes at Scrappin' Valley used underground retreats other than pocket gopher burrows more frequently ($\chi2$ = 29.31, df = 1, $P < 0.001$).

The percent of time an individual utilized underground environments on days snakes were monitored was determined through visual observations and making inferences from temperature relationships based on the snakes' body temperature compared to air and substrate temperatures. Snakes at Scrappin' Valley (Table 1) spent a significantly lower proportion of daylight hours underground (45%) compared to snakes at Foxhunter's Hill (74%) (χ^2 =19.96, df = 1, P<0.05).

generally involved movement from one *G. breviceps* burrow system to another and consequently reflect the dispersed distribution of these burrow systems.

Pituophis ruthveni, during this and associated studies were found to move very little while underground in *G. breviceps* burrows, typically remaining near the point of entrance in the relatively shallow foraging tunnels. This suggests that *P. ruthveni* behave as sit-and-wait predators when hunting pocket gophers, rather than actively searching within the burrow system. *Geomys breviceps* maintain an intricate burrow complex that can reach 180 m in length (Schmidly 1983), and they can rapidly construct an earthen plug effectively limiting movement by *P. ruthveni* (Rudolph et al. 2003). These observations suggest that a sit-and-wait strategy combined with a brief pursuit may be the most effective strategy to capture *G. breviceps*.

Pituophis ruthveni behavior differed significantly, based on three criteria, between the Scrappin' Valley and Foxhunter's Hill study sites. Snakes at Scrappin' Valley moved more frequently, moved greater distances, and spent less time underground compared to snakes at Foxhunter's Hill. The Scrappin' Valley site was also characterized by a greater density of both *G. breviceps* burrows and other types of retreats compared to the Foxhunter's Hill site. It is possible that the greater availability of subterranean retreats at Scrappin' Valley resulted in fewer restrictions on above ground activity by *P. ruthveni*. The greater availability of *G. breviceps* burrows and other subterranean retreats (primarily burned stump and root channels) is presumably related to the more frequent prescribed fire regime at the Scrappin' Valley site.

The use of subterranean retreats during the active period of the year provided *P. ruthveni* with predictable escape from excessively high air temperatures. Conversely, snakes also had direct access to basking opportunities on the surface that allowed the snakes to maintain a higher body temperature during substantial periods. This general pattern is similar to the results of Himes et al. (2002) for this species in northern Louisiana.

The diel activity budget of *P. ruthveni* reveals a species that is diurnal and semifossorial as is generally typical of other members of the genus in the United States (Fitch & Shirer 1971; Parker & Brown 1980; Sweet & Parker 1990). The importance of burrows of Baird's pocket gophers when combined with previous data and observations (Rudolph &

Burgdorf 1997; Rudolph et al. 1998; 2003) supports the hypothesis that *P. ruthveni* is dependent on *G. breviceps* and ultimately on a frequent fire regime that maintains the herbaceous vegetation that supports *G. breviceps* populations.

ACKNOWLEDGMENTS

B. Autrey, S. J. Burgdorf, R. R. Schaefer, R. N. Conner, R. Maxey, and C. M. Duran provided assistance in collection of field data and other aspects of this research. Temple-Inland Forest Products Corp. provided access to the Scrappin' Valley study site. The U.S. Fish and Wildlife Service and Texas Parks and Wildlife Department provided partial funding under Section 6 of the U. S. Endangered Species Act and Texas Parks and Wildlife Department issued the required permits.

LITERATURE CITED

Burger, J. & R. T. Zappalorti. 1988. Habitat use by pine snakes (*Pituophis melanoleucus*) in the New Jersey Pine Barrens; individual and sexual variation. J. Herpetol., 23(1):68-73.

Collins, J. T. 1991. Viewpoint: A new taxonomic arrangement for some North American amphibians and reptiles. Herpetol. Rev., 22(2):42-43.

Conant, R. 1956. A review of two rare pine snakes from the Gulf coastal plain. Amer. Mus. Novitates, (1781):1-31.

Crother, B. I., J. Boundy, J. A. Campbell, K De Quieroz, D. Frost, D. M. Green, R. Highton, J. B. Iverson, R. W. McDiarmid, P. A. Meylan, T. W. Reeder, M. E. Seidel, J. W. Sites, Jr., S. G. Tilley & D. B. Wake. 2003. Scientific and standard English names of amphibians and reptiles of North America north of Mexico: update. Herp. Rev., 34(3):196-203.

Davis, W. B. & D. J. Schmidly. 1994. The Mammals of Texas. Texas Parks and Wildlife Press, Austin, 338pp.

Fitch, H. S. & H. W. Shirer. 1971. A radio telemetric study of spatial relationships in some common snakes. Copeia, 1971(1):118-128.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. Tall Timbers Fire Ecol. Conf., 18:17-43.

Gans, C. & W. R. Dawson. 1976. Reptilian physiology: An overview. Pp. 1-17, *in* Biology of the Reptilia. C. Gans and W. R. Dawson, (eds). Academic Press, London and New York, 556 pp.

Gibbons, J. W. & R. D. Semlitsch. 1987. Activity patterns. Pp. 396-421, *in* R. A. Siegel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology. McGraw Hill, New York, 529 pp.

Himes, J. G., L. M. Hardy, D. C. Rudolph & S. J. Burgdorf. 2002. Body temperature variations of the Louisiana pine snake (*Pituophis ruthveni*) in a longleaf pine ecosystem. Herpetol. Nat. History 9(2):117-126.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. Pp. 25-91, *in* Biology of the Reptilia. C. Gans, ed. Academic Press, London and New York, 502 pp.

Parker, W. S. & W. S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis taeniatus taeniatus and Pituophis melanoleucus deserticola*, in northern Utah.

Publ. Biol. Geol. No. 7, Milwaukee Publ. Mus., 104p.

Platt, W. J., G. W. Evans & S.L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Nat. 131(4):491-525.

Plummer, M. V. & J. D. Congdon. 1994. Radio telemetric study of activity and movement of racers (*Coluber constrictor*) associated with a Carolina Bay in South Carolina. Copeia, 1994(?):20-26.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanolecus ruthveni*) and its relevance to the evolutionary species concept. J. Herpetol., 29(2):186-198.

Rudolph, D. C. & S. J. Burgdorf. 1997. Timber rattlesnakes and Louisiana pine snakes of the west Gulf coastal plain: hypotheses of decline. Texas J. Sci., 49(3) Supplement:111-122.

Rudolph, D. C., S. J. Burgdorf, J. C. Tull, M. Ealy, R. N. Conner, R. R. Schaefer & R. R. Fleet. 1998. Avoidance of fire by Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. Herpetol. Rev., 29(3):146-148.

Rudolph, D. C., S. J. Burgdorf, R. N. Conner, C. S. Collins, D. Saenz, R. R. Schaefer, T. Trees, C. M. Duran, M. Ealy & J. G. Himes. 2003. Prey handling and diet of Louisiana pine snakes (*Pituophis ruthveni*) and black pine snakes (*P. melanoleucus lodingi*) with comparisons to other selected colubrid taxa. Herpetol. Nat. History, 9(1):57-62.

Schmidly, D. J. 1983. Texas mammals east of the Balcones fault zone. Texas A&M Univ. Press, College Station, 400p.

Secor, S. M. 1994. Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. Copeia, 1994(3):631-645.

Slip, D. J. & R. Shine. 1988. Habitat use, movements, and activity patterns of free-ranging diamond pythons, *Morelia spilota spilota* (Serpentes: Boidae): A radio telemetric study. Aust. Wild. Res., 15:515-531.

Stull, O. G. 1929. The description of a new subspecies of *Pituophis melanoleucus* from Louisiana. Occas. Papers Mus. Zool. Univ. Michigan, 205:1-3.

Sweet, S. S. & W. S. Parker. 1990. *Pituophis melanoleucus*. Catalogue of American Amphibians and Reptiles, 474:1-8.

Thomas, R., B. J. Davis & M. R. Culbertson. 1976. Notes on variation and range of the Louisiana pine snakes, *Pituophis melanoleucus ruthveni*, Stull (Reptilia, Serpentes, Colubridae). J. Herpetol., 10(3):252-254.

U. S. Fish and Wildlife Service. 1991. Animals proposed for review. Federal Register, 56(225):58804-58813.

Weatherhead, P.J. & F. W. Anderka. 1984. An improved radio transmitter and implantation technique for snakes. J. Herpetol., 18(3):264-269.

Young, R. A. & T. L. Vanderventer. 1988. Recent observations on the Louisiana pine snakes, *Pituophis melanoleucus ruthveni* (Stull). Bull. Chicago Herp. Soc., 23:203-207.

MJE at: ealy@wcnet.net

Herpetological Natural History, 9(1), 2002, pages 57–62.

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

D. Craig Rudolph, Shirley J. Burgdorf, Richard N. Conner, Christopher S. Collins, Daniel Saenz, Richard R. Schaefer, and Toni Trees
Wildlife Habitat and Silviculture Laboratory, Southern Research Station, U.S.D.A. Forest Service, Nacogdoches, Texas 75962, USA

C. Michael Duran
Mississippi Department of Wildlife, Fisheries and Parks, Hattiesburg, Mississippi 39401, USA

Marc Ealy
Department of Biology, Stephen F. Austin State University, Nacogdoches, Texas 75962, USA

John G. Himes[1]
Museum of Life Sciences, Louisiana State University, Shreveport, Louisiana 71115, USA

Abstract. Diet and prey handling behavior were determined for Louisiana pine snakes (*Pituophis ruthveni*) and black pine snakes (*P. melanoleucus lodingi*). Louisiana pine snakes prey heavily on Baird's pocket gophers (*Geomys breviceps*), with which they are sympatric, and exhibit specialized behaviors that facilitate 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* was also examined.

Key Words. Diet; *Geomys*; *Pituophis melanoleucus lodingi*; *P. ruthveni*; Predation.

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 radiotelemetry study of *P. ruthveni* (Rudolph and Burgdorf 1997; Rudolph et al. 1998) demonstrated 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 from that of *P. ruthveni* in that its range is allopatric with that of pocket gophers except in the extreme eastern part of its range where it intergrades with *P. m. mugitus*. In this limited area, it is sympatric with the southeastern pocket gopher (*G. pinetis*).

[1]Present address: Nevada Division of Wildlife, Southern Region Headquarters, 4747 Vegas Drive, Las Vegas, Nevada 89108, USA

Prey handling by constricting snakes is a behavioral pattern that has a long evolutionary history (Greene and Burghardt 1978). Hisaw and Gloyd (1926), Willard (1977), Greenwald (1978) and de Queiroz (1984) have described the basic patterns of constriction in the genus *Pituophis* and described variation in constriction behavior dependent on prey type and the physical setting in which constriction takes place. *Pituophis* is capable of substantial plasticity in the use of constriction to subdue a variety of prey species and, unlike many other colubrid genera, exhibits a strong tendency to use pinioning to subdue prey, especially relatively small or inactive prey (Willard 1977; de Queiroz 1984).

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. For comparative purposes we also observed prey handling behavior of *P. sayi sayi*, a closely related congener, and *Elaphe obsolete lindheimeri*, a sympatric constrictor without fossorial adaptations.

MATERIALS AND METHODS

Data on diet in the wild were taken 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, teeth, claw, bone, and eggshell were extracted from fecal samples and identified by comparison with a reference collection obtained from local animals. Hair samples were compared microscopically to the limited number of small mammal species occurring locally. Tooth and claw samples were compared macroscopically to available museum specimens and to remains of animals fed to captive snakes. Two additional prey records for *P. ruthveni* and one for *P. m. lodingi* were obtained during field observations of radio-transmittered 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. The space was filled with slightly moist sandy loam soil to a depth of 40 cm. The 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, 1–2 h, 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. The procedure was repeated 20 times with 14 individual *P. ruthveni* 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 for small sample size 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 used coils for constriction 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

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

Taxon	n
Pituophis ruthveni	
Geomys breviceps	10
Scalopus aquaticus	4
Peromyscus sp.	1
Sigmodon hispidus	1
unid. mammal	2
turtle eggs*	4
P. m. lodingi	
Sigmodon hispidus	2
Peromyscus sp.	2
Silvilagus sp.	1
Colinus virginianus (eggs)	1
spider	1

*probably *Trachemys scripta*, based on size and habitat

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 five of six 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 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 a third to half of the snake's total length and pinioned the gopher by muscular kinking of its extended body (Fig. 1A); (2) the snake rapidly proceeded past the gopher, doubled back, and pinioned the gopher using two lengths of its body (Fig. 1B); or (3) the snake briefly (< 2 s) 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 1 or 2 s. Otherwise, a snake's 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; cf. Hisaw and Gloyd 1926).

Pituophis m. lodingi reacted differently (Table 2). In nine 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 typ-

TABLE 2. Foraging behavior of selected snakes within burrows of Baird's pocket gophers and in open situations. Abbreviations used are Pr = *Pituophis ruthveni*, Ps = *P. sayi sayi*, Pm = *P. melanoleucus lodingi*, Eo = *Elaphe obsolete lindheimeri*.

Taxon	n	Successful Attempts		Pursuit Rate		Mouth Used		Constriction*	
		Trial 1	All Trials	Slow	Rapid	Yes	No	Yes	No
Burrow Trials									
Pr	14	14 of 14	19 of 20	0	19	0	19**	0	19
Pm	9	1 of 9	2 of 11	10	1	1	1	1	1
Ps	2	2 of 2	6 of 6	0	6	0	6	0	6
Eo	7	3 of 7	7 of 12	12	0	7	0	7	0
Open Trials									
Pr	11	11 of 11		NA		11	0	11	0
Pm	3	2 of 3	6 of 11***	NA		6	0	6	0
Ps	2	2 of 2	5 of 5	NA		5	0	5	0
Eo	7	3 of 3	8 of 8	NA		8	0	8	0

*see text for definition
**includes two trials in which mouth grasp was used for < 2 s.
***Three individual *P. m. lodingi* refused *G. breviceps* a total of five times.

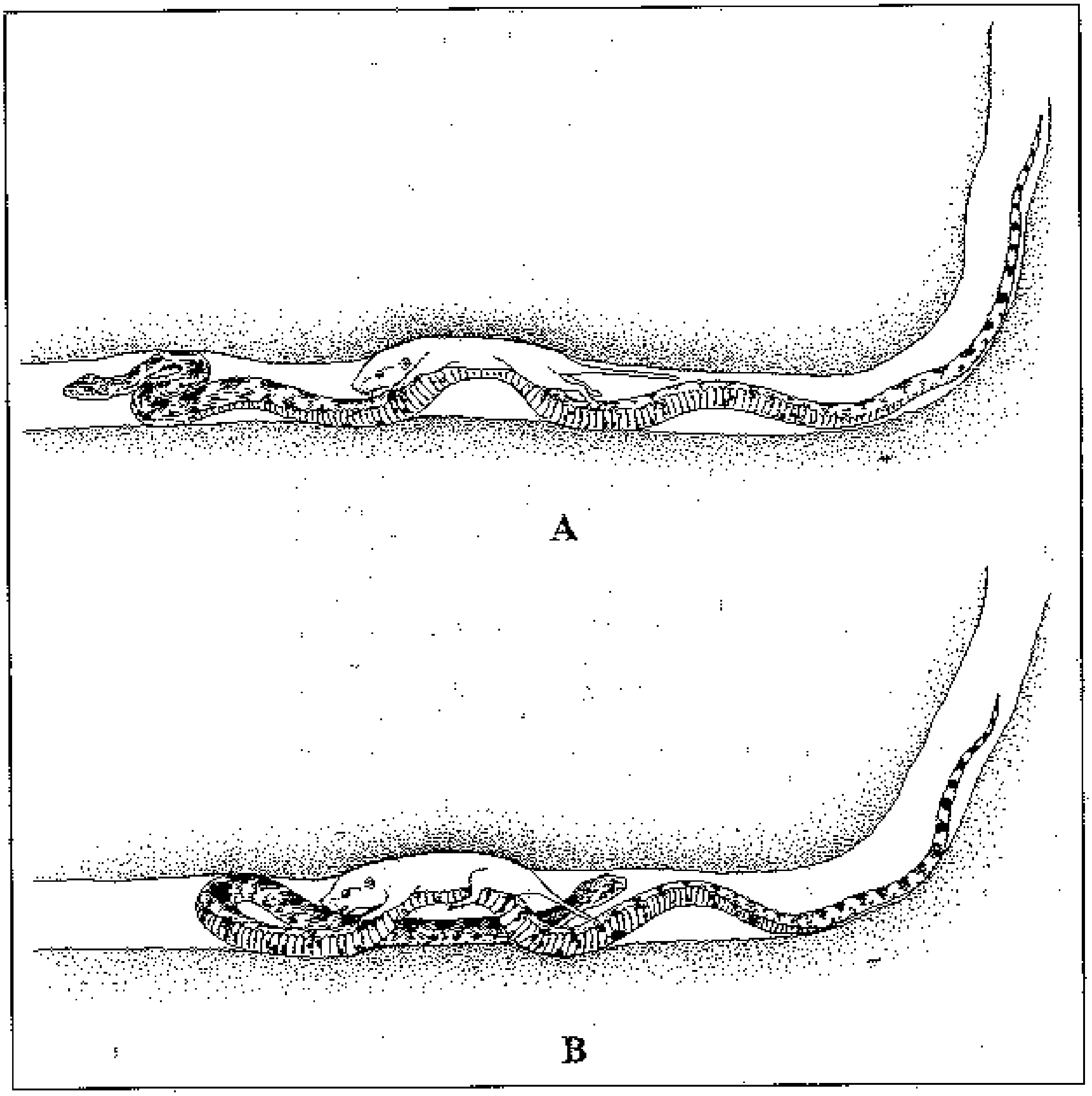


Figure 1. Prey handling behavior of *Pituophis ruthveni* during trial interactions with *Geomys breviceps* showing gopher pinioning (A) by muscular kinking of the extended body and (B) by using two lengths of body.

ically 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 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. Subjectively, this individual seemed 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 (five 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 (seven of 12 trials) the snake then grasped the gopher in it's 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 pinioning the gopher against the burrow wall, typically at the end of a burrow or at a sharp bend in the passage, with 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 (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 shelters 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 (mean = 4) and large hatchling size (mean = 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 may be 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. lodingi* 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 pinioning the prey using a kink in the snake's extended body rather than coils, 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 species of *P. ruthveni*.

ACKNOWLEDGEMENTS

The authors thank S.B. Reichling, R.R. Fleet, R.E. Thill, and two anonymous reviewers for helpful comments on earlier drafts of this manuscript. N.B. Koerth provided statistical assistance. The U.S. Fish and Wildlife Service, Louisiana Department of Game and Fisheries, and Texas Parks and Wildlife Department provided funding under Section 6 of the U.S. Endangered Species Act. Texas Parks and Wildlife Department and Louisiana Department of Game and Fisheries issued the necessary permits. We also thank the Mississippi Museum of Natural Science for access to specimens for prey analysis.

LITERATURE CITED

Carpenter, C.C. 1982. The bullsnake as an excavator. Journal of Herpetology 16:394–401.

Collins, J.T. 1991. Viewpoint: a new taxonomic arrangement for some North American amphibians and reptiles. Herpetological Review 22:42–43.

Conant, R. 1956. A review of two rare pine snakes from the Gulf coastal plain. American Museum Novitates 1781:1–31.

de Queiroz, A. 1984. Effects of prey type on the prey-handling behavior of the bullsnake, *Pituophis melanoleucus*. Journal of Herpetology 18:333–336.

Greene, H.W. and G.M. Burghardt. 1978. Behavior and phylogeny: constriction in ancient and modern snakes. Science 200:74–77.

Greenwald, O.E. 1978. Kinematics and time relations of prey capture by gopher snakes. Copeia 1978:263–268.

Hisaw, F.L. and H.K. Gloyd. 1926. The bull snake as a natural enemy of injurious rodents. Journal of Mammalogy 7:200–205.

Knight, J.L. 1986. Variation in snout morphology in the North American snake *Pituophis melanoleucus* (Serpentes: Colubridae). Journal of Herpetology 20:77–79.

Komarek, E.V. 1968. Lightning and lightning fires as ecological forces. Proceedings of the Tall Timbers Fire Ecology Conference 8:169–197.

Platt, W.J., G.W. Evans, and S.L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). American Naturalist 131:491–525.

Platt, W.J., J.S. Glitzenstein, and K.R. Strent. 1989. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. Proceedings of the Tall Timbers Fire Ecology Conference 17:143–191.

Reichling, S.B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). Southwestern Naturalist 35:221–222.

Reichling, S.B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. Journal of Herpetology 29:186–198.

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 49:111–122.

Rudolph, D.C., S.J. Burgdorf, J. 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 29:146–148.

Sweet, S.S. and W.S. Parker. 1991. *Pituophis melanoleucus*. Catalog of American Amphibians and Reptiles 474:1–8.

Thomas, R.A., B.J. Davis, and M.R. Culbertson. 1976. Notes on variation and range of the Louisiana pine snake, *Pituophis melanoleucus ruthveni*, Stull (Reptilia, Serpentes, Colubridae). Journal of Herpetology 10:252–254.

Willard, D.E. 1977. Constricting methods of snakes. Copeia 1977:379–382.

Young, R.A. and T.L. Vandeventer. 1988. Recent observations on the Louisiana pine snake, *Pituophis melanoleucus ruthveni*, Stull. Bulletin of the Chicago Herpetological Society 23:203–207.

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 adu[illegible]ber 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) [illegible] 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 presumably 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 wide-spread 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.
All Points			
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	$t = -2.68$ $P < 0.0088$
Points w/in 3 km of Permanent Streams			
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; Sulentich 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 (Vandeventer & Young 1989).

Causes of mortality and population decline.—Louisiana pine snake populations are thought to have declined in recent decades (Jennings & Fritz 1983; Young & Vandeventer 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 & Vandeventer 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; Sutentich 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-

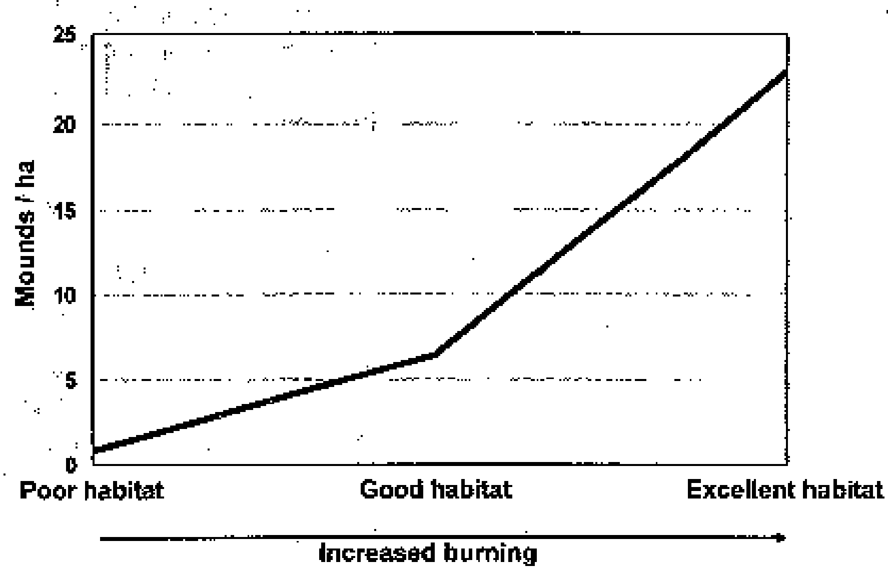


Figure 1. Hypothesized relationship between effectiveness of burning and pocket gopher (*Geomys breviceps*) density based on preliminary data on mound density.

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

The authors wish to thank Robert R. Fleet, James A. Neal, Ronald E. Thill, Daniel Saenz and two anonymous reviewers for commenting on earlier drafts of this manuscript. The U.S. Fish and Wildlife Service, Texas Parks and Wildlife Department and the Louisiana Department of Game and Fisheries provided funding for the research on *Pituophis* under Section 6 of the U.S. Endangered Species Act. Texas Parks and Wildlife Department issued the necessary scientific collecting permits.

LITERATURE CITED

Andersen, D. C. 1987. *Geomys bursarius* burrowing patterns: influence of season and food patch structure. Ecology, 68:1306-1388.

Adams, C. E., J. K. Thomas, K. J. Strnadel & S. L. Jester. 1994. Texas rattlesnake roundups: implications of unregulated commercial use of wildlife. Wildl. Soc. Bull., 22:234-330.

Andersen, D. C. 1987. *Geomys bursarius* burrowing patterns: influence of season and foodpatch structure. Ecology, 68:1306-1318.

Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pp. 99-118 *in* Nature Conservation II: The role of Corridors (D. A. Saunders & R. J. Hobbs, eds.). Surrey Beatty & Sons, Heidelberg, Victoria, Australia, 442 pp.

Bridges, E. L. & S. L. Orzell. 1989. Longleaf pine communities of the West Gulf Coastal Plain. Natural Areas Journal, 9:246-253.

Brown, W. S. 1991. Female reproductive ecology in a northern population of the timber rattlesnake, *Crotalus horridus*. Herpetologica 47:101-115.

Brown, W. S. 1993. Biology, status, and management of the timber rattlesnake (*Crotalus horridus*): a guide for conservation. Society for the Study of Amphibians and Reptiles. Herpetological Circular No. 22.

Brown, W. S. & D. B. Greenberg. 1992. Vertical-tree ambush posture in *Crotalus horridus*. Herpetol. Rev., 23:67.

Conant, R. 1956. A review of two rare pine snakes from the Gulf coastal plain. Amer. Mus. Novitates, 1781:1-31.

Davis, W. B., R. R. Ramsey & J. M. Arendale, Jr. 1938. Distribution of pocket gophers (*Geomys breviceps*) in relation to soils. J. Mammology, 19:412-418.

Dundee, H. A. & D. A. Rossman. 1989. The amphibians and reptiles of Louisiana. Louisiana State Univ. Press, Baton Rouge, Louisiana, 300 pp.

Ehmann, H. & H. Cogger. 1985. Australia's endangered herpetofauna: a review of criteria and policies. Pp. 435-437 *in* Biology of Australian Frogs and Reptiles (G. Gregg, R. Shine, & H. Ehmann, eds.). Surrey Beatty & Sons, Sydney, New South Wales, Australia, 527 pp.

English, P. F. 1932. Some habits of the pocket gopher, *Geomys breviceps breviceps*. J. Mammalogy, 12:253-256.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. of the Tall Timbers Fire Ecology Conf. 18:17-43.

Frost, C. C., J. Walker & R. K. Peet. 1986. Fire dependent savannas and prairies of the Southeast: original extent, preservation status and management problems. Pp. 348-357 *in* Wilderness and Natural Areas in the Eastern United States: a Management Challenge (D. L. Kulhavy & R. N. Conner, eds.). Center for Applied Studies, School of Forestry, Stephen F. Austin State Univ., Nacogdoches, Texas, 416 pp.

Galligan, J. H. & W. A. Dunson. 1979. Biology and status of timber rattlesnake (*Crotalus horridus*) populations in Pennsylvania. Biol. Conserv., 15:34-28.

Jennings, R. D. & T. H. Fritz. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni*. U. S. Fish and Wildl. Serv. and the Univ. of New Mexico Mus. of Southwestern Biol. pp 1-32.

Klauber, L. M. 1956. Rattlesnakes: their habits, life histories, and influence on mankind. University of California Press, Berkeley, California, 1533 pp.

Komarek, E. V. 1964. The natural history of lightning. Proc. of the Tall Timbers Fire Ecology Conf., 3:139-183.

Lalo, J. 1987. The problem of roadkill. American Forests 50:50-52.

Martin, W. H. 1992. The timber rattlesnake: Its distribution and natural history. Pp. 13-22 *in* Conservation of the timber rattlesnake in the northeast (T. F. Tyning, ed.). Massachusetts Audubon Society, Lincoln, Massachusetts, 40 pp.

Mount, R. H. 1975. The reptiles and amphibians of Alabama. Auburn Univ. Agri. Exp. Sta., Auburn, Alabama.

Outcalt, K. W. & P. A. Outcalt. 1994. The longleaf pine ecosystem: an assessment of current conditions. Unpubl. report on USDA Forest Service Forest Inventory and Analysis Data. 23 pp.

Platt, W. J., G. W. Evans, & S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Naturalist 131:491-525.

Reichling, S. B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). SW Naturalist, 35:221-222.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. J. Herpetology, 29:186-198.

Reinert, H. K., D. Cundall & L. M. Bushar. 1984. Foraging benhavior of the timber rattlesnake, *Crotalus horridus*. Copeia 1984:976-981.

Saenz, D., S. J. Burgdorf, D. C. Rudolph & C. M. Duran. 1996. *Crotalus horridus* (timber rattlesnake). Climbing. Herpetol. Rev., 27:145.

Sulentich, J. M., L. R. Williams & G. N. Cameron. 1991. *Geomys breviceps*. Mammalian Species, 383:1-4.

Sweet, S. S. & W. S. Parker. 1991. *Pituophis melanoleucus*. Catalogue of American Amphibians and Reptiles, 474:1-8.

TPWD. 1992. Texas threatened and endangered species. Texas Parks and Wildlife Department, Austin, Texas, 4 pp.

Young, R. A. & T. L. Vandeventer. 1988. [illegible]ent observations on the Louisiana pine snake, *Pituophis melanoleucus ruthveni*, Stull. Bull Chicago Herp. Soc., 23:203207.

breeding season, males searched for mates while on migration routes to the stream (Tsuji 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 (Tsuji 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 Tsuji 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.

Acknowledgments.—We thank M. Kishimoto (Miyazaki), T. Mizuta, and T. Teraoka for field assistance; D. H. Olson and two anonymous reviewers for their valuable comments on earlier versions of the manuscript; M. Brazil for assistance with the English manuscript; the staff of Mie University's Misugi Forest for kindly allowing us to study there, and we especially thank the Sakamoto family for their willing help during the time spent living at the study site.

LITERATURE CITED

DAVIES, N. B., AND T. R. HALLIDAY. 1979. Competitive mate searching in male common toads, *Bufo bufo*. Anim. Behav. 27:1253–1267.

HOWARD, R. D. 1980. Mating behavior and mating success in wood frogs, *Rana sylvatica*. Anim. Behav. 28:705–716.

JAMESON, D. L. 1955. Evolutionary trends in the courtship and mating behavior of Salientia. Syst. Zool. 4:105–119.

KUSANO, T., AND K. FUKUYAMA. 1989. Breeding activity of a stream-breeding frog (*Rana* sp.). *In* M. Matsui, T. Hikida, and R. C. Goris (eds.), Current Herpetology in East Asia, pp. 314–322. Herpetol. Soc. Japan, Kyoto.

MAEDA, N., AND M. MATSUI. 1989. Frogs and Toads of Japan. Bun-ichi Sogo Shuppan, Tokyo. 206 pp. (In Japanese with an English abstract).

OLSON, D. H. 1989. Predation on breeding Western toads (*Bufo boreas*). Copeia 1989:391–397.

TSUJI, H., AND T. KAWAMICHI. 1996a. Breeding activity of a stream-breeding toad, *Bufo torrenticola*. Japan. J. Herpetol. 16:117–128.

———, AND ———. 1996b. Breeding habitats of a stream-breeding toad, *Bufo torrenticola*, in an Asian mountain torrent. J. Herpetol. 30:451–454.

———, AND ———. 1998. Field observations of the spawning behavior of stream toads, *Bufo torrenticola*. J. Herpetol. 32:34–40.

WELLS, K. D. 1977. The social behavior of anuran amphibians. Anim. Behav. 25:666–693.

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

D. CRAIG RUDOLPH
S. J. BURGDORF
JOHN C. TULL
Wildlife Habitat and Silviculture Laboratory, Southern Research Station U.S.D.A. Forest Service, Box 7600 SFA Station Nacogdoches, Texas 75962, USA

MARC EALY
Department of Biology, Stephen F. Austin State University Nacogdoches, Texas 75962, USA

RICHARD N. CONNER
RICHARD R. SCHAEFER
Wildlife Habitat and Silviculture Laboratory, Southern Research Station U.S.D.A. Forest Service, Box 7600 SFA Station Nacogdoches, Texas 75962, USA

and

ROBERT R. FLEET
Department of Biology, Stephen F. Austin State University Nacogdoches, Texas 75962, USA

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 Vandeventer 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 breviceps*) and ultimately on Louisiana pine snakes.

Since 1993, radio-transmitters (Holohil 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 prescribe-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 Februrary 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; ie. 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.

Acknowledgments.—We thank J. A. Neal for reviewing earlier drafts of this manuscript. The U. S. Fish and Wildlife Service, Louisiana Department of Game and Fisheries, and Texas Parks and Wildlife Department provided funding for research on *Pituophis* under Section 6 of the U.S. Endangered Species Act. Texas Parks and Wildlife Department issued the necessary scientific collecting permits.

Literature Cited

Conant, R. 1956. A review of two rare pine snakes from the gulf coastal plain. Amer. Mus. Novitates 1781:1–31.

Conner, R. N., and D. C. Rudolph. 1989. Red-cockaded woodpecker colony status and trends on the Angelina, Davy Crockett, and Sabine National Forests. U.S.D.A. For. Serv. Res. Pap. SO-250, New Orleans, Louisiana.

Erwin, W. J., and R. H. Stasiak. 1979. Vertebrate mortality during the burning of a reestablished prairie in Nebraska. Am. Midl. Nat. 101:247–249.

Frost, C. C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. Tall Timbers Ecol. Conf. 18:17–43.

Komarek, E. V. 1968. Lightning and lightning fires as ecological forces. Proc. Tall Timbers Ecol. Conf. 8:169–197.

———. 1974. Effects of fire on temperate forests and related ecosystems: southeastern United States. *In* T. T. Koslowski and C. E. Ahlgren (eds.), Fire and Ecosystems, pp. 251–277. Academic Press, New York.

Landers, J. L. 1987. Prescribed burning for managing wildlife in southeastern pine forests. *In* J. G. Dickson and O. E. Maughan (eds.), Managing Southern Forests for Wildlife and Fish, pp. 19–27. U.S.D.A. For. Serv. Gen. Tech. Rept. SO-65, New Orleans, Louisiana.

Means, B. D., and H. W. Campbell. 1981. Effects of prescribed burning on amphibians and reptiles. *In* G. W. Wood (ed.), Prescribed Fire and Wildfire in Southern Forests, pp. 89–97. Clemson Univ., Georgetown, South Carolina.

Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). Amer. Nat. 131:491–525.

———, J. S. Glitzenstein, and K. R. Strent. 1989. Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. Proc. Tall Timbers Fire Ecol. Conf. 17:143–191.

Reichling, S. B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. J. Herpetol. 29:186–198.

Rudolph, D. C., and S. J. Burgdorf. 1997. Timber rattlesnakes and Louisiana pine snakes of the west Gulf Coastal Plain: hypotheses of decline. Texas J. Sci. 49:111–122.

Seigel, R. A. 1986. Ecology and conservation of an endangered rattlesnake, *Sistrurus catenatus*, in Missouri. USA. Biol. Cons. 35:333–346.

Van Lear, D. H. 1985. Prescribed fire—its history, uses, and effects in southern forest ecosystems. *In* D. D. Wade (ed.), Prescribed Fire and Smoke Management in the South, pp. 57–75. U.S.D.A. Forest Ser., Southern Forest Exp. Sta., Asheville, North Carolina.

Weatherhead, P. J., and F. W. Anderka. 1984. An improved transmitter and implantation technique for snakes. J. Herpetol. 1

Young, R. A., and T. L. Vandeventer. 1988. Recent observa the Louisiana pine snake, *Pituophis melanoleucus ruthven* Chicago Herpetol. Soc. 23:203–207.

Diel and Monthly Variations in Capture Su of *Phrynosoma cornutum* via Road Cruisin Southern Texas

SCOTT E. HENKE
Caesar Kleberg Wildlife Research Institute
Texas A&M University-Kingsville, Kingsville, Texas 78363, USA
e-mail: kfteh00@tamuk.edu

and

MELISA MONTEMAYOR*
Texas Parks and Wildlife Department
4200 Smith School Road, Austin, Texas 78744, USA
**Present address: Texas Department of Transportation,*
1817 Bob Bullock Loop, Laredo, Texas 78043, USA

Road cruising may be a time-efficient capture method for Texa horned lizards (*Phrynosoma cornutum*) and may yield better cap ture success per unit effort than systematic searches and funne 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) and ambient temperature (Prieto and Whitford 1971). We hypothesized 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.

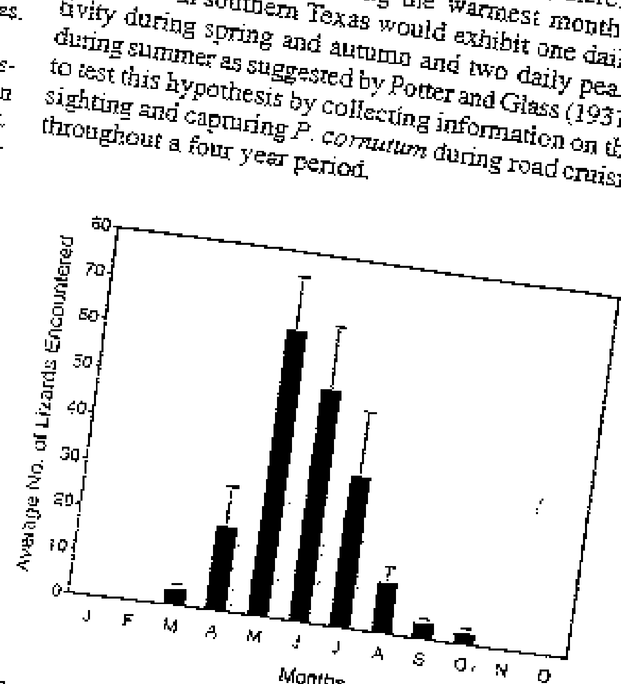
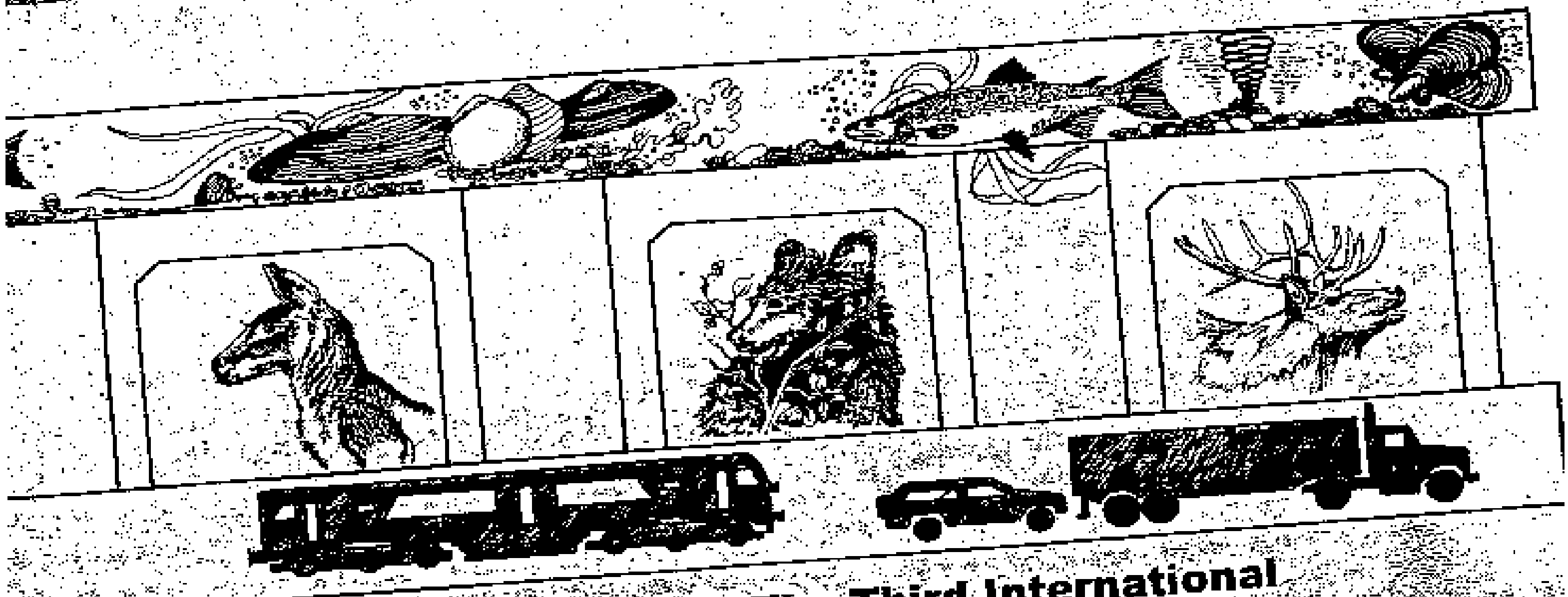


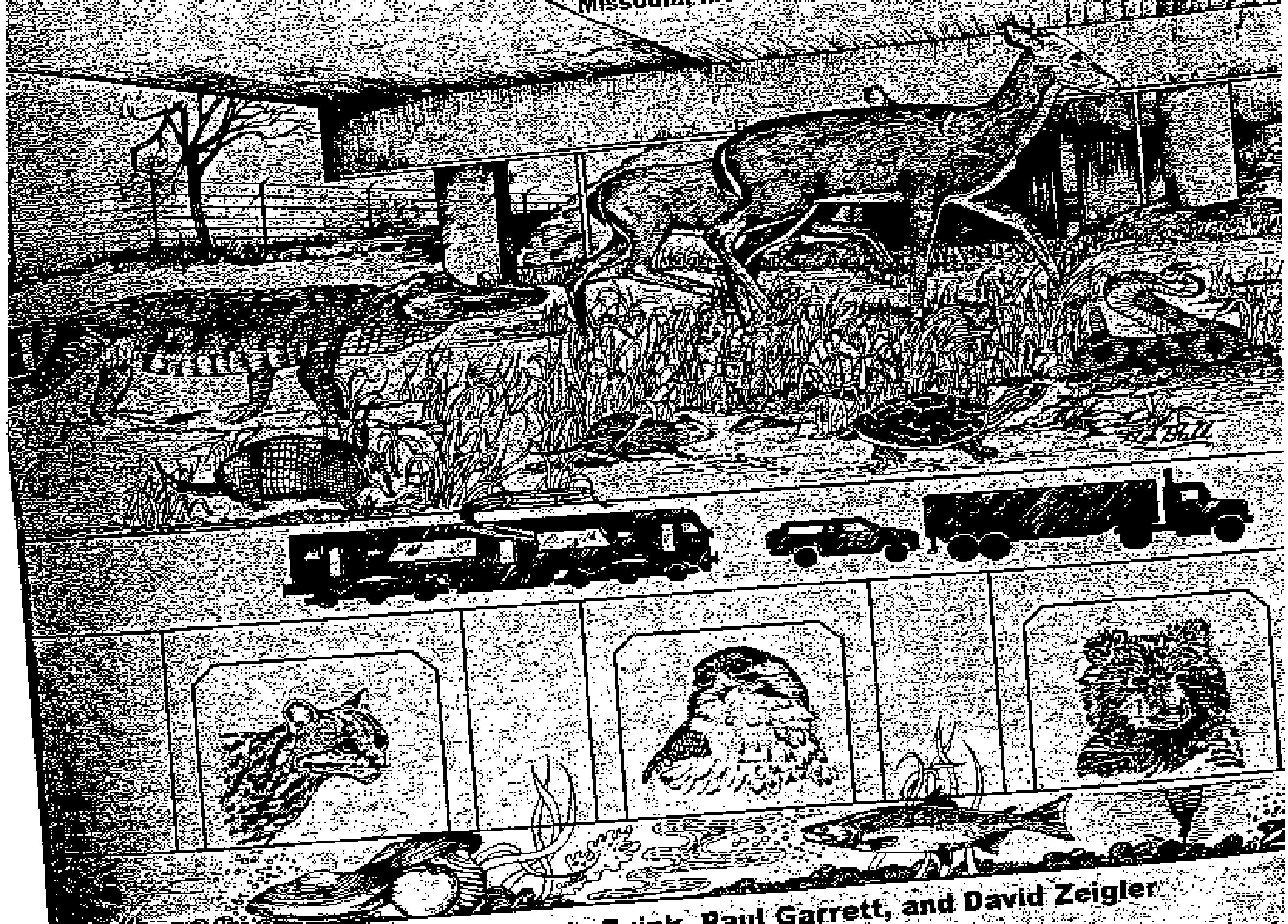
Fig. 1. Average number of *P. cornutum* collected monthly via road cruising during March 1991 to October 1994 in southern Texas. Bars extending above the means are the standard errors of the means. Average number of *P. cornutum* for January, February, November, and December was calculated using three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



Proceedings Of The Third International Conference On Wildlife Ecology And Transportation

September 13-16, 1999

Missoula, Montana



Edited by: Gary L. Evink, Paul Garrett, and David Zeigler

FL-ER-73-99

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

D. Craig Rudolph, Shirley J. Burgdorf, Richard N. Conner, and Richard R. Schaefer,
U. S. D. A. Forest Service, Nacogdoches, Texas

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 X 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.

Acknowledgements

We thank the Texas Parks and Wildlife Department and the U. S. Fish and Wildlife Service for partial support for this study through Section 6 of the Endangered Species Act. We thank M. B. Keck and R. R. Fleet for constructive comments on an early version of the manuscript and N. E. Koerth for statistical assistance. We also thank C. Collins, T. Trees, and J. Niederhofer for assistance in the field.

References Cited

Adams, L. W. and A. D. Geis. 1983. Effects of roads on small mammals. Journal of Applied Ecology 20:403-415.

Ashley, E. P. and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point causeway, Lake Erie, Ontario. Canadian Field Naturalist 110:403-412.

Bennett, A. F. 1991. Roads, roadsides and wildlife conservation: a review. Pages 99-118 *in* D. A. Saunders and R. J. Hobbs (eds.), Nature Conservation II: the Role of Corridors. Surrey Beatty & Sons, Heidelberg, Victoria, Australia.

Fowle, S. C. 1996. Effects of roadkill mortality on the western painted turtle (*Chrysemys picta bellii*) in the Mission Valley, western Montana. In G. L. Evink, P. Garrett, D. Zeigler and J. Berry, eds. Trends in Addressing Transportation Related Wildlife Mortality, Proceedings of the transportation related wildlife mortality seminar in Tallahassee, Florida, June 1996. Florida Department of Transportation, Tallahassee, FL (unpaginated).

Lalo, J. 1987. The problem of roadkill. American Forests (Sept.-Oct.):50-52.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

Rosen, P. C. and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran desert of southern Arizona. Biological Conservation 68:143-148.

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.

		Trap Distance from Road (m)					
Transect	Year	50	250	450	650	850	total
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.

	Trap Distance from Road (m)					
Year	50	250	450	650	850	total
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.

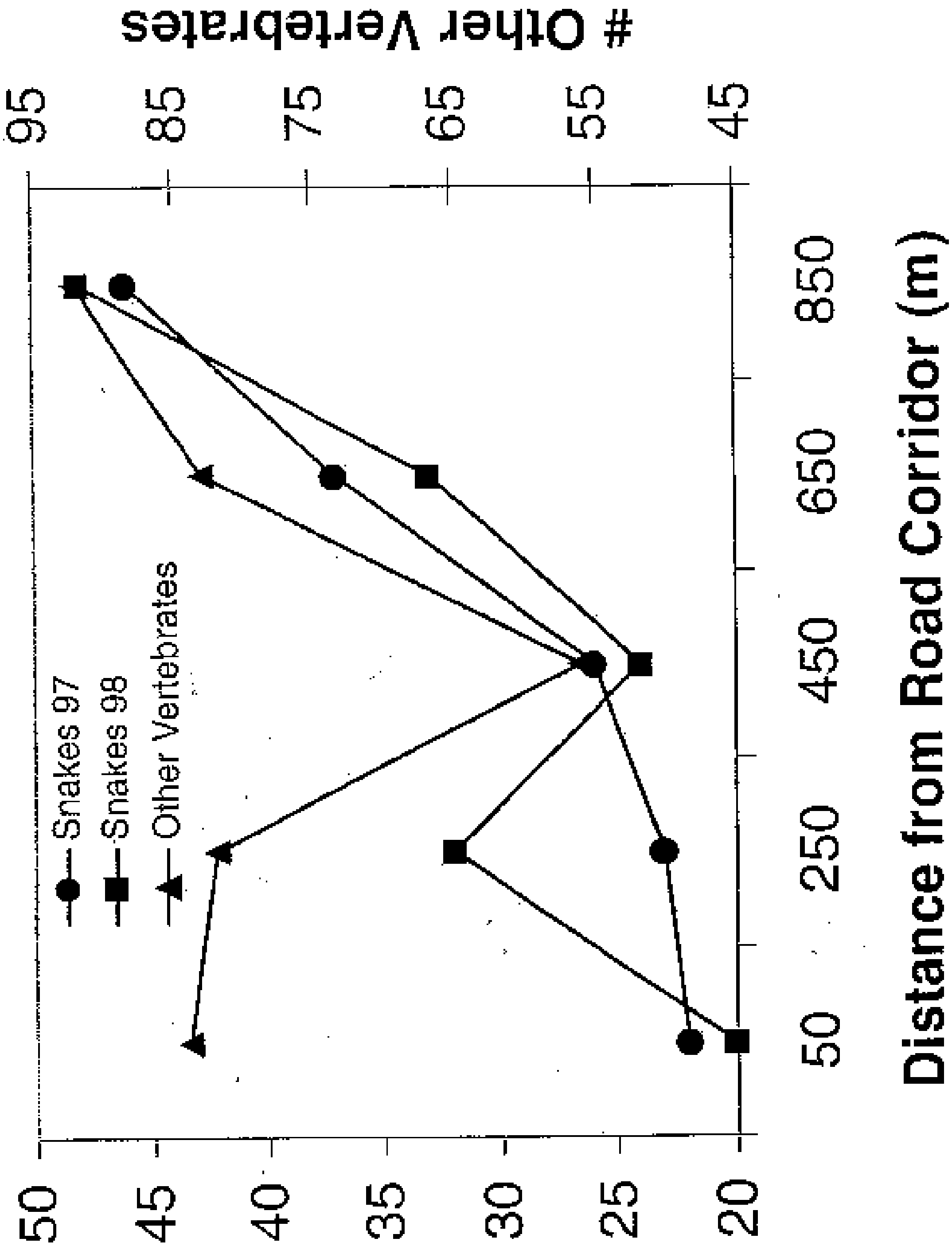


Figure 1.
Number of snakes and other vertebrates captured at 50, 250, 450, 650, and 850 m from road corridors.

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

Habitat Variable	Transect A	Transect B	Transect C	Transect D	Transect 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 ($P < 0.05$).

Ruby, D. E., J. A. Spotila, S. K. Martin, and S. J. Kemp. 1994. Behavioral responses to barriers by desert tortoises: implications for wildlife management. Herpetological Monographs 8:144-160.

Rudolph, D. C., S. J. Burgdorf, R. N. Conner, and J. G. Dickson. 1998. The impact of roads on the timber rattlesnake, (*Crotalus horridus*), in eastern Texas. Pages 236-240 *in* G. L. Evink, P. Garrett, D. Zeigler and J. Berry (eds.), Proceedings of the International Conference on Wildlife Ecology and Transportation. FL-Er-69-98, Florida Department of Transportation, Tallahassee, Florida.

Herpetological Natural History, 9(2), 2002, pages 117–126.

BODY TEMPERATURE VARIATIONS OF THE LOUISIANA PINE SNAKE (*PITUOPHIS RUTHVENI*) IN A LONGLEAF PINE ECOSYSTEM

John G. Himes[1,2] and Laurence M. Hardy
Museum of Life Sciences, Louisiana State University in Shreveport,
One University Place, Shreveport, Louisiana 71115-2399, USA

D. Craig Rudolph and Shirley J. Burgdorf[3]
Wildlife and Habitat Silviculture Laboratory, Southern Research Station,
USDA Forest Service, Nacogdoches, Texas 75962, USA

Abstract. The thermal ecology of the Louisiana pine snake, *Pituophis ruthveni*, was studied from 1993–97 in Louisiana and Texas. All snakes were implanted with temperature-sensitive radiotransmitters. Temperatures were recorded from snakes located above ground and underground and were compared between size and sex classes (juveniles, adult males, adult females). Associated air and substrate temperatures were also recorded. Collectively, body temperatures of snakes were lowest during winter (11.4°C), increased during spring (22.3°C), peaked during summer (27.7°C), and decreased during autumn (22.7°C). Seasonal body temperatures were most similar between juveniles and adult males, primarily because adult females had higher body temperatures during summer. During spring and autumn, snake, air, and substrate temperatures were generally 3–4°C higher above-ground than underground. Temperatures of snakes of all size and sex classes increased from morning through evening and most closely approximated the air and substrate temperatures at 1800 h and 1900 h, when snakes were located predominantly underground. Temperatures of juveniles and adult males showed no consistent relationship to air or substrate temperatures from 0700–1700 h. However, temperatures of adult females were significantly lower than air temperature from 1000–1600 h. Temperatures of juveniles and adult males were significantly higher above ground than underground from 1100–1400 h and 1100–1700 h, respectively, with no consistent relationship between hourly above-ground and underground temperatures of adult females. Overall, temperature patterns of *P. ruthveni* and *P. catenifer deserticola* appear to be similar, except that *P. c. deserticola* maintains higher temperatures in the spring than does *P. ruthveni*.

Key Words. Body temperature; Longleaf pine; Louisiana pine snake; *Pituophis ruthveni*; Thermal ecology.

The body temperature of snakes has a profound effect on most, if not all, facets of their ecology. Snakes are nearly exclusively ectothermic, deriving their body heat primarily from external (environmental) sources. Thus, body temperature in snakes (and thus the level and type of activity in which snakes are physiologically capable of engaging) is limited by the range of thermal conditions available in the environment (Peterson et al. 1993). The thermal environment itself is subject to daily and seasonal fluctuations and thus body temperature in snakes may be expected to fluctuate accordingly. However, most snakes are very adept at behavioral thermoregulation in an effort to offset (at least partially) the potentially debilitating effects of suboptimal thermal conditions, resulting in a corresponding change in the types of activities in which snakes may engage (Heatwole and Taylor 1987).

[1]Present address: Nevada Division of Wildlife, 4747 Vegas Drive, Las Vegas, Nevada 89108, USA. Email: jhimes@ndow.state.nv.us
[2]Please use for correspondence.
[3]Present address: US Fish and Wildlife Service, 510 Desmond Drive, Suite 102, Lacey, Washington 98503-1263, USA.

Consequently, the timing of basic and essential activities, such as those associated with foraging and reproduction, is proximately determined by body temperature and ultimately determined by the thermal environment (Lillywhite 1987).

Peterson et al. (1993) posed five fundamental questions about thermal ecology and associated body temperature variation. These questions aim to assess (1) the range of possible body temperatures under natural conditions; (2) the proximate factors that determine which body temperatures a snake selects from that range of possibilities; (3) the variation of body temperatures of individual snakes under natural conditions over extended periods of time; (4) the functional effects (i.e., developmental, physiological, behavioral) of body temperature variation; and (5) the ecological consequences of body temperature variation. Ideally, studies on the thermal ecology of snakes should cover each of these five areas.

Our main objective was to assemble data to cover these five areas of Peterson et al. (1993) for the Louisiana pine snake, *Pituophis ruthveni*. This species is a highly threatened endemic of the relictual longleaf pine forests of western Louisiana and adjacent Texas (Jennings and Fritts 1983; Reichling 1988; Rudolph and Burgdorf 1997). The few remaining natural populations of *P. ruthveni* are highly disjunct and occur at extremely low densities. Until the 1990s, when *P. ruthveni* was known in the wild from only 100 specimens (Rudolph, unpubl. data) and the U.S. Forest Service initiated an intensive ecological project on this species, no quantitative studies had been conducted on the natural history of *P. ruthveni*. In fact, what little information is available on *P. ruthveni* (e.g., morphological variation, reproductive biology) was collected from snakes maintained in captivity (e.g., Reichling 1989), and nothing, to our knowledge, has been reported on the thermal ecology of *P. ruthveni*.

Pituophis ruthveni occurs in a unique habitat that is distinctive from that of other species of *Pituophis*. In addition, clutch sizes of *P. ruthveni* (n = 4 eggs; no deviation from mean) are smaller than those of all other species of *Pituophis*, and its eggs (mean length = 11.94 ± 0.88 [95% CI] cm, 10.00–13.00 cm, n = 8; mean width = 3.56 ± 0.33 cm, range 3.00–4.00 cm, n = 8) and hatchlings (mean total length = 54.4 ± 2.5 cm, range 52.0–55.5 cm, n = 4; mean mass = 106.7 ± 5.7 g, range 104.0–108.0 g, n = 3) are the largest of all snakes in the United States (Reichling 1989, 1990). Thus, the energetics of growing the exceedingly large eggs would suggest that gravid females spend more time basking, thus gaining heat energy needed for the physiological demands of vitellogenesis. On the other hand, this species is highly fossorial (Himes et al. 2003), which would seem to contradict the higher thermal needs of egg development. Therefore, understanding more about the thermal relationship of the Louisiana pine snake to its environment might contribute to a better understanding of the thermal ecology of species with extreme reproductive characteristics.

Mean cloacal temperatures of other taxa of *Pituophis* include 25.5°C in *P. c. catenifer* (Cunningham 1966), 28.0°C in *P. c. sayi* (Fitch 1956), and 28.6°C in *P. c. deserticola* (Diller and Wallace 1996). In all three studies, temperatures were recorded from snakes only once and thus daily and seasonal fluctuations in body temperature could not be determined. Daily fluctuations in body temperature single individuals of *P. c. sayi* (Dill 1972) and *P. c. deserticola* (Parker and Brown 1980) varied from 26–32°C and 19–35°C, respectively. However, snakes were monitored over a one- to two-day period and thus seasonal fluctuations in body temperature could not be determined.

Parker and Brown (1980) recorded 155 cloacal temperatures from *P. c. deserticola* that emerged from or retreated into a communal hibernaculum during spring (n = 44) and autumn (n = 38), respectively. Cloacal temperatures were significantly higher in spring (mean = 27.88°C) than in autumn (mean = 24.43°C). However, no temperatures were recorded from snakes during winter and temperature differences by size and sex class were not noted.

Parker and Brown (1980) also recorded 416 body temperatures from nine *P. c. deserticola* implanted with temperature-sensitive radiotransmitters. The mean body temperature of surface-active snakes from spring through autumn averaged 27.9°C. Mean inactive body temperatures of snakes underground and under rocks varied from 19.68°C (autumn) to 27.01°C (summer) and approximately 12°C (autumn) to 24°C (summer), respectively. Body temperatures of snakes underground were below air and insolated substrate temperatures, similar to shaded substrate temperatures, and significantly higher in summer compared to autumn. When snakes were under rocks, body temperatures were similar to air and shaded substrate temperatures, consistently below insolated substrate temperatures, and significantly higher during cloudy days in summer compared to spring. Again, no temperatures were recorded from snakes during winter and temperature differences by size and sex class were not noted.

Greenwald (1971) determined that the aerobic energy available for activity (metabolic scope) of *P. catenifer affinis* was maximum at a body temperature of 30°C. In 1974, Greenwald determined that strike velocity and frequency of prey capture were maximum at body temperatures of 27°C and 33°°C, respectively. This was a rather surprising finding because it indicated that snakes captured prey less frequently at a lower temperature (27°C), when strike velocity was greatest. Thus, from these data, it is difficult to determine the preferred range of active body temperature in *P. c. affinis*. However, it is clear from these findings that there is a complicated relationship among body temperature, behavior, and the metabolic scope in *Pituophis*.

All *Pituophis* for which body temperature data are available occur in open habitats with few trees (e.g., grasslands, brushlands, deserts) of the midwestern and western United States. In contrast, *P. ruthveni* occurs predominantly in pine forests (Dundee and Rossman 1989; Rudolph and Burgdorf 1997). These habitats have different thermal qualities that may result in different thermal relationships between the snakes and their environment. For example, solar radiation and conduction should be less intense on the forest floor than in a desert. In fact, thigmothermy is an important heat exchange mechanism used by many ectotherms, including *Pituophis* living in deserts (Sullivan 1981).

As part of a range-wide natural history study on *P. ruthveni*, eight juveniles, 17 adult males and 13 adult females were implanted with temperature-sensitive radiotransmitters and individually studied for up to 43 mo in Louisiana and Texas from 1993–97. Temperatures were recorded of all 38 snakes, during all seasons and hours of the day (over the course of the five-year period), and when snakes were located above-ground (on the surface and generally amid thick herbaceous vegetation) and underground (generally in self-made burrows or in burrows excavated by pocket gophers [*Geomys breviceps*] or moles [*Scalopus aquaticus*]). Comparisons of body, substrate, and air temperatures helped us determine the thermoregulatory capability of *P. ruthveni*. In addition, we determined the effects that size and sex class of snakes and the time of year and day have on the thermal ecology of *P. ruthveni*.

MATERIALS AND METHODS

Study Areas

This study was conducted within the historic longleaf pine (*Pinus palustris*) region of Bienville, Sabine, and Vernon Parishes in Louisiana, and in Angelina, Jasper, Newton, and Sabine Counties in Texas. Sandhills that are dissected by intermittent and small perennial streams characterize all sites. Pine forest consisting of longleaf pine, shortleaf pine (*P. echinata*), loblolly pine (*P. taeda*), and the introduced slash pine (*P. elliottii*), with occasional hardwoods, dominates the uplands. By contrast, several species of hardwoods (*Carya* spp., *Fagus grandifolia*, *Liquidambar styraciflua*, *Nyssa sylvatica*, *Quercus* spp., etc.) dominate the lowland areas. At most sites, silvicultural practices have resulted in the formation of clearcuts and pine plantations, as well in as the suppression of fire, leading to hardwood encroachment and consequential suppression of herbaceous vegetation.

Survey Methods and Study Subjects

Snakes were trapped and hand-captured from 1993–97. Traps were constructed of a plywood frame, top, and bottom, and hardware cloth walls (6-mm mesh), forming 1.3 x 1.3 x 0.3 m boxes with a funnel entrance on each side to permit entry of snakes. Drift fences, also of 6-mm hardware cloth (height = 0.5 m), extended for 16 m from each funnel entrance. Traps were operated on a variable schedule at 10–15 sites during the months of March–October.

Wild-caught snakes were obtained at (n = 26 snakes) or near (n = 4) one of the study sites. In addition, eight captive-bred snakes obtained from the Memphis Zoo and Aquarium (MZA) were used in this study. These latter snakes were the offspring of snakes from Bienville Parish that were used to establish a captive breeding program (S. Reichling, pers. comm. 1995). Prior to shipping from Memphis, these snakes were inspected by an accredited veterinarian from the American Association of Zoo Veterinarians and were determined to show no signs of disease. Specific identification numbers were assigned to each snake, and sex, length, and mass were recorded of all snakes immediately before and after the study (see Table 1 in Himes et al. 2002).

Surgical Procedures and Transmitter Implantation

Snakes were implanted either subcutaneously (Sabine Parish, Vernon Parish, and Texas snakes) or intraperitoneally (Bienville Parish and MZA snakes) with SI-2T transmitters (44 x 10 mm, 12 g; Holohil Systems LTD, Carp, Ontario, Canada), each of which was equipped with a 20 cm whip antenna (see Reinert and Cundall [1982] and Weatherhead and Anderka [1984]). The transmitter mass exceeded 5% of the body mass of one snake (a juvenile); this individual survived and showed no ill effects throughout the study. Anesthesia was achieved by intramuscular injection (80 mg kg^{-1} $snake^{-1}$) of Ketamine (Mallinckrodt Veterinary, Inc., Mundelein, Illinois, USA; Sabine Parish, Vernon Parish, and Texas snakes) or inhalation of Halothane (Ayerst Labs, Inc., New York, USA; Bienville Parish and MZA snakes). All transmitters had an approximate battery life of 18 mo and were replaced as necessary.

Each snake was only handled during surgery (once every 14–15 mo). Thus, reproductive status could not be determined and gravid and non-gravid females were not distinguished. Sexual maturity, although not known for *P. ruthveni* in the wild, is attained at 3–4 yr of age in other species of *Pituophis* (Fitch 1970). Therefore, we considered our captive snakes, which were 1-yr-olds (and did not exceed 101 cm in total length) at the time of their release, to be juveniles. One wild-caught snake, 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. All other wild-caught snakes exceeded 120 cm in total length at the time of their release and thus were considered to be adults.

When not in surgery, one to two snakes were maintained in fiberglass and plastic cages (56 x 30 x 23 cm) at 20–25°C, with an approximate 12 h:12 h light:dark photoperiod. Additional heat was supplied by lamps and heating pads. Fresh water was provided *ad libitum* and one freshly killed mouse was offered as food once a day to each snake. The interior of each cage was washed with soap and rinsed clean every other day and the exterior was covered with newspaper to minimize disturbance to snakes.

Release and Radiotracking Protocols

Snakes were allowed 2–14 d 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 by local residents in nearby areas of Bienville Parish that were not accessible for telemetry studies and were at risk because of adjacent highways. These snakes were released at safe distances (5-40 km from their point of capture) and where other snakes were under observation. The risks to the four repatriated snakes and their receiving populations were considered to be less than the imminent danger posed by a busy highway and much human activity; the extreme rarity of this species justified the repatriation of snakes to a safer habitat. MZA snakes were individually released at habitat edges (to give the snakes a choice of habitat) at the Bienville Parish study site; each snake was released at least 100 m from all other snakes under study. Following their release into the field, all snakes were relocated 1–7 times per week.

Upon locating a transmitter-bearing snake, date, time, and location were recorded. The snake's position was recorded as above-ground or underground. For each location, transmitter pulse rate was recorded for three consecutive 10-sec periods and then averaged and converted to a per minute pulse rate. Shaded air and substrate temperatures were recorded with an alcohol thermometer within 5 min of locating a snake and generally within 2 m of the snake (unless the snake was on the surface, when temperatures were recorded 2–5 m from the snake to prevent disturbance). Substrate temperatures were recorded at a depth of 10–15 cm, corresponding to the approximate depth at which snake and mammal burrows were located (and in which snakes were located when underground). Radiotracking seasons were defined as winter (December–February), spring (March–May), summer (June–August), and autumn (September–November).

A temperature calibration equation for each transmitter was plotted (x-axis = pulse rate in ms; y-axis = transmitter temperature in °C), allowing determination of snake body temperature (because pulse rates were recorded when transmitters were located within the snake, transmitter and body temperatures were assumed to be equal). Snake body temperatures were then plotted with the associated air and substrate temperatures by month and hour. Temperatures are listed below, giving the mean ± 95% CI, as well as the temperature range. To prevent biased statistical analyses due to unequal or low sample sizes, a minimum of ten body temperatures each of juveniles, adult males, and adult females was used to analyze size and sex class temperature differences by month and hour. An ANOVA ($P \leq 0.05$) was used to test for temperature differences between all size and sex classes within the same season, month, or hour. A t-test ($P \leq 0.05$) was used to test for temperature differences between two size/sex classes within the same season, month, or hour.

RESULTS

Mean snake temperatures were lower during winter (11.4 ± 1.97°C, 5.0–18.0, n = 78), increased during spring (22.3 ± 1.28°C, 8.5–36.5, n = 372), peaked during summer (27.7 ± 0.71°C, 20.0–38.5, n = 563), and decreased during autumn (22.7 ± 0.36°C, 10.0–38.5, n = 824; Fig. 1A–C). Snake temperatures ranged from a mean of 10.0 ± 2.25°C (5.0–16.0, n = 12) in adult males located underground during January (Fig. 1B) to a mean of 32.2 ± 3.72°C (24.5–38.5, n = 16) in adult females located above ground during August (Fig. 1C). Air and substrate temperatures showed similar seasonal trends. During spring and autumn, snake, air, and substrate temperatures were generally 3–4°C higher above ground than underground (Fig. 1A–C). However, during summer, temperatures between juveniles and adult males were not significantly different above ground (t = 0.78, $P > 0.05$; Fig. 1A, B) or underground (t = 0.03, $P > 0.05$; Fig. 1A, B), whereas temperatures of adult females were significantly higher above ground than underground (t = 2.93, $P \leq 0.05$; Fig. 1C).

During summer, temperatures were significantly higher in adult females than in juveniles (t = 2.25, $P \leq 0.05$; Fig. 1A, 1C) and adult males (t = 3.69, $P \leq 0.05$; Fig. 1B, C). Moreover, during summer, temperatures of adult females were significantly higher above ground than underground (t = 2.86, $P \leq 0.05$; Fig. 1C), whereas above-ground and underground temperatures were not significantly different in juveniles (t = 1.72, $P > 0.05$; Fig. 1A) or adult males (t = 1.18, $P > 0.05$; Fig. 1B).

Few monthly temperatures were significantly different between size and sex classes. Above-ground temperatures during March were significantly higher in adult males than in juveniles (Table 1) and during May were significantly higher in adult females than in juveniles (Table 1). Above-ground temperatures were also significantly higher in adult females than in adult males during August and September (Table 1). Underground temperatures during June were significantly higher in adult males than in juveniles and adult females (Table 1).

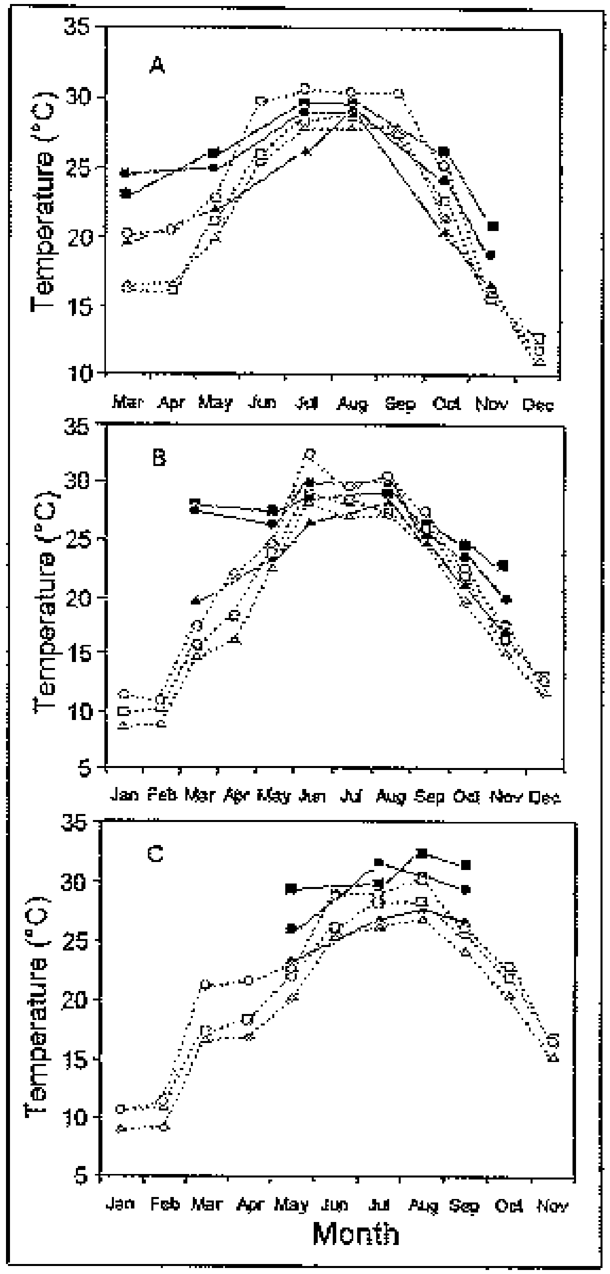


Figure 1. Monthly mean body temperatures (°C; squares) of juveniles (A), adult males (B), and adult females (C) of *Pituophis ruthveni* located above ground (solid lines; black symbols) and underground (dashed lines; open symbols), with means for associated air (circles) and substrate (triangles) temperatures. Each temperature plotted on the graph represents the mean of ≥ 10 recordings; temperatures are not plotted for months with < 10 recordings. See Table 1 for statistics on significant differences.

Some general trends are apparent in daily variations in temperatures. Mean above-ground snake

TABLE 1. Monthly mean (±1 SD) body temperatures (°C) recorded from juvenile, adult male, and adult female *Pituophis ruthveni* located above ground (T_{ab}) and underground (T_{be}); ranges and samples sizes in parentheses. Months during which (1) neither T_{ab}s or T_{be}s differed significantly between at least two size/sex classes, or (2) < 10 recordings of T_{ab}s and T_{be}s were taken for each size/sex class, have been omitted. An ANOVA tested for temperature differences between all size and sex classes within the same month. A *t*-test (P ≥ 0.05) tested for temperature differences between two size/sex classes within the same month; *t*-tests between pairs that are not identified in the *t*-test column were not significant.

Month	Class			ANOVA	*t*-test
	Juveniles	Males	Females		
March (T_{ab})	23.0 ± 5.4 (16.0–30.5, *n* = 10)	27.9 ± 4.4 (18.5–34.5, *n* = 10)	–	–	*t* = 2.23
May (T_{ab})	26.0 ± 4.9 (19.0–36.0, *n* = 53)	27.4 ± 5.8 (15.0–35.0, *n* = 28)	29.2 ± 5.6 (19.0–36.5, *n* = 18)	*	*t* = 2.29 (Juveniles, Females)
June (T_{be})	25.9 ± 2.8 (20.5–34.5, *n* = 38)	28.7 ± 3.3 (25.0–38.0, *n* = 20)	26.1 ± 1.8 (22.5–30.5, *n* = 27)	*	*t* = 2.64 (Juveniles, Males)
					t = 3.78 (Males, Females)
August (T_{ab})	29.7 ± 1.9 (26.5–33.5, *n* = 11)	28.8 ± 3.5 (22.5–33.5, *n* = 14)	32.2 ± 4.8 (24.5–38.5, *n* = 16)	*	*t* = 2.22 (Males, Females)
September (T_{ab})	-	26.2 ± 5.3 (14.0-35.5, n = 36)	31.4 ± 3.7 (23.0-38.5, n = 17)	-	*t* = 3.45

*$P \geq 0.05$

temperatures increased from 19.6°C in juveniles (9th hour) and 21.5°C in adult males (10th hour) to a respective 28.7°C (11th hour) and 29.8°C (13th hour; Fig. 2A, B). Mean underground snake temperatures increased from 20.1°C in juveniles (8th hour), 20.4°C in adult males (10th hour), and 21.5°C in adult females (8th hour) to 27.0°C (18th hour), 27.5°C (18th hour), and 26.5°C (19th hour), respectively (Fig. 2A–C).

Snake temperatures most closely approximated the air and substrate temperatures during the 18th and 19th hours, when snakes were located predominantly underground (Fig. 2A–C). The temperatures of juveniles and adult males showed no consistent relationship to the associated air and substrate temperatures from the 7th to the 17th hours (Fig. 2A, B). However, air temperatures were significantly higher than the associated temperatures of adult females from the 10th to the 16th hours ($t = 2.49$; $P \leq 0.05$; Fig. 2C), whereas these latter temperatures were not significantly different from the associated substrate temperatures ($t = 1.08$, $P > 0.05$; Fig. 2C).

There was no consistent relationship between the hourly temperatures of snakes located above ground versus underground, particularly for adult females, which were infrequently located above ground. However, juvenile temperatures were significantly higher above ground than underground from the 11th through the 14th hours ($t = 2.76$, $P \leq 0.05$; Fig. 2A), and adult male temperatures were significantly higher above ground than underground from the 11th through the 17th hours ($t = 7.88$, $P \leq 0.05$; Fig. 2B).

The only significant difference in hourly temperatures between size classes occurred during the fifteenth hour, when above-ground temperatures were significantly higher in adult males than juveniles ($t = 2.09$, $P \leq 0.05$; Fig. 2A, B), whereas there were no significant differences in hourly temperatures between sex classes.

DISCUSSION

Because the magnitude of most pathways of heat exchange between an animal and its environment is dependent in part on the size of the animal (Pough et al. 1998), similarly sized individuals of the same species (that are exposed to the same environmental conditions) should exhibit similar temperature patterns. In particular, the smaller size and correspondingly higher body surface to volume ratio of juveniles may enable them to more efficiently thermoregualate than the adults since juveniles increase locomotor speed more than adults (Heckrotte 1967), probably due to ontogenetic increases in both aerobic and anaerobic capacity (Pough 1978), and since net energy gains are maximized at environmental temperatures very close to their preferred body temperature of about 29°C (Stephenson et al. 1985 for *Thamnophis elegans*). In turn, this should result in different temperature patterns between size classes because the juveniles can exchange heat with external sources more readily than can the adults. For example, juveniles may be able to access more underground microhabitats (e.g., small mammal tunnels) while attempting to locate a site that offers thermally optimal conditions. Moreover, juveniles are probably less conspicuous to potential predators while thermoregulating above ground due to their small size (J. Himes, pers. obs. 1996) and tend to move less frequently and over shorter distances compared to adults (Himes et al., unpubl. data).

In spite of this predicted relationship between animal size and temperature, the seasonal and hourly temperature patterns of juveniles and adult males were more similar to each other than either was to the temperature patterns of adult females. Assuming adult females and males have similar physiological capacities, the former may exhibit different behavioral and activity patterns (particularly when they are gravid) that result in a different thermal regime for adult females than for juveniles and adult males. While all snakes tended to avoid direct exposure to sunlight (each snake was found in sunlight in < 10% of the total observations on each individual), particularly during summer (< 5%), the most notable difference was the higher summer temperatures in adult females than in juveniles and adult males. No information is available on the reproductive biology of natural populations of *P. ruthveni*. However, adult females that were

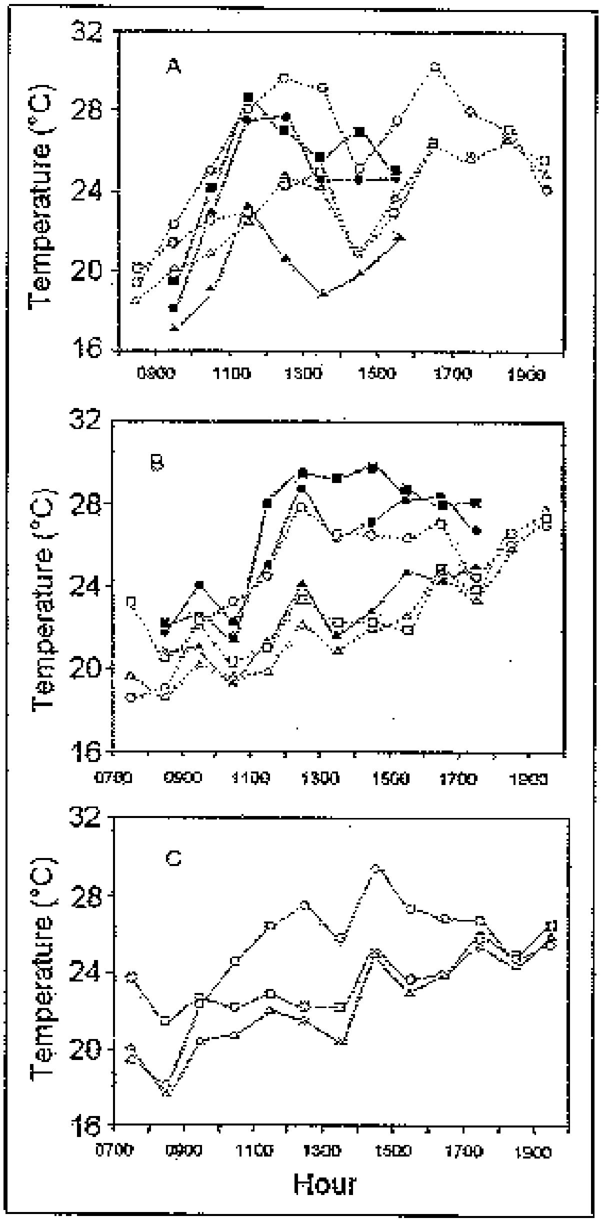


Figure 2. Hourly mean body temperatures (°C; squares) of juveniles (A), adult males (B), and adult females (C) of *Pituophis ruthveni* located above ground (solid lines) and underground (dashed lines), with means for associated air (diamonds) and substrate (triangles) temperatures. Each temperature plotted on the graph represents the mean of ≥ 10 recordings; temperatures are not plotted for hours with < 10 recordings (including all hourly aboveground temperatures of adult females). Temperatures are pooled across months. See text for statistics on significant differences.

emaciated and thought to have recently oviposited have been found above ground in July and August (T. Vandeventer, pers. comm. 1995). Therefore, adult females may maintain higher temperatures during late spring-early summer to enhance the development of their eggs.

Conversely, adult males move more frequently and over longer distances than do adult females (Himes et al., unpubl. data), probably in part because males are searching for mates and gravid females tend to be sedentary. However, juveniles move even less frequently and over shorter distances than do adult females. Thus, the disparate temperature patterns between size and sex classes are probably attributable to the behavioral and activity patterns exhibited by the adults and juveniles. However, because all but one of the juvenile snakes was captive-bred, the disparate temperature patterns between size classes may also be due in part to captive-bred snakes exhibiting different thermal behavior than wild-caught snakes.

Adult females were located above ground less frequently than were juveniles and adult males. Yet, it was during three of the four months in which an adequate number of temperatures (≥ 10) was recorded (for statistical analysis) of adult females above ground (May, August, September) when there was a significant difference in temperatures between size and sex classes. Therefore, it appears that adult females spend less time above ground than do juveniles and adult males, but maintain a higher body temperature when they are above ground.

In contrast to *P. c. deserticola* in northern Utah (Parker and Brown 1980), *P. ruthveni* did not have significantly higher temperatures in spring than in autumn. In fact, the mean temperatures of *P. ruthveni* were higher in autumn (22.7°C) than in spring (22.3°C); these temperatures were lower than those of *P. c. deserticola* in autumn (24.43°C) and spring (27.88°C). *Pituophis c. deserticola* may have attained higher temperatures than did *P. ruthveni* during the spring because the former taxon frequently basked on the surface shortly after emerging from hibernation. By contrast, *P. ruthveni* was located above ground only about 20% of the time, when it was usually secluded amid the shade of thick herbaceous vegetation.

Because individuals of *P. c. deserticola* emerged in the spring after spending 210–229 d in hibernation (Parker and Brown 1980), they probably needed to maintain elevated body temperatures during the first several weeks of activity to be physiologically capable of engaging in sustained types of activity (e.g., foraging and mate seeking). In contrast, *P. ruthveni*, which inhabit an area with a far milder winter and spring compared to the foothills of northern Utah inhabited by individuals of *P. c. deserticola*, spent only approximately 150 d in hibernation, during which they occasionally moved up to 200 m (J. Himes, pers. obs. 1996, 1997). Thus, unlike *P. c. deserticola*, individuals of *P. ruthveni* that have recently emerged from hibernation in the spring may already be physiologically capable of sustained activity without further elevation of their body temperatures.

Despite these temperature differences between *P. ruthveni* and *P. c. deserticola*, the mean temperatures of snakes located above ground from spring through autumn were similar (26.6°C [*P. ruthveni*] versus 27.9°C [*P. c. deserticola*]; Parker and Brown 1980). Moreover, the mean temperatures of snakes located underground were actually higher in *P. ruthveni* than in *P. c. deserticola* during autumn (22.5°C [*P. ruthveni*] versus 19.68°C [*P. c. deserticola*]) and summer (27.9°C [*P. ruthveni*] versus 27.01°C [*P. c. deserticola*]). Therefore, *P. c. deserticola* maintained higher temperatures than did *P. ruthveni* only at the beginning of its active season (spring), before temperatures of both taxa became more similar in the summer.

The relationship between snake, air, and substrate temperatures is very similar between *P. ruthveni* and *P. c. deserticola*. In both taxa, underground body temperatures were below air temperatures and were similar to shaded substrate temperatures (Parker and Brown 1980). Thus, snakes may have been thermoregulating at similar capacities. However, unlike *P. ruthveni*, *P. c. deserticola* occurred in an area containing numerous surface boulders and rock piles, under which it frequently sheltered. When *P. c. deserticola* was sheltering under this additional microhabitat, its body temperature was similar to the associated air and shaded substrate temperatures (no significant difference between temperatures).

In addition to *P. ruthveni*, three other taxa of *Pituophis* inhabit similar sandy-soiled pine forests in the southeastern United States: *Pituophis m. melanoleucus*, *P. m. lodingi*, and *P. m. mugitus* (Tennant and Bartlett 2000). Therefore, studies on the thermal ecology of these latter *Pituophis* would help determine whether the seasonal and diel temperature patterns of *P. ruthveni* are typical of southeastern *Pituophis* or are unique to *P. ruthveni*. However, *P. ruthveni* is most closely related to *P. c. sayi* (Reichling 1995; Rodríguez-Robles and De Jesús-Escobar 2000), which inhabits the open plains of the midwestern United States and northeastern Mexico (Tennant and Bartlett 2000). Therefore, studies on the thermal ecology of *P. c. sayi* could provide valuable insight into the origin of temperature patterns of *P. ruthveni*. In fact, the temperature patterns of *P. ruthveni* may be more similar to *P. c. sayi* than to the other southeastern *Pituophis*, depending on the relative importance of historical versus present-day factors in shaping the natural histories and associated temperature patterns of snakes.

In answer to the questions posed by Peterson et al. (1993), as they apply to *P. ruthveni*, (1) the range of possible body temperatures (°C) under natural conditions is 5.0–18.0 (winter), 8.5–36.5 (spring), 20.0–38.5 (summer), and 10.0–38.5 (autumn), (2) the proximate factors that determine which body temperatures a snake selects from that range of possibilities include its size and sex class, reproductive status, and location relative to the surface (above ground versus underground), and the time of year and day, (3) the variation of body temperatures of individual snakes under natural conditions over extended periods of time is 5.0 (winter) to 38.5°C (summer and autumn), (4) the functional effects of body-temperature variation include enhanced rates of growth in juveniles and perhaps adult males, and enhanced rates of egg development in adult females, and (5) the ecological consequences of body-temperature variation include relatively limited time spent on the surface and no surface activity from December-February.

ACKNOWLEDGMENTS

Stephen Reichling of the Memphis Zoo and Aquarium and J. Jordan (private reptile collector) provided nine and four study snakes, respectively. All MZA snakes were screened for diseases by the American Association of Zoo Veterinarians (Standard Certificate of Veterinary Inspection Number 020369). The Louisiana Department of Wildlife and Fisheries, U.S. Fish and Wildlife Service, and Texas Parks and Wildlife Department provided financial support through Section 6 funding. We thank the International Paper Company and Temple-Inland, Inc. for permission to conduct portions of this study on their land and the Magnolia Road Hunt Club for providing lodging. This study was conducted in accordance with U.S. Department of Agriculture guidelines.

LITERATURE CITED

Cunningham, J.D. 1966. Additional observations on the body temperatures of reptiles. Herpetologica 22:184–189.

Dill, C.D. 1972. Reptilian core temperatures: variation within individuals. Copeia 1972:577–579.

Diller, L.V. and R.L. Wallace. 1996. Comparative ecology of two snake species (*Crotalus viridis* and *Pituophis melanoleucus*) in southwestern Idaho. Journal of Herpetology 52:343–360.

Dundee, H.A. and D.A. Rossman. 1989. *The Amphibians and Reptiles of Louisiana*. Louisiana State Univ. Press, Baton Rouge, Louisiana, USA.

Fitch, H.S. 1956. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. University of Kansas Publications, Museum of Natural History 8:417–476.

Fitch, H.S. 1970. Reproductive cycles of lizards and snakes. University of Kansas Miscellaneous Publications, Museum of Natural History 52:1–247.

Greenwald, O.E. 1971. The effect of body temperature on oxygen consumption and heart rate in the Sonora gopher snake, *Pituophis catenifer affinis* Hallowell. Copeia 1971:98–106.

Greenwald, O.E. 1974. Thermal dependence of striking and prey capture by gopher snakes. Copeia 1974:141–148.

Heatwole, H.F. and J. Taylor. 1987. *Ecology of Reptiles*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.

Heckrotte, C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, *Thamnophis s. sirtalis*. Copeia 1967:759–763.

Himes, J.H., L.M. Hardy, C.D. Rudolph, and S.J. Burgdorf. 2002. Growth rates and mortality of the Louisiana pine snake (*Pituophis ruthveni*). Journal of Herpetology 36:683–687.

Himes, J.H., L.M. Hardy, C.D. Rudolph, and S.J. Burgdorf. 2003. Movement patterns and habitat selection by native and repatriated Louisiana pine snakes (*Pituophis ruthveni*): implications for conservation. Herpetological Natural History 9:000–000.

Jennings, R.D. and T.H. Fritts. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni*. Report submitted to the U.S. Fish and Wildlife Service and University of New Mexico Museum of Southwestern Biology, pp. 1–32.

Lillywhite, H.B. 1987. Temperature, energetics, and physiological ecology. In: R.A. Seigel, J.T. Collins, and S.S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 442–477. McGraw-Hill, New York, USA.

Parker, W.S. and W.S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee Public Museum Publications in Biology and Geology 7:1–104.

Peterson, C.R., A.R. Gibson, and M.E. Dorcas. 1993. Snake thermal ecology: the causes and consequences of body-temperature variation. In: R.A. Seigel and J.T. Collins (eds.), Snakes: Ecology and Behavior, pp. 241–314. McGraw-Hill, New York, USA.

Pough, F.H. 1978. Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): Physiological correlates and ecological consequences. Copeia 1978:69–75.

Pough, F.H., R.M. Andrews, J.E. Cadle, M.L. Crump, A.H. Savitzky, and K.D. Wells. 1998. *Herpetology*. Prentice Hall, Inc., Upper Saddle River, New Jersey, USA.

Reichling, S.B. 1988. Louisiana's rare and elusive snakes. Louisiana Conservationist 40:12–14.

Reichling, S.B. 1989. Reproductive biology and current status of the Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. In: M.J. Uricheck (ed.), *Proceedings of the 13th Annual International Herpetological Symposium*, pp. 95–98. International Herpetological Symposium, Inc., Danbury, Connecticut, USA.

Reichling, S.B. 1990. Reproductive traits of the Louisiana pine snake *Pituophis melanoleucus ruthveni* (Serpentes: Colubridae). Southwestern Naturalist 35:221–222.

Reichling, S.B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. Journal of Herpetology 29:186–198.

Reinert, H.K. and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705.

Rodríguez-Robles, J.A. and J.M. De Jesús-Escobar. 2000. Molecular systematics of New World gopher, bull, and pinesnakes (*Pituophis*: Colubridae), a transcontinental species complex. Molecular Phylogenetics and Evolution 14:35–50.

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 49:111–122.

Stevenson, R.D., C.R. Peterson, and J.S. Tsuji. 1985. The thermal dependence of locomotion, tongue flicking, digestion and oxygen consumption in the wandering garter snake. Physiological Zoology 58:46–57.

Sullivan, B.K. 1981. Observed differences in body temperature and associated behavior of four snake species. Journal of Herpetology 15:245–246.

Tennant, A. and R.D. Bartlett. 2000. *A Field Guide to Snakes of North America; Eastern and Central Regions*. Gulf Publishing Co., Houston, Texas, USA.

Weatherhead, P.J. and F.W. Anderka. 1984. An improved radio transmitter and implantation technique for snakes. Journal of Herpetology 18:264–269.

HERPETOLOGICAL NATURAL HISTORY

VOL. 9 2002 NO. 2

Herpetological Natural History, 9(2), 2002, pages 103–116.

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

John G. Himes[1,2] and Laurence M. Hardy
Museum of Life Sciences, Louisiana State University in Shreveport,
One University Place, Shreveport, Louisiana 71115-2399, USA

D. Craig Rudolph and Shirley J. Burgdorf[3]
Wildlife and Habitat Silviculture Laboratory, Southern Research Station,
USDA Forest Service, Nacogdoches, Texas 75962, USA

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

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

The genus *Pituophis* (Serpentes: Colubridae) contains three species in the United States: *P. catenifer*, *P. melanoleucus*, and *P. ruthveni* (Collins 1997). The Louisiana pine snake, *P. ruthveni*, was recently elevated to specific status (Reichling 1995) and is endemic to northern and western Louisiana and eastern Texas (Conant and Collins 1991; Reichling 1995; Thomas et al. 1976). Few data

[1]Present address: Nevada Division of Wildlife, 4747 Vegas Drive, Las Vegas, Nevada 89108, USA. Email: jhimes@ndow.state.nv.us
[2]Please use for correspondence.
[3]Present address: U.S. Fish and Wildlife Service, 510 Desmond Drive, Suite 102, Lacey, Washington 98503-1263, USA

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

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

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

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

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

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

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

MATERIALS AND METHODS

Study Site

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

Snake Collection

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

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

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

Experimental Protocol and Radio Implantation

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

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

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

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

Radiotracking

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

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

Data Collection

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

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

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

Data Analysis

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

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

RESULTS

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

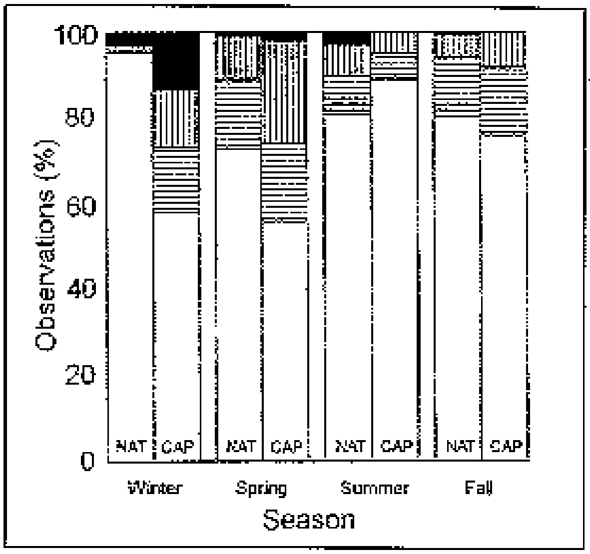


Figure 1. Frequency of positions of naturally occurring (NAT; n = 1358) and captive-bred (CAP; n = 705) pine snakes by season. Positions are in a hollow stump or log (black bars), under debris (leaves, pine needles, branches, or log; vertical bars), in the open (horizontal bars), and in mammal burrows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

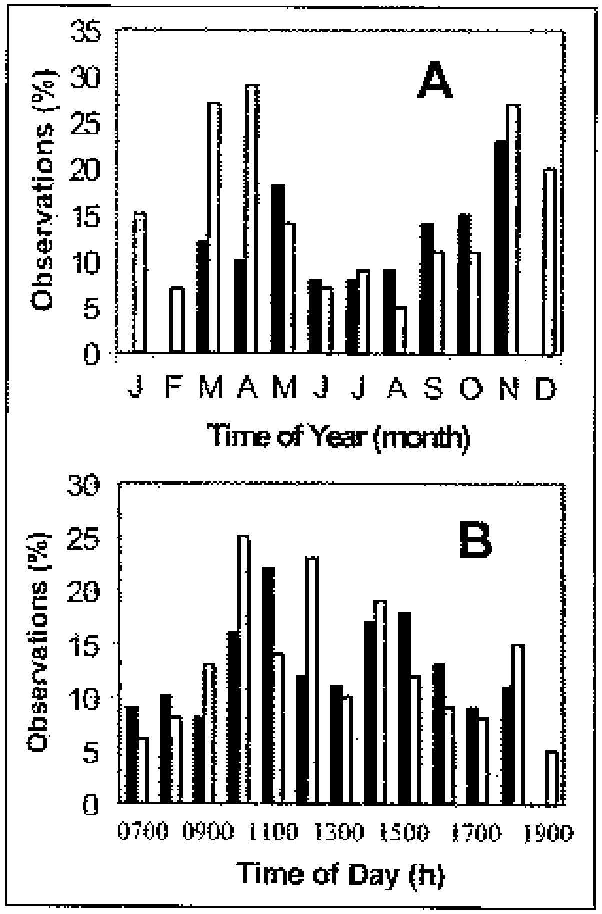


Figure 2. Frequency of NAT (n = 173, closed bars) and CAP (n = 93, open bars) snakes located in the open by month (A) and hour (B). Hours during which no snakes were located in the open (0100–0600 h and 2000–2300 h) are not shown.

CAP snakes that were tracked for at least ten days. Habitat data were analyzed for the 519 and 179 plots from the nine NAT and six CAP snakes, respectively, that each contributed at least ten plots.

Movement Patterns

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

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

Macrohabitat

NAT snake plots were more frequent in pine forests (where 56% of all NAT snake plots were located) than expected (RAN plots; Fig. 3). NAT and CAP snake plots were more frequent in pine plantations (23 and 38%, respectively) and grasslands (6 and 5%, respectively), and were less frequent in pine-hardwood, hardwood-pine, and hard-

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

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

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

wood forests (5 and 13%, respectively, for all three habitats combined) than expected ($P < 0.05$ [hardwood forests]; RAN plots; Fig. 3). Of the six CAP snakes with a minimum of five expected locations per habitat, one individual each was found significantly more often ($P < 0.05$) in a forest, pine plantation, and clearcut (Table 2). Of the remaining three CAP snakes, one individual each was found relatively more often ($P \geq 0.05$) in a forest, grassland, and clearcut (Table 2).

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

Microhabitat

Most NAT and CAP snake plots (80 and 88%, respectively) contained relatively few (< 10) trees as expected (RAN plots; Fig. 5A). Moreover, nearly 50% of all CAP snake plots lacked trees (Fig. 5A). NAT snake points (point = center of NAT

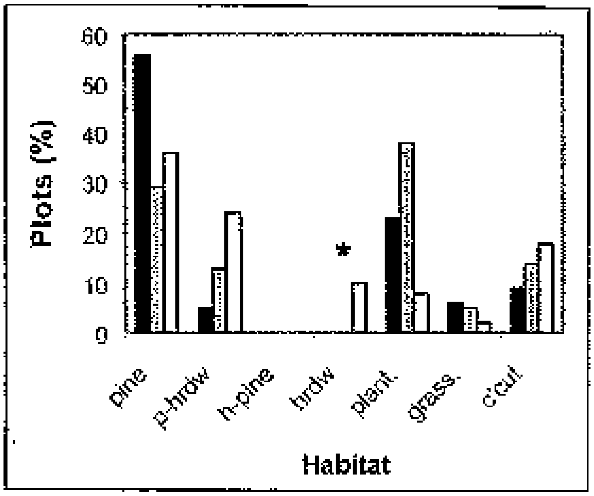


Figure 3. Habitats where NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots (radius = 11.2 m) were located compared to available habitats (random plots [RAN]; n = 100, open bars). Abbreviations used are pine (pine forest), p-hrdw (pine-hardwood forest), h-pine (hardwood-pine forest),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

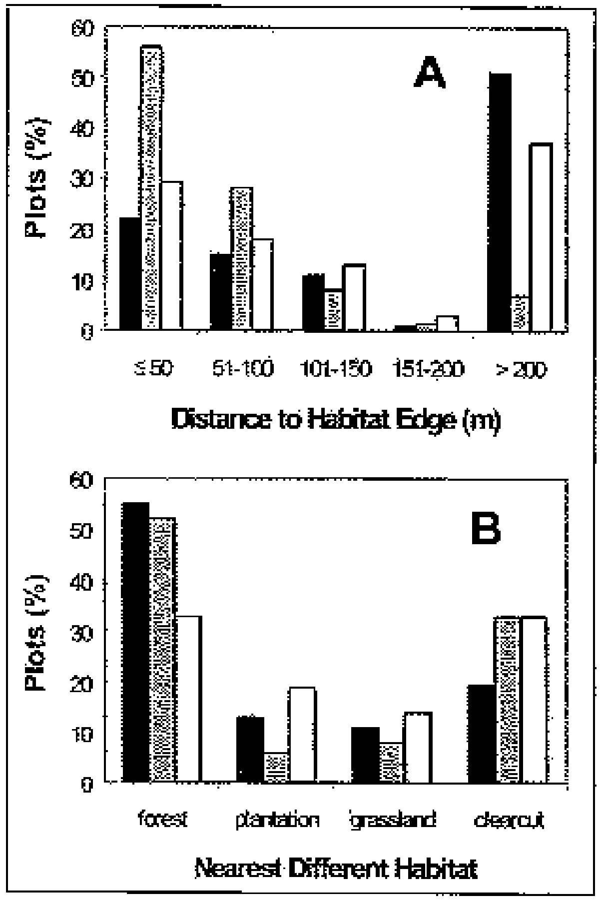


Figure 4. (A) Proximity of NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots to nearest habitat edge compared to RAN plots (n = 100, open bars). (B) Nearest different habitat (≤ 200 m; all forest types grouped together) to NAT (n = 265, black bars) and CAP (n = 172, grey bars) snake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

snake plot where snake was located) were more frequently nearer loblolly pines (40%) than expected, and nearer longleaf (12%) and slash pines (33%) as expected (center of RAN plot; Fig. 5B). CAP snake points were more frequently nearer longleaf (23%) and slash pines (46%) than expected (center of RAN plot; Fig. 5B). NAT and CAP snake points each were more and less frequently nearer shortleaf pines (9 and 7%, respectively) and hardwoods (5 and 8%, respectively), respectively, than expected (center of RAN plot; Fig. 5B).

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

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

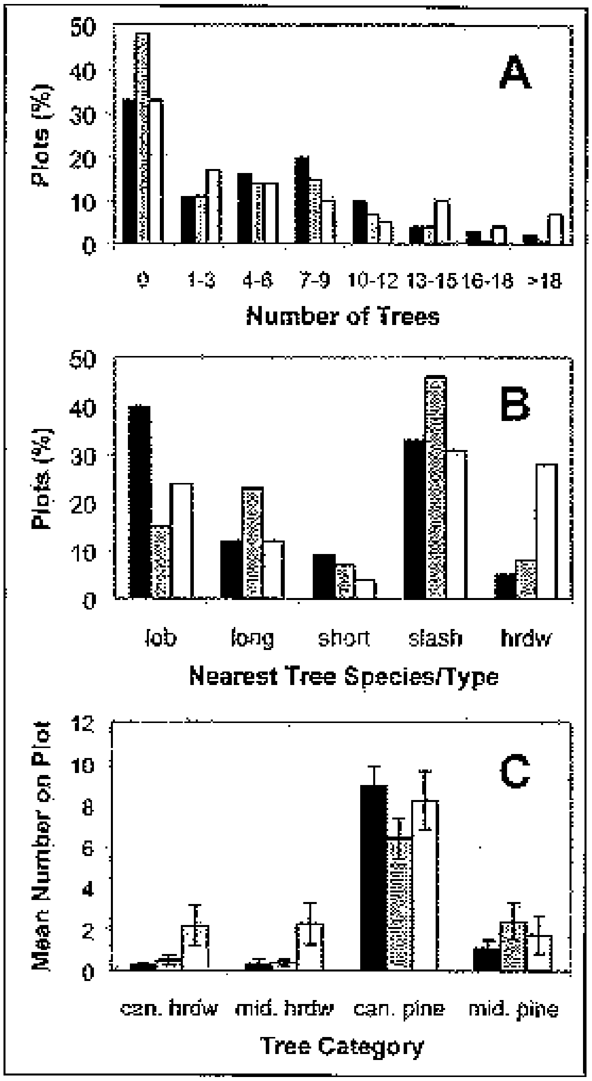


Figure 5. (A) Mean number of trees on NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots compared to RAN plots (n = 100, open bars). (B) Nearest tree species/type (≤ 15 m; all non-pines grouped together) to NAT (n = 349, black bars) and CAP (n = 92, grey bars) snake points compared to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

Pocket Gopher Mounds and Open Mammal Burrows

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

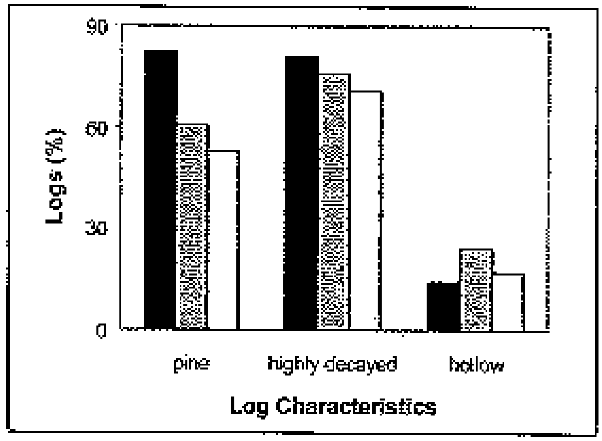


Figure 6. Characteristics of logs on NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots compared to RAN plots (n = 100, open bars). Abbreviation used is highly decayed (< 50% of bark remaining on log).

2.5, range = 0–211, n = 519; 27 ± 4.2, 0–104, n = 179) than expected, but few open mammal burrows (mean number of burrows ± 95% CI on NAT and CAP snake plots, respectively, 3 ± 0.1, 0–24, n = 519; 4 ± 0.1, 0–23, n = 179) as expected (RAN plots; Fig. 8A). Pocket gopher mounds were less frequently located on NAT and CAP snake plots in clearcuts (3 and 1%, respectively, of plots containing mounds) than expected (RAN plots; Fig. 8B). Mounds were more frequently on CAP snake plots in pine plantations (45%) and less frequently in pine forests (35%) than expected (RAN plots; Fig. 8B). Mounds were more frequent as expected on NAT and CAP snake plots where the most abundant trees were loblolly (37 and 34%, respectively, of plots containing mounds and trees) and shortleaf pine (7 and 3%,

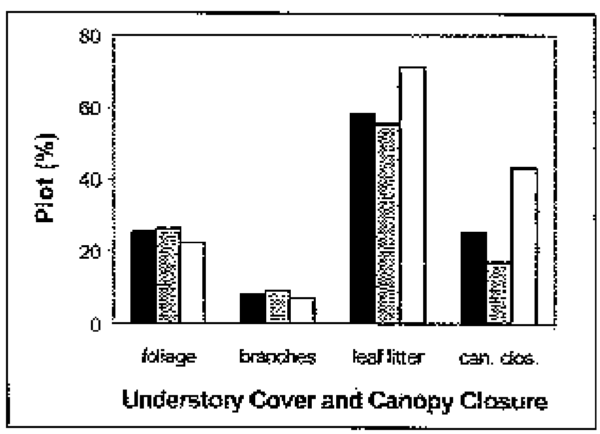


Figure 7. Understory cover percents on NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots and canopy closure percent over the center of NAT and CAP snake plots compared to RAN plots (n = 100, open bars). Abbreviation used is can. clos. (canopy closure).

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

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

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

Soil

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

DISCUSSION

Movement Patterns

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

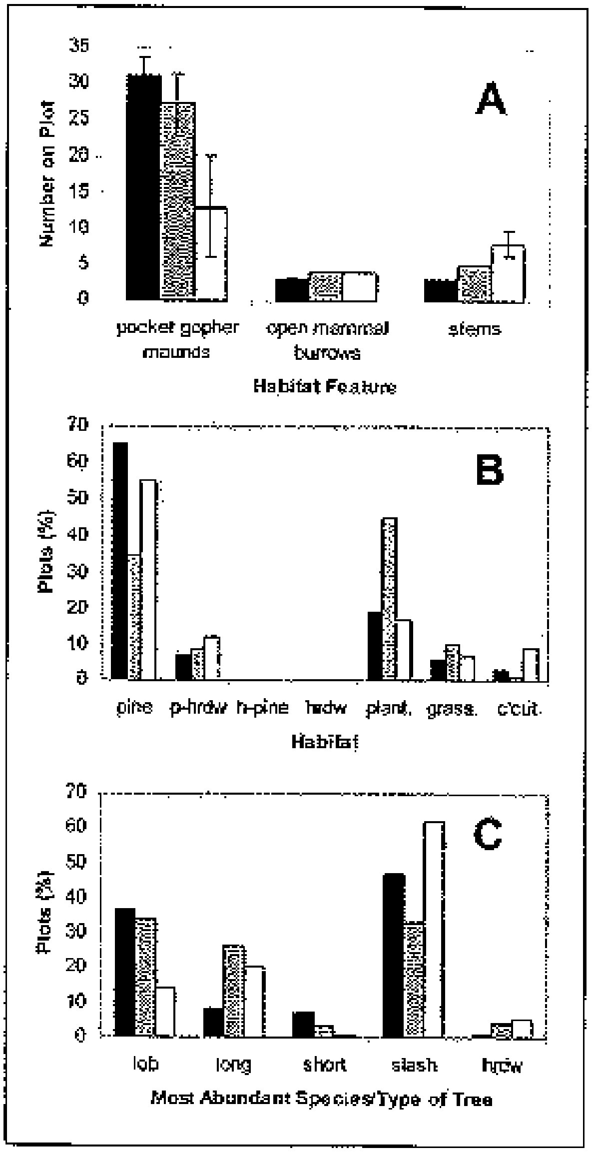


Figure 8. (A) Mean number of pocket gopher mounds, open mammal burrows, and stems (= trees with DBH < 25 cm) on NAT (n = 519, black bars) and CAP (n = 179, grey bars) snake plots compared to RAN plots (n = 100, CI = 0.95, open bars). (B) Habitats where pocket gopher mounds were located on NAT (n = 519,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

and Wright 1957). In addition, extreme surface temperatures can be avoided by sheltering underground, where temperatures are less variable.

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

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

The lower vagilities and smaller home ranges of CAP snakes may have been due to the snakes' introduction into an unfamiliar habitat after a lifetime in captivity, as well as to their levels of endurance, which are typically lower in younger and smaller snakes (Pough 1978). Alternatively, the smaller size of CAP snakes may have enabled them to access more mammal burrows, particularly of small rodents, thereby potentially increasing the snakes' foraging success within a relatively small area. Also, because smaller individuals of *P. ruthveni* are more vulnerable to predation than are larger individuals (J. Himes and L. Hardy, pers. obs. 1996, 1997), the smaller snakes may limit the extent of their movements to lessen their conspicuity to predators.

Habitat Relations

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

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

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

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

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

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

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

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

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

Conservation

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

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

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

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

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

ACKNOWLEDGMENTS

Nine and four study snakes, respectively, were provided by S. Reichling of the Memphis Zoo and Aquarium and J. Jordan (private reptile collector). All CAP snakes were screened for diseases by the American Association of Zoo Veterinarians (Standard Certificate of Veterinary Inspection Number 020369). The Louisiana Department of Wildlife and Fisheries and the US Fish and Wildlife Service provided partial financial support. We thank the International Paper Company for permission to conduct this study on their land and the Magnolia Road Hunt Club for providing study site lodging. Assistance was provided during various aspects of this study by R. Conner, R. Schaefer, and C. Collins. This study was conducted in accordance with U.S. Department of Agriculture guidelines.

LITERATURE CITED

Bogert, C.M. 1949. Thermoregulation in reptiles: a factor in evolution. Evolution 3:195–211.

Bogert, C.M. 1959. How reptiles regulate their body temperature. Scientific American 200:105–120.

Boyer, W.D. 1980. Longleaf pine. In: F.H. Eyre (ed.), *Forest Cover Types of the United States and Canada*, pp. 51–52. Society of American Foresters, Washington, D.C., USA.

Brattstrom, B.H. 1965. Body temperatures of reptiles. American Midland Naturalist 73:376–422.

Brown, W.S. and W.S. Parker. 1982. Niche dimensions and resource partitioning in a Great Basin desert snake community. In: N.J. Scott, Jr. (ed.), *Herpetological Communities: a Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977*, pp. 59–81. U.S. Fish and Wildlife Service, Wildlife Research Report 13, Lawrence, Kansas, USA.

Buckman, H.O and N.C. Brady. 1969. *The Nature and Properties of Soils. Seventh Edition*. Collier Macmillan Co., Ltd., Toronto, Canada.

Burger, J. and R.T. Zappalorti. 1986. Nest site selection by pine snakes, *Pituophis melanoleucus*, in the New Jersey Pine Barrens. Copeia 1986:116–121.

Burger, J. and R.T. Zappalorti. 1988. Habitat use in free-ranging pine snakes, *Pituophis melanoleucus*, in the New Jersey Pine Barrens. Herpetologica 44:48–55.

Clark, D.R., Jr. 1988. Environmental contaminants and the management of bat populations in the United States. In: R.C. Szaro, K.E. Severson, and D.R. Patton (eds.), *Management of Amphibians, Reptiles, and Small Mammals in North America*, pp. 409–413. General Technical Report RM-166, Flagstaff, Arizona, USA.

Collins, J.T. 1997. Standard common and current scientific names for North American Amphibians and Reptiles. Fourth Edition. Society for the Study of Amphibians and Reptiles, Herpetological Circular 19:1–40.

Conant, R. 1956. A review of two rare pine snakes from the Gulf Coastal Plain. American Museum Novitates 1781:1–31.

Conant, R. and J.T. Collins. 1991. *A Field Guide to Reptiles and Amphibians of Eastern and Central North America. Third Edition*. Houghton Mifflin Co., Boston, Massachusetts, USA.

Cowles, R.B. and C.M. Bogert. 1944. A preliminary study of the thermal requirements of desert reptiles. Bulletin of the American Museum of Natural History 83:261–296.

Dodd, C.K., Jr. 1987. Status, conservation, and management. In: R.A. Seigel, J.T. Collins, and S.S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 478–513. McGraw-Hill, New York, USA.

Dodd, C.K., Jr. 1993. Strategies for snake conservation. In: R.A. Seigel and J.T. Collins (eds.), *Snakes: Ecology and Behavior*, pp. 363–393. McGraw-Hill, New York, USA.

Dodd, C.K., Jr. and R.A. Seigel. 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Fitch, H.S. 1949. Road counts of snakes in western Louisiana. Herpetologica 6:87–90.

Gibbons, J.W. and R.D. Semlitsch. 1987. Activity patterns. In: R.A. Seigel, J.T. Collins, and S.S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*, pp. 396–421. McGraw-Hill, New York, USA.

Heckrotte, C. 1962. The effect of the environmental factors in the locomotory activity of the plains garter snake (*Thamnophis radix radix*). Animal Behavior 10:193–207.

Himes, J.H., L.M. Hardy, C.D. Rudolph, and S.J. Burgdorf. 2002. Growth rates and mortality of the Louisiana pine snake (*Pituophis ruthveni*). Journal of Herpetology 36:683–687.

James, F.C. and H.H. Sugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

Jennings, R.D. and T.H. Fritts. 1983. The status of the black pine snake *Pituophis melanoleucus lodingi* and the Louisiana pine snake *Pituophis melanoleucus ruthveni*. Report submitted to the U.S. Fish and Wildlife Service and University of New Mexico Museum of Southwestern Biology, pp. 1–32.

Landreth, H.F. 1973. Orientation and behavior of the rattlesnake *Crotalus atrox*. Copeia 1973:26–31.

Lowery, G.H., Jr. 1974. *The Mammals of Louisiana and its Adjacent Waters*. Louisiana State University Press, Baton Rouge, Louisiana, USA.

Parker, W.S. and W.S. Brown. 1980. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*, in northern Utah. Milwaukee Public Museum Publications in Biology and Geology 7:1–104.

Platt, D.R. 1969. Natural history of the hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. University of Kansas Publications, Museum of Natural History 18:253–420.

Pough, F.H. 1978. Ontogenetic changes in endurance in water snakes (*Natrix sipedon*): physiological correlates and ecological consequences. Copeia 1978:69–75.

Reichling, S.B. 1988*a*. Louisiana's rare and elusive snakes. Louisiana Conservationist 40:12–14.

Reichling, S.B. 1988*b*. Reproduction in captive Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. Herpetological Review 19:77–78.

Reichling, S.B. 1989. Reproductive biology and current status of the Louisiana pine snakes, *Pituophis melanoleucus ruthveni*. In M.J. Uricheck (ed.), *Proceedings of the 13th Annual International Herpetological Symposium*, pp. 95–98. International Herpetological Symposium, Inc., Danbury, Connecticut, USA.

Reichling, S.B. 1993. *North American Regional Studbook for the Black Pine Snake,* Pituophis melanoleucus lodingi, *and the Louisiana Pine Snake,* Pituophis melanoleucus ruthveni. Memphis Zoo and Aquarium, Memphis, Tennessee, USA.

Reichling, S.B. 1995. The taxonomic status of the Louisiana pine snake (*Pituophis melanoleucus ruthveni*) and its relevance to the evolutionary species concept. Journal of Herpetology 29:186–198.

Reinert, H.K. 1991. Translocation as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. Herpetologica 47:357–363.

Reinert, H.K. and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705.

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 49:111–122.

Rudolph, D.C., S.J. Burgdorf, R.R. Schaefer, R.N. Conner, and R.T. Zappalorti. 1998. Snake mortality associated with late season radio-transmitter implantation. Herpetological Review 29:155–156.

Speake, D., D. McGlincy, and C. Smith. 1987. Captive breeding and experimental reintroduction of the eastern indigo snake. In: R.R. Odom, K.A. Riddleberger, and J.C. Ozier (eds.), *Proceedings of the Third Southeastern Nongame and Endangered Wildlife Symposium*, pp. 84–90. Georgia Department of Natural Resources, Athens, Georgia, USA.

Stull, O.G. 1929. The description of a new subspecies of *Pituophis melanoleucus* from Louisiana. Occasional Papers of the Museum of Zoology, University of Michigan 205:1–3.

Thomas, R.A., B.J. Davis, and R. Culbertson. 1976. Notes on variation and range of the Louisiana pine snake, *Pituophis melanoleucus ruthveni* Stull (Reptilia, Serpentes, Colubridae). Journal of Herpetology 10:252–254.

Vandeventer, T.L. and R.A. Young. 1989. Rarities of the longleaf: the black and Louisiana pine snakes. Vivarium 1:32–36.

Wright, A.H. and A.A. Wright. 1957. *Handbook of Snakes of the United States and Canada*. Cornell University Press, Ithaca, New York, USA.