ECOLOGY OF THE WESTERN COTTONMOUTH (*AGKISTRODON PISCIVORUS LEUCOSTOMA*) IN NORTHEASTERN TEXAS

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ABSTRACT: There are few long-term studies of North American pitvipers using mark and recapture methods. In particular, the ecology of the Cottonmouth (*Agkistrodon piscivorus*) has only been examined for relatively short periods. A total of 607 records from 247 individuals of the Western Cottonmouth (*A. p. leucostoma*) were collected from 1984 to 1997 at Sheff's Wood, a 32.2 ha preserve in northeastern Texas. The site is a flat, open deciduous woodland with several small streams, standing pools of water, a sphagnum bog, and a shallow, permanent stream that leads to a pond outside of the preserve. The snakes were captured in drift fence traps, measured, sexed, and individually marked for future identification. Snakes were found in lowland areas (ca. 5 ha), and in the first five years of the study ca. 25 individuals were captured in the active season (5 snakes/line, March to November), but in the next six years ca. 85 were obtained each year (10 snakes/line). Recapture rates increased each year from 20% to 75% until the winter of 1995, when a drought occurred. The only *A. p. leucostoma* recorded in 1996 was unmarked, as were two captured in 1997. From marked neonates it was established that maturity could be reached in the fourth year, but growth was highly variable. Males continued to grow and reached larger sizes than females. Population estimates ranged from 130 to 170 for the 5 ha area. Although the adult female to male sex ratio was 52/47, females were more commonly captured in the spring and males in the late summer. Neonates and juveniles were predominately captured in the fall. Litter size averaged five, and parturition was in late August to early September. Less than 50% of the adult females were pregnant in a year, but some females reproduced in consecutive years.

INTRODUCTION

Long-term studies of snake populations have lagged woefully behind those of other vertebrates. For these ectothermic animals, basic life-history characteristics such as growth and reproduction are strongly influenced by stochastic events, such as prey availability during or preceding the period in which sampling occurs (Parker and Plummer, 1987; Seigel, et al. 1995), and the need for long-term studies is evident (see Tinkle, 1979). Historically, data on the population ecology of snakes have been obtained from short-term examination of populations, and for many species, such as the Western Cottonmouth (*Agkistrodon piscivorus leucostoma*), information is only anecdotal (see Gloyd and Conant, 1990 for a review of the literature on this taxon). The explanation for the paucity of long-term demographic and life-history studies relates to the difficulty of assessing information about individual snakes in nature (Parker and Plummer, 1987; Plummer, 1997; for an alternative explanation see Seigel, 1993). As a group, snakes tend to be reclusive and are often difficult to capture repeatedly. Long-term studies that have been conducted on vipers have been primarily in northern regions, where they utilize communal den sites and can be collected in numbers (e.g., *Vipera berus*, Andrén and Nilson, 1983; *Crotalus horridus*, Brown, 1993; *Crotalus viridis*, Diller and Wallace, 1996). For southern North America, data on individual snakes over extended periods are only now being acquired, and primarily through the technology of radiotelemetry.

The Cottonmouth (*A. piscivorus*) is a medium to large-sized pitviper that occurs throughout much of the southeastern United States, as far west as central Texas (Gloyd and Conant, 1990). Its diet consists of expected prey such as fish and frogs, but also includes mammals, birds, and reptiles, including turtles, small alligators, and even other Cottonmouths (Savitzky, 1992). *Agkistrodon piscivorus* can be found in high densities in lowland swamp habitats (Barbour, 1956; Kofron, 1978). They have small litters of relatively large young that may have a higher survival rate than other neonate snakes (Fitch, 1985). These factors make *A. piscivorus* a good candidate for long-term studies in terms of numbers that can be collected and the likelihood of recapture of individuals.

METHODS

Study Site

Sheff's Wood is a small (32.2 ha) second-growth forest that in 1969 was donated to the Texas Nature Conservancy by O. C. Sheffield (Gehlbach, 1975). Lands adjacent to the preserve have been utilized as cattle range, oil exploration, and timber harvesting, but Sheff's Wood has been relatively undisturbed since 1950. Wooded corridors into the preserve are primarily through riparian habitat, although some borders have second-growth forest. Species diversity and seasonal abundance of 21 species of snakes found in the preserve were evaluated from 1984 to 1987 (Ford et. al. 1991); presently 22 species are docu-

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Table 1. Study site characteristics and capture/recapture data for *Agkistrodon piscivorus leucostoma* by year. Population estimates were calculated by the Schabel method (see text). Sample period for the calculation was each year so recaptures of individuals within years were used only once.

Year	N traplines	Total N captures	Total N individuals	N recaptures from previous years	Population estimate (95% confidence limits)
1984 (Oct-Nov only)	3	2	2	0	—
1985	3	11	9	2	—
1986	5	22	17	1	153 + 69
1987	5	25	25	5	130 + 47
1988	7	28	24	5	169 + 67
1989	8	81	64	10	284 + 62
1990	8	85	55	26	265 + 110
1991	8	84	51	20	298 + 65
1992	8	77	48	15	347 + 134
1993	8	78	56	27	370 + 77
1994 (excluded in July)	8	61	43	29	367 + 46
1995 (May-July only)	8	19	17	12	366 + 38
1996	8	1	1	1	—
1997	8	2	2	0	—

mented. Much of the preserve is upland oak and hickory forest, but about 5 ha of flat bottomland hardwood forest is present, and *A. p. leucostoma* is restricted to this small floodplain (Ford et al., 1991). This area contains several small streams and oxbow pools, a sphagnum bog, and a shallow permanent stream (3 m wide) that leads to a pond (ca. 1 ha) located in the preserve boundaries. The trees in this area (*Acer rubrum*, *Betula nigra*, *Liquidambar styraciflua*, and *Quercus nigra*) are typical bottomland hardwoods. In general, the forests are mature and multiple trees fall each year creating logs and root cavities along with debris. The soil is loamy and sand rich with decaying vegetation. Because the main stream is spring-fed, the basic nature of the floodplain was similar each year. In wetter years, water flowed from upland sites through additional streams, but even during droughts water flowed in the main creek. During the midpoint of the study, oil exploration upstream caused silting in the main stream, lowering its depth and partially filling the pond.

Data Acquisition

Snakes were live-trapped using 45 cm high aluminum drift fences with box-shaped traps (L120 x W35 x H35 cm) as described in Ford et al. (1991). Traps were placed at the ends and in the middle of 15 m long drift fences. A series of three to eight lines were monitored every two to three days from 1984 to 1997, usually starting in March and running until the first cold period in November. The first three lines were established in fall of 1984, two were added in 1986 and 1988, and one in 1989 (Table 1). Initial lines were placed near the sphagnum bog and the permanent stream, and subsequent lines were placed near the pond. During surveys, *A. p. leucostoma* were occasionally captured outside the traps. For each snake captured the following was recorded: trap location, snout-vent length (SVL), mass, and sex. Snakes were marked with unique ventral scale clips until 1989, and thereafter with passive integrated transponder (PIT) tags that were injected into the body cavity (Avid Corp. Norco, California; Jemison et al., 1995). Animals were released near their capture location within two days, except in 1989 and 1990 when several pregnant females were transported to the laboratory and held until parturition occurred. The offspring of those females were measured, marked, and released in the area where their respective mother was collected.

The number of *A. p. leucostoma* captured and recaptured was totaled each year. For each year from 1985 to 1995, population size (95% confidence intervals) was calculated by the Schnabel method

(Ecological Analysis-PC; Eckblad, 1986–89). Mark-recapture models for snakes have been criticized because of low rates of recapture (generally < 30%; see Parker and Plummer, 1987). In this study we had high recapture rates; a regression of the proportion of recaptured animals to the number previously marked increased linearly, which supports the model of equal catchability (Krebs, 1989). Admittedly, rates of emigration and immigration are unknown for this population, but because population estimates have not been reported for *A. piscivorus*, it is worthwhile to present them for comparisons to other snakes.

From 1984 to 1987, capture rates per drift fence line were calculated by dividing the number of snakes captured (including recaptures separated by at least one month) by the number of lines present. For 1994 and 1995, capture rates were adjusted for the shorter length of time that traps were run, by considering the number of months the traps were open relative to the eight months they were normally open, and multiplying that ratio by the number of captures. Drift fences as a method of examining seasonal and yearly variation in activity through capture rates is less subjective than hand captures or collection of snakes from roads. Sources of error related to unequal catchability of all individuals, however, are unknown.

Growth and Age

Duration of the growing season varies in relation to a variety of climatological events, but because *A. p. leucostoma* were most often observed active from 1 March to mid-November, growth was assumed to be limited to an eight-month period. Date of birth was considered to be early September, based on eight litters born in the laboratory. Free-living animals were determined to be in their first year (= 0) of life based on the size of neonates and juveniles in the laboratory. A snake captured in October that was slightly larger than neonate size, for example, would be considered in its first year. The growth of neonates captured in their first year or the following spring was examined during subsequent recaptures. Due to variation in the size of animals within one year after birth, only the growth of adult males, and females captured in their first and subsequent years, was analyzed. The growth of animals first captured at a larger size was plotted as the size at first capture, and then the size at recapture relative to the number of active months after the initial capture. These animals could not be accurately aged, but a range was estimated from the graphs of the snakes marked as neonates.

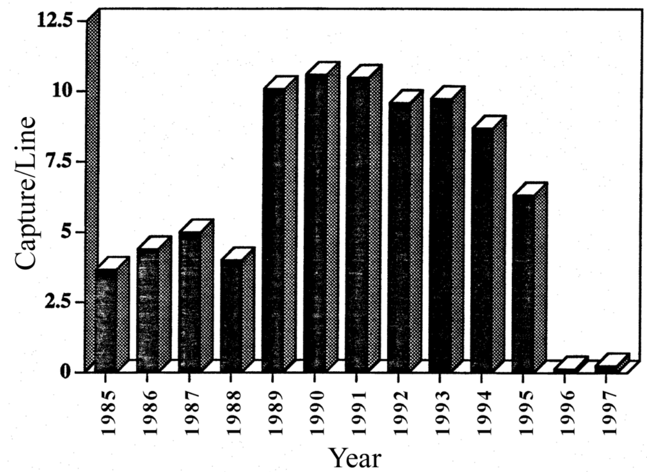

Fig. 1. Number of yearly captures of *Agkistrodon piscivorus leucostoma* per 15 m drift fence at Sheff's Wood. Capture rates were calculated by dividing the total number of snakes captured (including recaptures separated by at least one month) by the number of lines present in that year. For 1994 and 1995, capture rates were adjusted for the shorter time traps were open by multiplying the number of snakes captured by the appropriate ratio (the 8 month period they were normally open divided by number of months the traps were open during that year).

Reproduction

Reproductive data for three *A. p. leucostoma* from this population were reported by Ford et al. (1991), and for this study five additional pregnant females were held in the laboratory until parturition. In 1989 adult females were routinely palpated for presence of embryos, and the percentage of pregnant individuals was calculated.

Survival

Survival rates were calculated for a small cohort of neonates that were PIT-tagged and released in 1989, and a second group in 1990. We considered that animals not recaptured in the subsequent seven years had died. No method for evaluating emigration rate was available. Larger snakes were grouped as subadults and adults (using a reproductive size of 50 cm SVL; Burkett, 1966). Annual survival rates were calculated based on recaptures the next year, plus snakes not recaptured the next year but recaptured some later year. Obviously, animals collected in later years survived each subsequent year from first capture to last capture date.

RESULTS

Capture Rates

A total of 607 usable records were collected from 247 different *A. p. leucostoma* during the study period

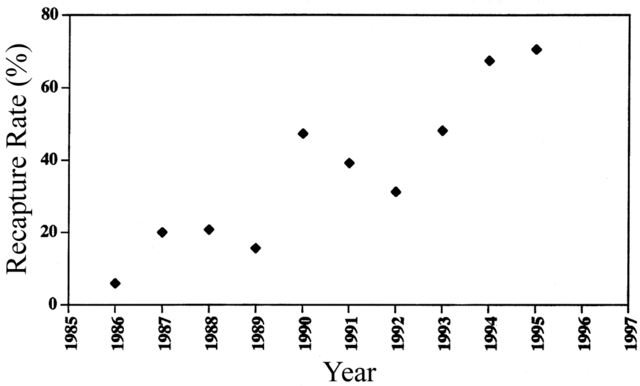

Fig. 2. Cumulative rate of recaptures of *Agkistrodon piscivorus leucostoma* at Sheff's Wood.

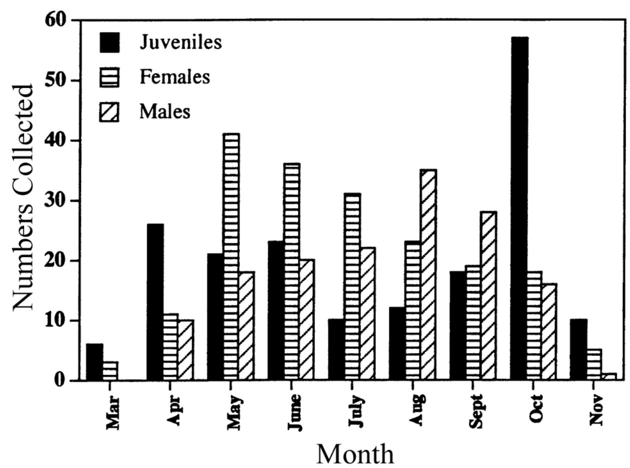

Fig. 3. Seasonal captures of *Agkistrodon piscivorus leucostoma* at Sheff's Wood for all years combined. Number collected each month is separated by sex for adults. Juveniles are considered those below 45cm SVL.

of 14 years. For the first four years, approximately five *A. p. leucostoma* were captured each year for each 15 m line (Fig. 1). In 1988 and 1989 additional lines closer to the stream and pond were included. From 1989 to 1994 about 10 snakes were recorded per line. The data for 1995 is lower, at seven per line, but this is data for three months the traps were open, adjusted for eight months. In winter 1995, a severe drought occurred and in the two years following less than one *A. p. leucostoma* was collected per line.

Starting with nine snakes marked in 1984 and 1985, I calculated the population sizes each year until 1995 (Schnabel method with year as sampling period: Krebs, 1989). Values ranged from a low of 130 to a high of 370 (Table 1). As more animals were marked the recapture rates generally increased each year to approximately 70% for 1994 and 1995 (Fig. 2). Population estimates from 1993 to 1995 were consistent (366 to 370 individuals) with relatively low 95%

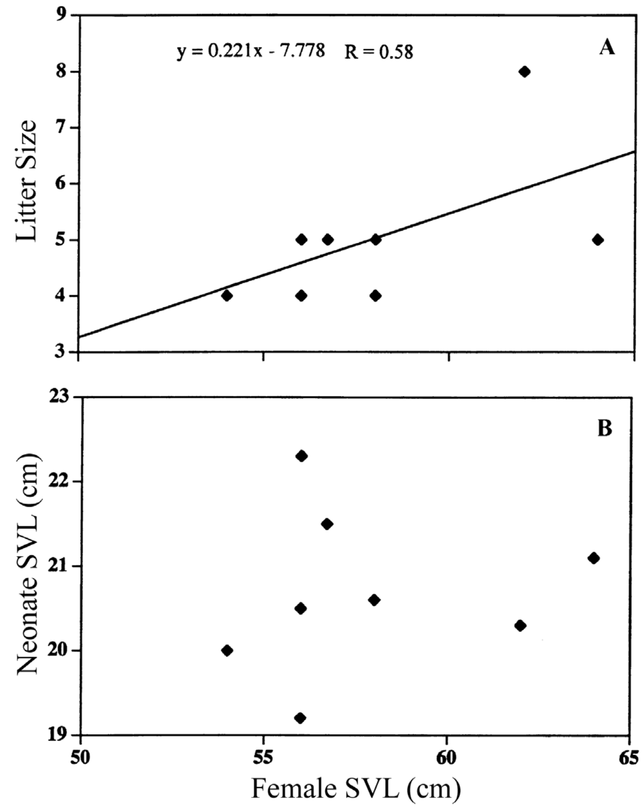

Fig. 4. Reproductive data on *Agkistrodon piscivorus leucostoma* from Sheff's Wood frpm 1989 and 1990. Adult females collected in 1989 and 1990. (A) litter size (N of offspring) vs maternal SVL. (B) Snout-vent length of neonates vs maternal SVL.

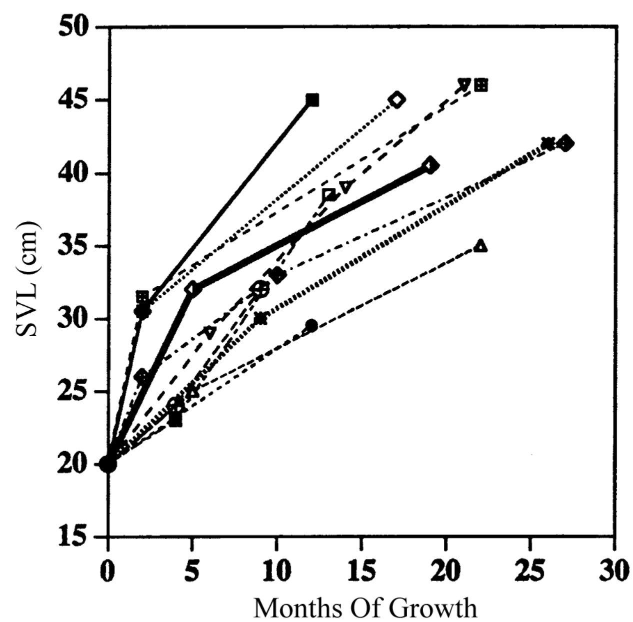

Fig. 5. Growth of juvenile *Agkistrodon piscivorus leucostoma* from Sheff's Wood relative to months of active growth (March to November). Symbols denote individual animals.

confidence intervals (38 to 77). Density of individuals/ha was approximately 30 individuals for the years 1986 to 1988, 56 for 1989 to 1992, and 73 for 1993 to 1995. In 1996 only one snake was captured and in 1997 only two were recorded, thus the density in those years was calculated at less than one snake/ha.

Seasonal Activity and Sex Ratio

The total number of adult males and females, as well as neonates, captured each month is shown in Figure 3. The sex ratio for 132 adult animals was nearly even (47.7% male). Adult females, however, made up a larger proportion of the snakes trapped in May, June, and July, whereas adult males were more abundant in August and September. Neonates and juveniles were collected in larger numbers in October, November, and April.

Reproduction

Females gave birth in late August and early September. The smallest pregnant female collected was 54 cm SVL (mean reproductive characteristics for eight females is given in Table 2). Although the sample size for these regressions was small, litter size was positively correlated to female SVL but neonate size was not (Fig. 4). In 1989 and 1990 less than 50% of the females collected were pregnant, which corresponds with values for the Eastern Cottonmouth (*A. p. piscivorus*; Scott et al., 1995). Percentages of 50% or lower are usually taken as evidence that the population has a biennial cycle (Burkett, 1966; Wharton, 1966). One female at Sheff's Wood, however, produced offspring in two consecutive years. Both Kofron (1979) and Blem (1981) suggest an annual cycle for some populations of *A. piscivorus*.

Survival

Twelve neonates were marked in 1989, three were captured in 1990, and one in 1992, yielding a 30% minimum survival rate for the first year of life (Table 3). Of six marked in 1990, none were collected the next year but three were eventually collected, bringing the annual survival rate to 50%. Medium-sized snakes had annual survival rates ranging from 33 to 89%, and adults had survival rates of 75 to 100% (Table 3). Some of these animals were not recaptured until several years after their initial marking, so actual yearly survival rates could be higher as animals that survived one year might die in subsequent years before being captured again. No sexual difference was evident in survival rate.

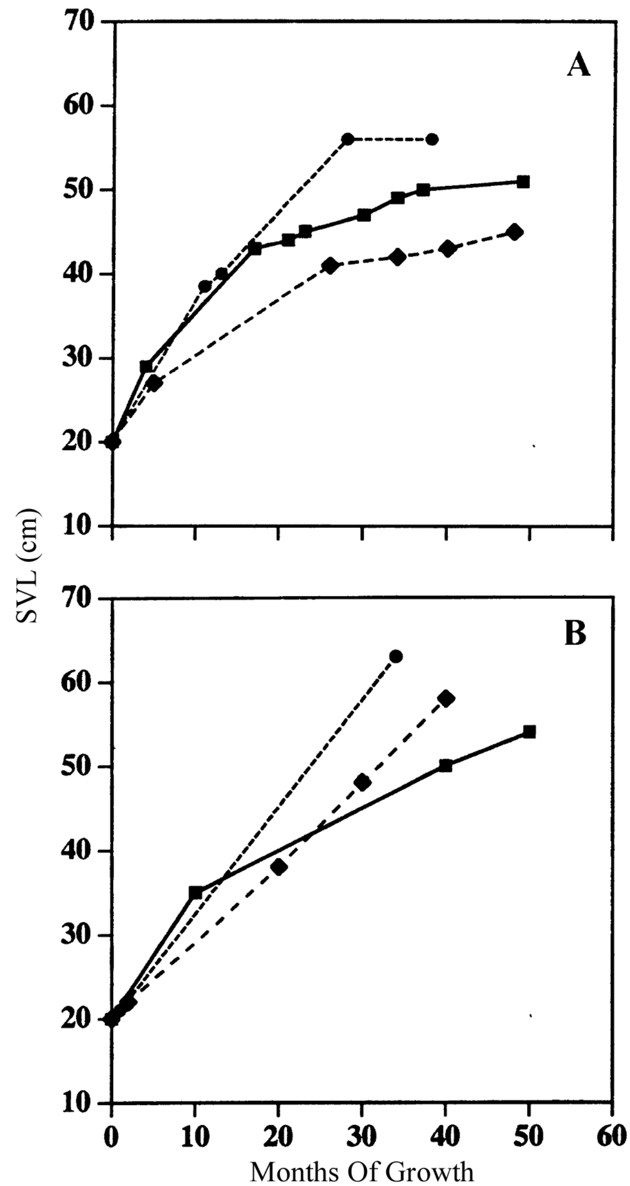

Fig. 6. Growth of female (A) and male (B) *Agkistrodon piscivorus leucostoma* of known age from Sheff's Wood during months of active growth (March to November). Symbols denote individual animals.

Growth

The growth of unsexed neonates is shown in Figure 5. Snout-vent length varied up to 15 cm (25 to 40 cm) within the first year. The growth of three females of known age and growth of three males first marked as neonates are shown in Figure 6. Males continued to grow at older ages and reached a larger size than females. The SVL of these three males had not become asymptote by the last capture date when they were six-years-old. Fourteen females in the population that had slower growth rates averaged 57.5 cm SVL.

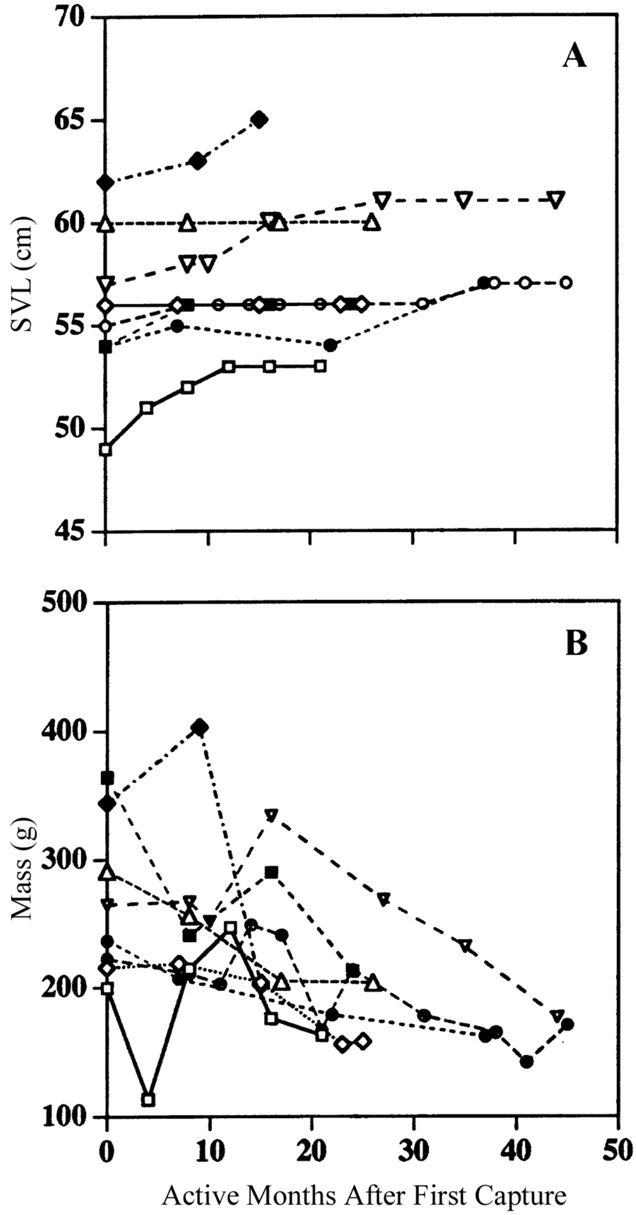

Fig. 7. Changes in SVL (A) and mass (B) of female *Agkistrodon piscivorus leucostoma* from their first capture.

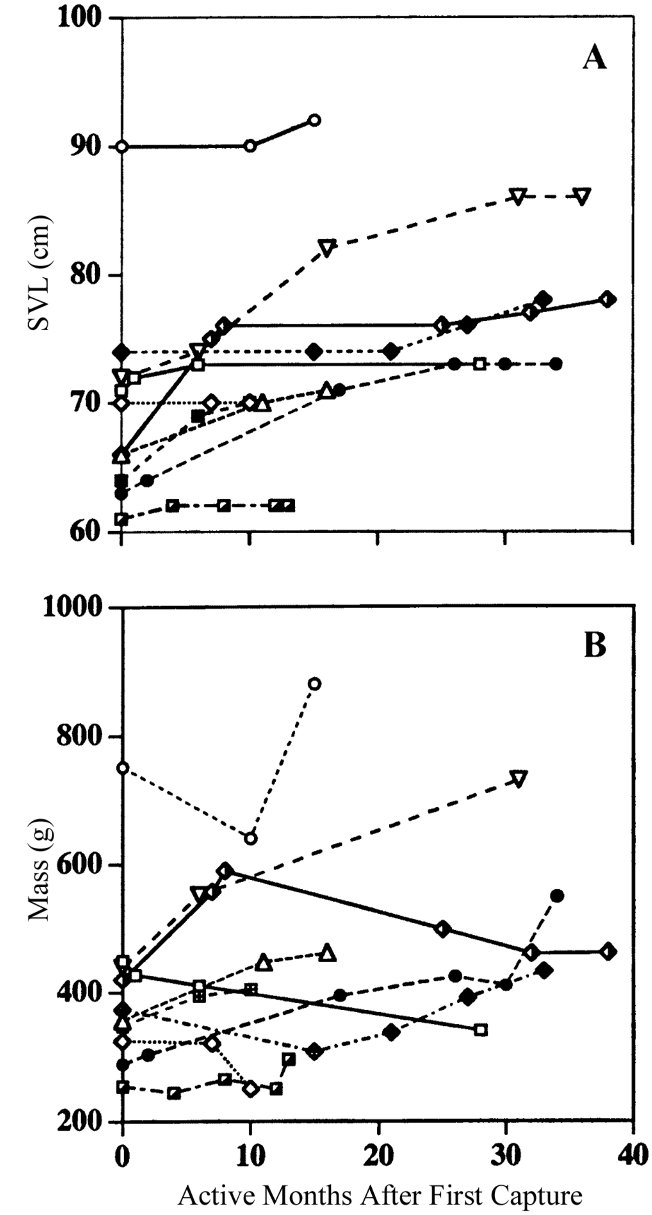

Fig. 8. Changes in SVL (A) and mass (B) of male *Agkistrodon piscivorus leucostoma* from their first capture.

The SVL of females first caught as adults rarely increased in recaptures (Fig. 7). Also, female mass fluctuated greatly within and between years (Fig. 7). Only five females were found over 60 cm SVL, whereas six adult males in the population were greater than 70 cm SVL with masses exceeding 800 g (Fig. 8). Male masses were more static over time. If these larger males and females were at least three years of age at first capture (most were likely several years older) then some were at least nine years of age at the time of their last recapture.

DISCUSSION

The capture of snakes in drift fences is not a fail-safe method to examine all aspects of their ecology. When traps are placed in a variety of habitats and used in conjunction with mark-recapture techniques over long periods, this technique can provide insight into population dynamics. Plummer and Parker (1987) stressed that indicating population sizes of snakes in the absence of long-term studies is inappropriate, yet in most reports *A. piscivorus* is considered to be abundant without such data. Barbour (1956) indicated

Table 2. Reproductive characteristics of *Agkistrodon piscivorus leucostoma* from Sheff's Wood collected in 1989 and 1990. Mean ± SD for eight females is given. Correlation coefficients (R) are for each trait relative to female SVL.

Female SVL (cm)	Female mass (g)	Litter size	Neonatal SVL (cm)	Neonatal mass (g)
57.9 ± 3.19	213 ± 19.6	5.0 ± 1.22	20.7 ± 0.89	14.9 ± 2.49
	R = 0.61	R = 0.58	R = 0.12	R = 0.18

Table 3. Annual survivorship data for *Agkistrodon piscivorus leucostoma* at Sheff's Wood. Numbers recaptured/number marked and percent recaptured in the following year and all years after marking are given.

		35-50 cm		> 50 cm	
Year	Juvenile	Female	Male	Female	Male
1989					
Next year	3/12 (25%)	2/6 (33%)	1/6 (17%)	5/5 (100%)	7/9 (78%)
All years after	4/12 (30%)	2/6 (33%)	3/6 (50%)	5/5 (100%)	7/9 78%)
1990					
Next year	0/6 (0%)	7/9 (77%)	3/4 (75%)	8/12 (67%)	10/13 (76%)
All years after	3/6 (50%)	8/9 (89%)	3/4 (75%)	9/12 (75%)	11/13 (85%)

that *A. p. piscivorus* occurs in high density (300 per acre) near a pond in Kentucky. Gloyd and Conant (1990) suggested that all subspecies of *A. piscivorus* may occur in high numbers in ideal environments. The present 14-year-old study showed that *A. piscivorus* can show dramatic yearly variation in population density. In addition, seasonal activity patterns suggest that behavior has a major impact on apparent abundance. Life history traits, such as survival and growth, showed characteristics that would require multiple years of study to be accurately addressed (see Seigel and Pilgrim, this volume). The current study also indicates that short-term data on individuals (i.e., mortality, estivation times) are important too, and techniques such as radiotracking of individuals would have been necessary to get satisfactory resolution to those kinds of questions. With such constraints in mind, it is worthwhile to make some evaluations of the ecology of this species in northeastern Texas.

Although equivalent numbers of drift fences were located in two upland sites, and some in transition areas within several hundred meters of the lowland, *A. p. leucostoma* was never recorded in any other trapline in the preserve. Twenty-one other species of snakes have been documented at Sheff's Wood, 17 of those occurring in the lowland area. Yellow-bellied Watersnakes (*Nerodia erythrogaster flavigaster*), Broad-banded Watersnakes (*N. fasciata confluens*), Diamond-backed Watersnakes (*N. r. rhombifer*), Gulf Crayfish Snakes, (*Regina rigida sinicola*) and Western Mudsnakes (*Farancia abacura reinwardtii*) are other semi-aquatic snakes found in the preserve, but only *N. fasciata confluens* showed the same restricted habitat utilization. From this and observations at other sites, it appears that *A. p. leucostoma* in northeastern Texas predominantly occurs in lowland, hardwood forests.

Initially, *A. p. leucostoma* often appears abundant at sites in northeast Texas, but the results from this study suggest that it can be relatively sedentary and thus the same individuals may be seen on repeated visits. At Sheff's Wood, for example, one female was captured 17 times in one summer. In addition, because the site was bordered by farmland and upland forests less suitable for *A. piscivorus*, it appears that this population is restricted to the small 10 ha bottomland areas. Indeed, new unmarked adult immigrants were rare, but some individuals, nonetheless, disappeared for long periods. In an ongoing study in another eastern Texas bottomland (Old Sabine Bottomland Wildlife Management Area), it appears that watersnakes (*Nerodia*) move greater distances than *A. p. leucostoma* on a daily basis (M. Doles pers. comm.). Obviously, their types of movement patterns influence the perception of snake abundance during short-term observations.

Even with capture-recapture data, population estimates of *A. p. leucostoma* at Sheff's Wood ranged widely, from 130 to 370 individuals (Table 1). Some variation may be due to violation of an assumption of the Schnabel method (e.g., no addition or removal of individuals during sampling). I suspect, however, that much of the variation is likely related to factors of trapping technique. The lowest numbers occurred during the first few years of the study, when most of the drift fences were several hundred meters up from the pond. The later estimates mirror the increase in capture rates per line, when additional lines were added closer to the water sources. This variation in population estimates may indicate the collection of new animals occurring only near the pond or reflect some variation in snake activity there. Alternatively, the increase in numbers could relate to some unknown factor in the environment. What might produce a rapid short-term increase in *A. p. leucostoma* in a limited area is unknown, but possibly some individuals were inactive at the beginning of the study.

Acknowledging the unknown causes of variation in numbers, the density of *A. p. leucostoma* for most of these 14 years is still much higher than any numbers/ha recorded for viperids (1–14 individuals/ha in Parker and Plummer, 1987). Sheff's Wood had about 30 individuals/ha the first years of the study, and in succeeding years, densities over 70 individuals/ha. Using similar techniques, Fitch (1960) found that a congener, the Copperhead (*A. contortrix*), exhibited a density of only 6–9/ha in eastern Kansas.

The proportion of marked animals captured each year increased in a linear fashion (Fig. 2). The cumulative recapture rate for *A. p. leucostoma* was nearly 75%, a higher level than is typical for snakes (Plummer, 1997). This high recapture rate suggests fidelity of individuals to the area, as most were eventually recaptured. Some *A. p. leucostoma* were captured infrequently (even less than yearly), whereas a few were recaptured on nearly a monthly basis. This indicates variation in the movements of individuals, with some staying near the drift fences and others only occasionally present in the area.

The decrease in percentage of recaptures in 1989 is explained by the new animals collected using the additional lines, but the reason for the drop in 1992 is unknown. It is especially noteworthy that in the last two years of the study, only two individuals were captured (Fig. 1). In 1995, the winter drought had a major impact on the number of individuals recorded in the next two summers, but whether the snakes died or emigrated is unknown. It seems unlikely that all could remain dormant in the area and not be recaptured (sighted) for two seasons. Interestingly, the water in the spring-fed creek continued flowing throughout the drought and the pond was nearly full, so actual lack of water was not the cause of their disappearance. The density of snake species at Sheff's Wood was not affected similarly. Indeed, a large number of unmarked adult *N. erythrogaster* were collected in the upland drift fence lines in the year following the drought. These snakes may have been the result of animals leaving the surrounding farm ponds due to the drought and entering Sheff's Wood looking for water sources. In any case, the dramatic difference in the number of *A. p. leucostoma* in these years underscores the importance of long-term ecological studies.

Seasonal Activity

It is evident that adult females are more active than adult males in the spring (Fig. 3). Most likely these individuals were foraging, as many had food in their stomachs when they were collected. Female vipers are known to eat in the spring (Andrén and Nilsen, 1983) even when pregnant later that year. Males were trapped more frequently at Sheff's Wood in August and September. Although it is not known when mating occurs in this population, *A. piscivorus* in Alabama breed in late summer and it is possible that these males were moving around in search of females (Johnson, et al., 1982). The increased proportion of neonates in the late summer and early fall obviously relates to parturition dates. The increase in older juveniles in September and October likely relates to active foraging on Bronze Frogs (*Rana c. clamitans*) that were evident in large numbers during that season.

It is useful to examine the activity peaks of *A. p. leucostoma* at Sheff's Wood, as seasonal patterns of snakes often show a unimodal mid-summer peak, or a bimodal pattern with peaks in the spring and fall (Gibbons and Semlitsch, 1987). Adult females and males showed unimodal patterns with more females collected in May and June, but male numbers peaked in August and September. Interestingly, no other species in the preserve were active in mid- and late summer (Ford et al., 1991). Juveniles of *A. p. leucostoma* showed the bimodal pattern, like most of the other snake species at Sheff's Wood. In the preserve, July and August were the hottest and driest months, and very few snakes except for *A. p. leucostoma* were collected during this period (Ford, et al., 1991).

Reproduction

Dates of parturition and litter sizes for *A. p. leucostoma* in this study are similar to those of populations of this taxon from other localities (Fitch, 1985; Gloyd and Conant, 1990). Comparable offspring sizes for the subspecies are not available, but the neonates in this study were smaller than the eastern subspecies (Wharton, 1966). Although offspring from different females varied in SVL, particularly in mass (12.3 to 18.9 g; Table 2), offspring SVL was not correlated with female size (Fig. 4). This was based on only eight females, but the fact that this contrasts with the Adder, *Vipera berus*, (Andrén and Nilsen, 1983) in Sweden, the Southern Copperhead (*A. c. contortrix*) from Sheff's Wood (Ford et al., 1990), and the Eastern Cottonmouth (*A. p. piscivorus*) in Virginia (Blem, 1981), is interesting.

Survival

Limited conclusions about annual survival in this species can be made from this study. The minimum value for neonates surviving their first year in 1989 and 1990 was 30 and 50%, respectively, which is high relative to other snakes. For example, in a mark-recapture study of the cryptic Rough Greensnake (*Opheodrys aestivus*), Plummer (1997) found only a 20% first year survival rate. Most researchers working with New World gartersnakes (*Thamnophis*) have first year annual survival rates of less than 20% (Bronikowski and Arnold, 1999). The fact that offspring may gain protection by being venomous may explain their higher annual survival. A small sample of adults also showed high annual survival (75–100%, Table 3). Some animals captured as adults were given a minimum age for their size, and many of the snakes were at least nine years old at the end of the study. One important point about the analysis of annual survival was that several individuals were not recaptured in the first year after marking, but rather three or four years later. A two-year study, for example, would have significantly underestimated annual survival both in neonates and adults.

Growth

Newborn *A. p. leucostoma* were born ca. 20 cm in SVL and ca. 16 g (Table 2). In some years, they grew rapidly in their first fall and spring. In other years, growth rates were much slower, and animals not much larger than neonates were found the next summer. The prey of neonates was likely heavily impacted by the occurrence of fall rains. When rains occurred, large numbers of newly metamorphosed *R. c. clamitans* were present, but in dry years this species was rarely observed. By the middle of their first full season, *A. p. piscivorus* varied in SVL by as much as 10 cm. Accurate aging of any animal over 30 cm was difficult (they could be from two to 12 months old; Fig. 5) and thus was not done. Favorable prey abundance early in life may exert long-term effect on the growth trajectories of Water Pythons, the so-called "silver spoon" effect (Madsen and Shine, 2000). The silver spoon effect may explain the continued rapid growth of some, whereas others grew much slower. In addition, the asymptote of females at different SVLs might also relate to juvenile growth rate. However, because only three males and three females were marked as neonates and recaptured multiple years later, it is not possible to determine if early rapid growth ultimately contributes to greater maximum size.

Both sexes grew at approximately the same rate for the first three years (Fig. 6). Females began to slow their growth at an age of about 24 months, and their SVL becomes asymptotic between 40 and 55 cm. The fastest growing females, therefore, matured as early as three years, but slow-growers take eight years or more. Burkett (1966) suggested that *A. p. leucostoma* matured at two and one-half years at 45 cm SVL. Since Sheff's Wood females were mature and reproductive at 54 cm, slower growth after that size is likely explained by the energetics of reproduction (e.g., vitellogenesis). Note from Figure 7 that older females tended not to grow in length after reaching a SVL of 55 to 60 cm. As mentioned above, the final size might relate to rapid early growth, but it could alternatively relate to when the female produced her first litter. A female that waited an additional year to reproduce could continue to grow, and since litter size is correlated with female SVL she would thereafter be able to produce larger litters. Although the early breeder would have a year's head start on total reproduction, the late breeder could quickly catch up (see Ford and Seigel, 1994 for a discussion of this dichotomy of strategies).

Female mass fluctuated both within and between years, as a result of reproductive events (e.g., pregnant vs recently parturient; Fig. 7). Males continued to grow even after 4 years-of-age to at least the 70 cm range before slowing (Fig. 8), and some males grew larger than 80 cm SVL. Based on the literature, males attain sexually maturity at about 55 cm (Burkett, 1966), and males of this size were often found in traps with adult females, suggesting they were trailing the females. Because *A. piscivorus* exhibits combat behavior, sexual selection for large body may explain their continued growth (Blem, 1987).

CONCLUSIONS

Although *A. p. leucostoma* is not uncommon in northeastern Texas, the results of this study show how general impressions and studies of short duration of snakes can be misleading, causing either gross overestimation or under-representation of numbers of species and/or density. Bottomland forests in this region are being heavily impacted by hardwood logging, and many of the remaining larger bottomlands have been flooded by reservoirs and impoundments. It seems likely that *A. p. piscivorus* is undergoing declines, and the probable future for the survival of this snake in northeastern Texas will likely depend on the presence of large protected bottomlands.

Acknowledgments.—I would like to thank all the students that have helped me collect snakes in Sheff's Wood over the years, especially Vincent Cobb, Linda Allen, Debra Lancaster, Cherri Bell, and Sean Walker. My wife, Joan, and my son, David, also often helped check the traps and I thank them for their companionship. Richard Seigel helped with statistical analysis and a review of the manuscript. Rod Whittenburg and Rita Mehta also reviewed a draft of the manuscript. The Texas Nature Conservancy provided funds for establishing the drift fences at the preserve, as did the University of Texas at Tyler Faculty Research fund. Finally, I would like to thank Gordon Schuett, Mats Höggren, Michael Douglas, and Harry Greene for the opportunity to compile this report.

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