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

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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 at 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

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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 | 106.1, 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.

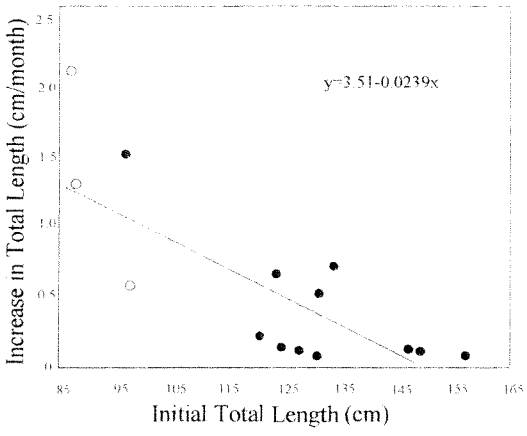


FIG. 1. Length increases of native (closed circles) and captive-bred (open circles) *Pituophis ruthveni* according to total length. Each symbol identifies the approximate growth rate of an individual snake. Regression line: y = 3.51 − 0.0239x.

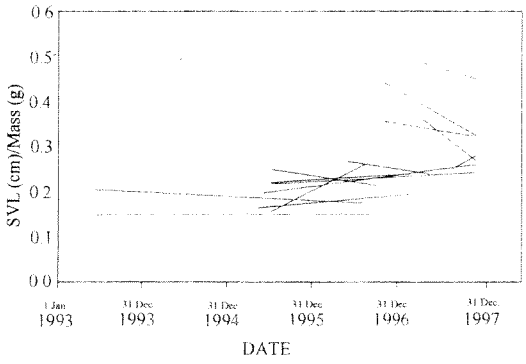


FIG. 2. Growth rates of *Pituophis ruthveni* ($N$ = 14). Lines represent individual adult snakes; dashed lines represent juveniles (all females).

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 (0.11–0.65, $N$ = 3), respectively. There was a negative relationship between increase in total length per month and total length of individual native ($N$ = 11) and captive-bred ($N$ = 3) snakes (Fig. 1; Table 1).

*Mass.*—Mean mass change (g) per month was 0.22 ± 6.81 (−30.04 to 18.25, $N$ = 14). Mean change in mass per month of juvenile snakes was 9.38 ± 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

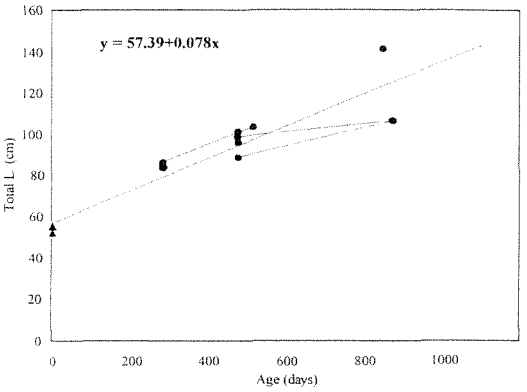


FIG. 3. Growth rates of nine individuals of *Pituophis ruthveni* of known age. Closed circles are captive snakes released during this study. Lines join two measurements of three individuals. The triangles represent four hatchlings (Reichling, 1990). Regression line: $y = 57.39 + 0.078x$.

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.

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