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Size and Age Structure of a Population of Western Terrestrial Garter Snakes (*Thamnophis elegans*)

HEATHER L. WAYE

The age structure of a population can reveal trends in growth and maturation and be used to describe other demographic processes. Accurate descriptions of age structure for populations of snakes are rare, limiting our ability to understand their population dynamics. In this study, I used skeletochronology to determine the age of individuals, and examined the relationship between age and size, in a population of western terrestrial garter snakes (*Thamnophis elegans*). Most of the adult snakes had between two and six growth layers, and the youngest gravid female had three growth layers. Although lengths and number of growth layers were positively correlated, it would not be possible to predict the age of an individual from its length.

DETERMINATION of the age of individual animals is an important component of the study of populations, because demographic processes (e.g., fecundity and survivorship) can be age specific. Knowledge of age structure therefore can yield essential data on the dynamics of the population and life history of the species as a whole (Parker and Plummer, 1987). Individual and population-specific patterns of growth and maturation, and individual and year-specific variations in these patterns, also can be determined if age structure is known; this information allows the dynamics of populations to be modeled and projected into the future more accurately. Besides contributing to our understanding of the fundamental ecological issue of limitation of distribution and abundance, such knowledge is critical to management or conservation plans for many species. Accurate data on age rarely have been collected for populations of snakes, greatly limiting our understanding of their population dynamics and life histories.

Skeletochronological determination of age has been verified for species in which toes or claws can be removed in subsequent years without sacrifice of the animals [e.g., *Bufo bufo* (Hemelaar and van Gelder, 1980), *Bufo calamita* (Tejedo et al., 1997), *Rana catesbeiana* (Schroeder and Baskett, 1968), *Rana temporaria* (Hemelaar, 1981), and turtles (Thomas et al., 1997)]. However, in the few studies in which this technique has been verified in snakes, the study animals all were sacrificed to obtain vertebrae or ectopterygoid bones (Castanet and Naulleau, 1974; Minakami, 1979), making the method unsuitable for use in long-term studies of population dynamics. For snakes, the only structure that can be removed very easily without sacrificing the animal is part of the tail. Jayne and Bennett (1989) found that 33% of the tail of garter snakes can be removed without affecting their

speed, making this a feasible way of obtaining bone for determining ages of living snakes. Whether removal of part of the tail affects other aspects of snake behavior (e.g., mating ability) is not known, but natural loss of the tail tip is common in most populations of garter snakes (unpubl. data; P. T. Gregory, pers. comm.).

My specific objectives were to test, by mark-recapture in the field, the hypothesis that growth rings are annual and to use skeletochronology to determine the age structure of a population of western terrestrial garter snakes (*Thamnophis elegans*) and examine relationships between life-history parameters and age and size in this population.

MATERIALS AND METHODS

The study site was the Canadian Wildlife Service wildlife reserve at the mouth of the Little Qualicum River, just north of Qualicum, British Columbia, Canada (49°24'N, 124°37'W). The first field season started at the end of March 1994. I captured snakes by hand while walking around the site, and each snake was given an individual mark by clipping a unique combination of subcaudal scales (Blanchard and Finster, 1933). The snout-vent length (SVL) and total length were measured to the nearest 5 mm, the snake was weighed to the nearest gram with a Pesola® hand-held spring scale, and the sex, coloring, markings, scars, and general condition of the snake were noted. Finally, the distal portion of the tail was cut off, using scissors cleaned in 70% ethanol. The length of the clipped portion varied, depending on the snake's length and whether the original tail was whole or not. Not more than one-third of the tail was taken and generally much less than that; on an adult snake, about 15 mm usually was removed from the tip of the tail. Several snakes were not sam-

pled at all, because too much of the tail was already missing. About 5 mm of the cut end of the piece of tail was removed and placed in 10% formalin in a labeled glass vial, and the rest was placed in a cryovial and stored in liquid nitrogen for DNA analysis in another project. During the second field season, any snakes that had been marked in 1994 and recaptured in 1995 were resampled by removing another small piece of tail, to determine whether one more ring had been added.

Samples were left in 10% formalin for at least 24 h, then soaked in water for several hours and placed in 70% ethanol until further processing. Embedding and sectioning followed standard histological techniques, and the slides were stained with 1% toluidine blue in 1% sodium borate. The growth layers were counted and verified as described in Wayne and Gregory (1998, see fig. 1 of that paper for a photograph showing growth layers).

RESULTS

I collected a total of 192 *T. elegans* from 29 April to 10 October 1994 and 25 March to 24 September 1995. Tail samples were not taken from three female *T. elegans*, because most or all of the tail was already missing. I read 92 bone samples from females and 75 from males (some bone sections failed to show any readable layers).

I recaptured 12 snakes in 1995 that originally were sampled in 1994 (eight female, four male). The difference between the two ages based on the number of growth layers was not significantly different from one year [paired *t*-test: $P(t_{0.05(2)11} \geq 0.4318) > 0.5$]. The patterns of the growth layers could be followed from the 1994 sample to the 1995 sample, even when the actual number of layers was difficult to count. Three of the 1995 sample had a false dark layer just inside or along the last layer, possibly a result of the trauma of the first sampling of the tail.

Very few snakes less than 300 mm SVL were captured; the majority of males were in the 325–500 mm SVL range and most of the females were between 400–700 mm SVL (Fig. 1). I combined the 1994 and 1995 length measurements to produce these size-frequency histograms because the rate of growth between the start of one season and the end of the same season would be more than that between the end of the first season and the start of the second and to increase sample size. Females attained greater lengths than males; many of the larger females were over 600 mm SVL, whereas none of

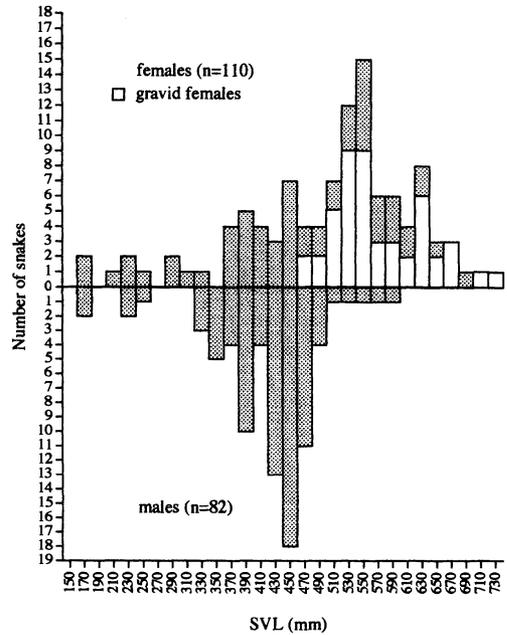


Fig. 1. Size frequency distribution of male and female *Thamnophis elegans* (1994 and 1995 lengths combined, not including recaptures). Bars are labeled at the middle of each interval.

the males reached this length. The two small clumps of individuals at 170 mm and 230 mm could indicate neonates and one-year olds (one hibernation), but any older putative age classes are impossible to define from these data. The smallest gravid female was 470 mm SVL, and there were gravid females throughout the distribution of body sizes above that.

The age-frequency distributions for 1994 (the 1995 ages were reduced by one and added to the 1994 ages) show some features that correspond to the size-frequency distributions; two neonates captured in 1995 were lost from this sample (Fig. 2). There were few individuals in both the smaller size classes and the lower age classes, although the numbers do not match perfectly. Most of the male and female snakes had undergone between two and six hibernation periods, with most of the males showing two, three, or four layers and most of the females showing three, four, or five layers; the youngest gravid female had three layers.

The SVL and the mass of the snakes compared to the number of layers showed a positive linear relationship with a large amount of scatter (Fig. 3). Each regression was significant. As the snakes get older and larger, the data points spread out more, indicating variability in individual growth rates. The average SVL in each age class increases in both males and females to

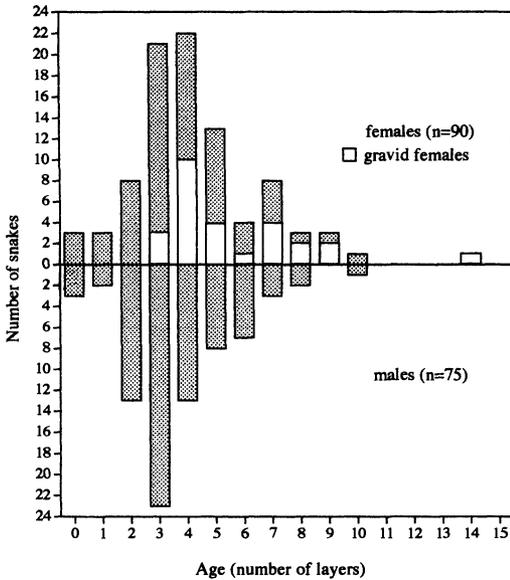


Fig. 2. Age frequency distribution of male and female *Thamnophis elegans*. Ages for 1995 samples were added to this figure by subtracting one to obtain the 1994 age. Only females that were known to be gravid in 1994 were included in the gravid female sample.

the fourth hibernation, then does not show much relationship to age (Fig. 4). The average female SVL is greater than the average male SVL for most age classes, although the 95% confidence limits overlap between males and females in most of the age groups, especially those with few individuals.

DISCUSSION

Reptiles generally show rapid growth to the time of first breeding, and from then on growth is slower. In those species that have been studied carefully, considerable variance is seen in the body size of individuals that have reached age of first breeding, and this variance is presumably maintained through the later age classes (Parker and Plummer, 1987). Body size and fecundity usually are positively correlated, at least in females, so it is important to know whether body size is a function of age or of early growth (Halliday and Verrell, 1988).

Adult female *T. sirtalis* in Manitoba grow faster than adult males (Gregory, 1977), and juvenile females have been found to grow faster than males in the first month after birth (Crews et al., 1985). The adult female *T. elegans* at Qualicum are on average larger for a given age than the males, which is consistent with other populations of garter snakes (e.g., Kephart, 1981, cited in Parker and Plummer, 1987); early growth

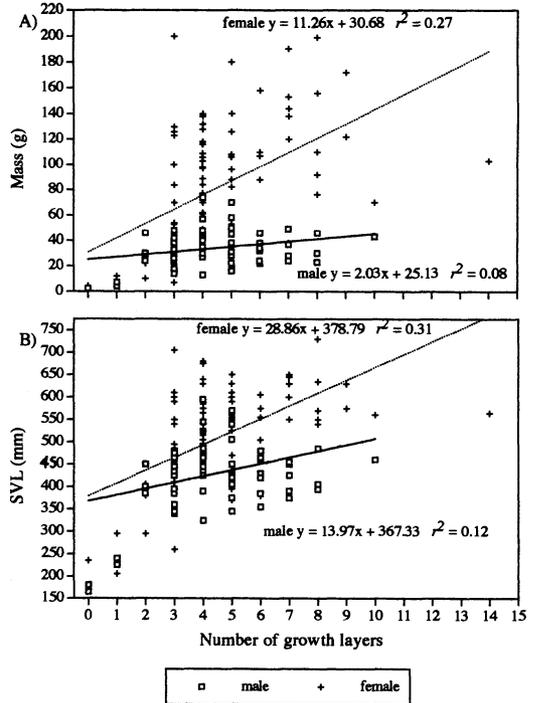


Fig. 3. Relationship between (A) age and mass and (B) age and length for male and female *Thamnophis elegans*, 1994 and 1995 combined.

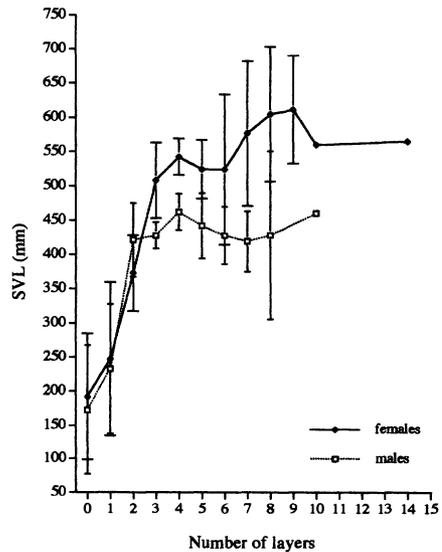


Fig. 4. Average snout-vent length for each age class, and 95% confidence limits, for male and female *Thamnophis elegans*, 1994 and 1995 combined.

is similar between the two sexes, as also shown by Gregory and Prelypchan (1994) for the same species. The growth rate generally slows after maturity is reached, then slows again after about the fifth hibernation. There appears to be only a rough correlation between the age of a snake and its size, especially after maturity is reached. The plot of SVL against number of layers suggests that the oldest snakes are not necessarily the longest; this could indicate that slower-growing snakes live longer.

Size-frequency data are occasionally used to define putative year classes (Parker and Plummer, 1987), and the first two year classes indeed could be defined from my data for *T. elegans*, but any older groups are impossible to define because the bulk of the snakes of 350 mm SVL and longer are mixed together. Age groups have been crudely estimated for *T. sirtalis* in Manitoba by Gregory (1977) but only by using body size. He found considerable overlap of size classes, especially in females, that made division into discrete classes difficult.

Males probably mature after two hibernations and females after three. The high number of two- to four-year-old males and three- to five-year-old females in the sample is possibly due to sampling bias; reproductive males and females are easier to find and catch, the males at the den sites in the spring and fall and the gravid females basking in the middle of summer. Parker and Plummer (1987), looking at medium-sized viviparous colubrids in general, found that females mature at about three years of age, whereas males are a year younger at maturity. In general, female *T. elegans* seem to live longer than the males; alternatively, older females are caught more often than older males.

Other studies seem to have found significant correlations between number of layers and size or age (e.g., Verrell and Francillon, 1986; Parham et al., 1996). I also found a significant relationship between number of layers and SVL and mass, but it is doubtful that this relationship could be used to predict age accurately from size for *T. elegans*.

The record for longevity in captivity for a garter snake is 15+ years for a *T. ordinoides* (Slavens and Slavens, 1992); the oldest female that I caught was gravid at age 14, suggesting that these snakes can reproduce many years after they mature. It is uncertain whether reproductive events have an effect on the number of layers that are recorded in the bones of females. I did not see any particular spacing patterns between the layers of females that would indicate this, but it is something to consider. Bone-marking of a population of snakes over several years

with oxytetracycline or another label would help to resolve this question; if certain years show two growth marks, and the individuals were known to be gravid in those years, then reproductive marks could be confirmed.

It is likely that many life-history parameters of garter snakes are more dependent on size than on age, but to prove this, the age of individuals must be compared with their size and with the parameters related to each. In this study, I have shown that size and age are not closely related in garter snakes, so any complete analysis of their demography will demand further attention to separating age-specific from size-specific effects.

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