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Seasonal Sexual Cycle of *Nerodia taxispilota* (Serpentes: Colubridae) At The Northeastern Edge Of Its Range

By
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Seasonal Sexual Cycle Of *Nerodia taxispilota* (Serpentes: Colubridae) At The Northeastern Edge Of Its Range

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Abstract

The seasonality of the sexual cycle of *Nerodia taxispilota* at the northeastern edge of its range was elucidated from specimens collected over a two-year period (1978-1979) from the Appomattox River near Hopewell, Virginia. The investigation centered on morphological changes in the testis of males and vitellogenesis and embryo development in females. Related reproductive parameters also studied were body size differences, seasonal sex ratios, comparative tail lengths, and tail mutilation.

Male and female cycles closely resembled those of other temperate zone colubrids. Spermatogenesis began in May and testis size peaked in late August. Testis length showed a time lag when compared with weight and volume. Sperm produced during summer were stored in the vas deferens through winter and used the following spring. The female cycle is apparently annual. Vitellogenesis occurred only in spring, ovulation was in mid-June, and parturition was probably in late August or early September. The number of young increased with increasing female body size with mean clutch size of full-term embryos 28.0.

Females were generally larger than males. Sex ratio was about 1:1 in spring and summer, however males predominated in fall. Males had comparatively longer tails than females. The amount of tail breakage was about equal for both sexes.

Introduction

Nerodia taxispilota (Holbrook), brown water snake, is a member of the North American genus of semiaquatic snakes that belongs to the large cosmopolitan family Colubridae. *Nerodia taxispilota* range from the southern tip of Florida and southeastern Alabama north to southeastern Virginia, chiefly in the coastal plain; occasionally ascending streams into the Piedmont (Conant, 1975). In Virginia, sympatric species include *Nerodia sipedon sipedon*, *Nerodia erythrogaster erythrogaster*, and *Agkistrodon piscivorous piscivorous*.

Fitch (1970) summarized the literature on reproductive cycles of snakes and lizards. He presented relatively extensive information for some species, but, for *N. taxispilota* he cited only the works of Franklin (1944) and Duellman and Schwartz (1958). Franklin (1944) reported the breeding season of Florida populations was in late May, parturition occurred in August, young were born out of water, and brood size ranged from 30-40 young. Duellman and Schwartz (1958) reported one brood of 16 young from a female captured in southern Florida.

Fitch (1970) stated that *N. taxispilota* was the geographical representative of *N. rhombifera*, an allopatric species whose range juxtaposes that of *N. taxispilota* in southeastern Alabama. He proposed that the two should be considered conspecific because of their ecological similarities. Mount and Schwaner (1970) considered them to be distinct species, after studying the distribution and ecology of each. They found no overlap in distribution and no significant evidence of overlap in several morphological and meristic characters. The only study to date on the life history of *N. taxispilota* is that of Herrington and Batson (1979), who concentrated on populations in the southern part of the range in central Georgia. Variations in important factors in the life history of a species emerge at the extremes of the range. It is the purpose of this study to document the seasonal sexual cycle of *N. taxispilota* at the northern limit of its range. Included are investigations of seasonal morphological changes in the testis of males, and seasonal vitellogenesis and embryo development in females. Additionally, the reproductive related parameters of body size differences, sex ratios, comparative tail length, and tail mutilation are considered.

Methods and Materials

One hundred six brown water snakes were collected over a two-year period in 1978 and 1979. Twenty-seven were taken on six trips from 27 May to 12 September, 1978; 79 on 16 trips from 11 May to 9 November, 1979. Areas sampled were the Appomattox River in Chesterfield County, Virginia between Hopewell and Colonial Heights, and Swift Creek in Chesterfield County between Interstate 95 and its confluence with the Appomattox River (Fig. 1). Collecting procedure was to move slowly downstream in a canoe and remove basking snakes from overhanging branches with Pillstrom tongs. Ninety-seven snakes were caught with this procedure; nine were taken from the banks and water. Specimens were placed in a metal box and transported to the laboratory where they were preserved, if not the same day, within two days of capture. Field notes included water and air temperatures (^{o}C), weather conditions, time of day, and activity of snakes when captured, e.g., basking or swimming. A record was made of other vertebrates seen in the vicinity.

Snakes were killed with ether-soaked paper towels that were placed in the metal box. Most of the snakes succumbed within 4-10 hours. The long period of time required for their death is attributed to the ability of water snakes to hold their breath for an extended period of time (pers. comm. Dr. Gerald C. Schaefer, former asst. prof. of biology, Univ. of Richmond). Sacrificed snakes were gently stretched, allowed to relax, and measurements were made of snout-vent length (SVL), tail length, and total length. As tail breakage has been used as an indicator of predation in snakes (Zug et al., 1979), tails were examined for completeness. Specimens were tagged and cut from vent to heart and placed in 10% formalin. Sex of the individual was confirmed and stomach contents were noted. Stomach contents were removed after the digestive tracts of several snakes ruptured and spoiled the reproductive system.

Reproductive systems were examined after all preservation was completed. This improved consistency between individual examinations. Snakes were transferred from formalin to a permanent preservative of 40% isopropyl alcohol. The entire reproductive tract of females, and the right testis and a 2-3 cm section of vas deferens of males were removed and stored in individually labeled jars containing 40% isopropyl alcohol.

The right testis was used to determine seasonality of male gonadal activity. Length (nearest mm) was measured with vernier calipers, weight (nearest mg) with an analytical balance, and volume (nearest .05 ml) by displacement of 40% isopropyl alcohol in a graduated cylinder. These values were divided by SVL to eliminate variation related to body size differences. Length and weight fractions were multiplied by 100 (vol. fractions by 1000) for the purpose of working with whole numbers, the computed ratio was used for comparative purposes. To determine maturity of males, a 3-4 mm section of vas deferens was squashed on a microscope slide. The tissue was stained with Toluidine Blue and examined under a microscope for the presence of sperm. If sperm were present, an estimation was made of the amount in the field of view and recorded as sparse, numerous, or abundant. The evaluation of seasonal gonadal activity was, with one exception, restricted to males judged mature by this technique.

Females were designated mature if yolking follicles and/or corpora lutea were present in the ovary. Ovarian follicles (yolking and non-yolking) and oviductal eggs and embryos were counted and measured with vernier calipers (nearest mm). Right and left sides of the system were considered separately except where ruptured oviducts prevented separate treatment. Where this occurred only the total number of oviductal eggs or embryos was noted. A description of the embryonic development of *N. taxispilota* is based on the embryos removed from gravid females at sequential intervals throughout the gestation period.

Statistical tests used in the analysis of data followed Zar (1974). The rejection level for statistical tests used in this thesis was P=.05, unless otherwise indicated.

Specimens used in this study will be deposited in the U.S. National Museum of Natural History.

Results

Although *N. e. erythrogaster* was not found in the area sampled, it is considered a sympatric species with *N. taxispilota* in southeastern Virgina. *Nerodia s. sipedon* and *A. p. piscivorous* were found along with *N. taxispilota* although the number of *A. p. piscivorous* seen during the two-year period (7) was considerably less than the number of *N. s. sipedon* (about 50) and *N. taxispilota* (194) encountered.

Body Size Differences

Gravid females were easily identified through a combination of large size and distention of the body that ended abruptly at the vent. Non-gravid females and males of similar size differed in appearance only at the base of the tail. In males, the base of the tail was stout and did not taper before 30-50 mm behind the vent. In females there was a uniform tapering of the tail beginning at the vent. This characteristic was not always apparent on small specimens (<500 mm SVL).

Males ranged from 239 mm (newborn) to 814 mm SVL with the mean size of 59 males being 602 mm SVL. The smallest mature male was 503 mm SVL; all males larger than this were mature. Size frequency distribution of males revealed the majority (48 of 59) were 500 to 800 mm SVL with a mode of 22 between 500 and 600 mm SVL (Fig. 2). There was a steady decline in the number of males as the SVL increased.

Females ranged from 396-1100 mm SVL with the mean size of 47 specimens 762 mm SVL. The smallest mature female (725 mm SVL) was also the smallest gravid female. All 26 females above 725 mm SVL were mature; all but 5 were gravid. Females were evenly distributed throughout most of their size range; however, the mode (12) was in the 800-900 mm SVL range (Fig. 2). Mean female SVL was not significantly different from that of males (t-Test, t=0.21).

Sex Ratios

The sex ratio over the two-year collecting period was 1.25:1 (59 males, 47 females) and was not statistically different from a 1:1 ratio. Although chi square tests indicated that all calculated ratios (Table 1) were not significantly different from 1:1, there were some notable trends, seasonal breakdown revealed about 1:1 ratio in spring and summer, and a 2.5:1 ratio in the fall with a predominance of males (Table 1). Considering mature individuals only, the proportion of males to females increased from 1.4:1 in spring to 1.9:1 in summer, and to 3.0:1 in fall (Table 1). Immature females outnumbered immature males except in the fall (Table 1). The relative abundance of adults of both sexes (i.e., number of snakes caught per trip) declined from May to November. Females exhibited a higher rate of increasing scarcity than males.

Tail Length Ratios

Males were found to have proportionally longer tails than females in all size groups (Fig. 3). The ratio of tail length/total length in males ($\bar{x}=.2519$) was significantly greater than that of females ($\bar{x}=.2270$) at the $P=.001$ level.

Tail Breakage

The overall occurrence of tail breakage was about equal for males (13 of 59, 22%) and females (10 of 47, 21%) (Fig. 2). Frequency of broken tails was low in immature snakes (males, 0 of 8, 0%; females 2 of 20, 10%) compared to mature individuals (males, 13 of 51, 25%;

females, 8 of 27, 29%). In males, the frequency of broken tails steadily increased with SVL to 100% (3 of 3 males) over 800 mm SVL. Females showed a high degree of tail breakage (50%) in some size classes; but, unlike males, no consistent pattern was evident.

Male Reproductive Cycle

Testes of snakes captured from May to July were compressed, elliptical, and flat-white in color with little vascularization on the surface. Snakes collected from August through November had swollen, elliptical testes that were cream-colored and vascularized over the entire surface. Small sample size (2) of October and November collections precluded analysis of their significance although all three measured parameters showed a decline in the fall.

Testicular weight of snakes taken in July and August increased to a mean of 33.5 from a mean of 4.8 in June (Table 2; Fig. 4). Volume showed the same monthly pattern as weight, increasing from a low of 0.4 in May to a high of 3.7 in August (Table 2; Fig. 5). Weight and volume began to decline in September ($\bar{x}$=21.5, 2.4 respectively) (Table 2). Testis length showed a similar trend from June ($\bar{x}$=4.1) through August ($\bar{x}$=6.1);

however, there was a small decrease from May ($\bar{x}=4.3$) to June and a small increase from August to September ($\bar{x}=6.2$) (Table 2; Fig. 6).

Sperm was present in the vas deferens of mature males from May through November. There was no indication that size of the male was a factor in the relative amount of sperm. The amount varied with time of year: abundant in May and early June, sparse to numerous in late June and July, and abundant in August through November. The increase in the amount of sperm in the vas deferens from July through August corresponded to testis size increase over the same period.

Male size at maturity was roughly 500 mm SVL. Maturity was confirmed in 50 of 51 males over 500 mm SVL by the presence of sperm in the vas deferens. The one male without sperm in the vas deferens was considered mature because its testis length, weight, and volume ratios were equal to or greater than another male with sperm in the vas deferens caught the same day. None of the nine males under 500 mm SVL had sperm in the vas deferens. All were considered immature although four specimens, 443-488 mm SVL and captured in late summer and early fall, had enlarged testes when compared to males caught in May and June. Testis mean length, weight, and volume ratios (5.0, 5.1, 0.56 respectively) of these four snakes were about the same or slightly greater than those recorded for mature males taken in May and June; however, they were not as great as values for the testes of mature males caught at the same time. (Table 2).

Female Reproductive Cycle

Twenty-seven of 47 females captured were mature and 22 of these were gravid (i.e., yolking follicles or embryos present). The five that were not gravid were designated mature because they had corpora lutea present in the ovaries, an indication that they had developed a brood the previous year. They were designated non-reproductive (as opposed to post-partum) because the oviducts showed no sign of recent stretching to accommodate developing embryos. Fourteen of the 17 mature females caught in 1978 were gravid (83%) as were 8 of 10 mature females (80%) caught in 1979.

Ovaries contained two types of developing follicles. Non-yolking follicles were white, elliptical, and measured from <1 to 11 mm in length with a modality of 7-8 mm. All females, regardless of time collected, possessed this type of follicle; however, total number, maximum size, and size range showed a positive correlation with increasing SVL. Small females (400-500 mm SVL) averaged 44 non-yolking follicles, maximum size 4 mm; large females (>980 mm) had up to 141 non-yolking follicles (usually 90-100) of all sizes (1-11 mm).

Yolking follicles were yellow, elliptical, and usually larger (>12 mm) than non-yolking follicles. Vitellogenesis (yolk deposition) was evident on the earliest collection date (11 May) although it was difficult to distinguish yolking from non-yolking in follicles 8-10 mm long.

Developing follicles and embryos were separated into three size classes based on the stage of vitellogenesis and location of the developing eggs. Non-yolking follicles were designated class I, yolking follicles in the ovary (9-36 mm) class II, and oviductal eggs (24-49 mm) class III. Class I follicles were present in the ovary year around and class II from May to mid-June; class III eggs were present in the oviducts from late June to late August (Fig. 7).

Length of yolked follicles increased rapidly from early May ($\bar{x}$=9.6 mm) to mid-June ($\bar{x}$=29.2 mm) (Fig. 8). Eggs were transferred from ovary to oviduct in late June.

In 1978, yolking follicles were found in the ovary on 13 June and eggs in the oviduct on 27 June; in 1979, in the ovary on 8 June and in the oviduct on 23 June. Vitellogenesis was observed only in spring (May-early June). There was a positive correlation between the number of yolking follicles or embryos and female SVL (Fig. 9). The mean number of yolking follicles or embryos for 22 gravid females was 33.9 (range 19-63); however, the mean number of full-term embryos among five females caught in late August was 28.0 (range 19-41). The smallest gravid female (725 mm SVL) contained the smallest number of yolking follicles (19). The largest gravid female (1100 mm SVL) contained 52 oviductal eggs; however, the largest clutch (63 yolking follicles) came from a female 1057 mm SVL. It was possible to make separate counts of yolking follicles or embryos from right and left ovaries in 19 of 22 gravid females. The right ovary contributed the greater number (R. $\bar{x}$=19.3, range 11-41; L. $\bar{x}$=13.7, range 8-24) in all 19 specimens; nevertheless the difference between the means was not statistically significant. The right ovary averaged 58.5% of the total brood, the left 41.5%.

Corpora lutea were visible in the ovaries of non-gravid mature females caught from May to September, and in gravid females after ovulation. In gravid females, they were small ($\bar{x}$=3 mm), orange, irregularly-shaped bodies located among the non-yolking follicles. Corpora lutea of non-gravid mature individuals agreed in shape, color, and location, but they were smaller (<2 mm).

Twelve of 21 gravid females showed some degree of atresia of yolking follicles in the ovary or resorption of egg masses in the oviduct. Atretic yolks were irregular in shape, smaller, and darker than normal eggs or yolking follicles. The occurrence of females with atretic yolks was greater in June (9 of 9) than in May (1 of 5) or August (2 of 7).

Embryonic Development

The following description of embryonic development was based on morphological features of yolking follicles or embryos removed from all gravid females caught throughout the collecting period. Gravid females captured on the same day were similar in mean size of yolking follicles or in degree of embryonic development. The only exception occurred in the embryos of the two females captured 15 August 1978, which differed in stage of development. Numbers in parentheses beside each date indicate the number of gravid females caught that day. A sample of two to four embryos was removed from each female and their SVL or total length determined.

11 May 1979 (1). Yolking of follicles apparent, distinction of yolking or non-yolking difficult at 8-10 mm size; yolking follicles light yellow as opposed to white non-yolking follicles; $\bar{x}$ lg.=9.6 mm.

27 May 1978 (4). Difference between all yolking and non-yolking follicles distinct; yolking follicles elliptical; $\bar{x}$ lg.=16.8 mm.

8 June 1979 (3) and 13 June, 1978 (4). Yolking follicles distinctly yellow, elliptical, and greatly enlarged; $\bar{x}$ lg.=29.2 mm.

23 June 1979 (1) and 27 June, 1978 (1). Eggs transferred to oviduct, shape changed from elliptical to spherical; $\bar{x}$ diameter=27.1 mm.

9 July 1979 (1) Eggs approximately same size ($\bar{x}$=25.8 mm) as 23 June; first date embryos visible (diameter 6-7 mm), coiled on surface of yolk mass; tubular purplish body; white bulbous head distinct with little detail.

6 August 1979 (2) Embryos comprise 25-33% of egg masses; head distinct, jaws developed and movable, brain visible and distinct, eyes blue-black with white iris, body purplish, ventral scutes visible, segmentation (i.e., rib divisions apparent, embryo $\bar{x}$ total lg.=85 mm.

15 August 1978 (2) Embryos of smaller female (831 mm SVL) not as developed (oviductal egg $\bar{x}$ diameter=30.3 mm) as those of larger female (1024 mm SVL) with oviductal egg $\bar{x}$ diameter=34.8 mm (Fig. 8). Smaller female with embryos well formed but not complete, lateral and ventral surfaces distinct, body scales apparent with keels visible; brown blotch pattern beginning to form; head well formed but not complete, eyes still oversized in relation to head, brain with four lobes bulging slightly above top of head, head scales few with only upper and lower labials distinct, nostrils present; embryos average about 100 mm SVL.

Larger female with embryos almost complete; body blotch pattern strong but not as dark as adult, background color grayish-brown, blotches darker; ventral body regions translucent, dorsal and lateral surfaces opaque; head complete with all scales distinct, brain barely visible and no longer bulges above rest of head, eyes proportional to head; embryo and yolk each comprise 50% of oviductal egg; embryos average about 150 mm SVL.

23 August 1978 (3). Two females with some yolk remaining on embryos (yolk now 33% of oviductal egg), one female with no yolk remaining on embryos; all embryos complete with intensity of color-pattern similar to adults; head and body opaque and sharp in detail; embryos average about 185 mm SVL.

Early to mid-September. Parturition (see discussion).

Discussion

The finding that female *N. taxispilota* SVL ($\bar{x}$=762 mm) was greater than male SVL ($\bar{x}$=602 mm) is consistent with the data of Franklin (1944), and Herrington and Batson (1979). Other natricines show similar relationships (*Thamnophis* sp.-Tinkle, 1957; Fitch, 1965; *N. rhombifera*, *N. erythrogaster*-Burton, 1970; *N. sipedon*-Feaver, 1977). The lack of significant difference between mean size of males and females is attributed to a considerable amount of overlap in SVL between the sexes.

Explanations for sexual size dimorphism were recently proposed by Feaver (1977) who pointed out that few attempts had been made to explain it, although it was a well-known phenomenon. He found that sexual size dimorphism resulted from different adult growth curves, i.e., it is only after maturity that growth rates of males and females differ. Species were put into two groups according to the sex of the larger sized individuals, and life histories of the species in each group were investigated. From these, Feaver concluded that growth rates and sexual sizes were functions of reproductive strategies and types of mating behavior. The "male larger" group included crotalids, viperids, Elaphe-like colubrids, and large elapids. This group generally had late maturity ($>$3 years), low adult mortality (Fitch, 1949; Gibbons, 1972), low rate of increase in female fecundity ($\bar{x}$=1.3 eggs/100 mm SVL increase) and small clutches of large young. Feaver attributed low adult mortality to the species being either powerful constrictors or venomous and therefore not as vulnerable as other types to predation. The "female larger" group included the natricine colubrids, the genus Coluber, the boids, and possibly some small elapids. This group usually had early maturity ($<$3 years), low adult survivorship (30% annual survival for N. sipedon according to Feaver), female with a high rate of increase in fecundity ($\bar{x}$=3.4 eggs/100 mm SVL increase) and large clutches of small young. The high mortality among adults and juveniles was attributed to poor predator defenses combined with the small size of individuals of some species when compared to those in the "male larger" group. Feaver suggested that life expectancy in species of this group is relatively short and therefore the selective advantage of the observed rapid growth of mature females is a steep increase in fecundity and the production of large clutches. Nerodia taxispilota in the present study conformed to the profile of the "female larger" group in respect to high fecundity increase ($\bar{x}$ 10.3 eggs/100 mm SVL increase) and large clutch size (33.2 oviductal eggs or embryos/female). When compared with the fecundity data for crotalids ($\bar{x}$=8-10 young) in the study by Klauber (1956), N. taxispilota produced approximately three times the number of young. Values for adult survivorship and age at maturity were not available from my study; however, Herrington and Batson (1979) stated that female N. taxispilota in Georgia matured in 3-4 years.

In the study by Feaver (1977), males from the "male larger" group were considerably larger than those of the "female larger" group. He stated that "growth of males to a large size is a function of whether or not male combat is advantageous in the mating system of a species." In most of the "male larger" species, dispersion of individuals was great from hibernating dens before mating. Therefore, chances were good that two males could battle for the opportunity to mate with a nearby female without risking the loss of the female to a third male. The larger male, whether suitor or intruder, usually won, hence selection would be expected to favor large males as they would probably enjoy greater reproductive success. Natricines, however, typically showed little dispersion from dens before mating and usually there were several males courting a single female (Breder, 1946; Fox, 1955; Gardner, 1955; Fitch, 1963a). Feaver did not report any literature references for male combat in natricines and did not observe any among male _N_. _sipedon_ in his study. The explanation was a courting male attempting to drive off another suitor would probably lose the female to other nearby males. The strategy in this type of mating would be for the first male to pursue courtship even if other males tried to interfere. There is no apparent selection for large males in natricines as male combat is not a factor in mating. Data from my study support the prediction of small males in natricines. Twenty-two of the 51 mature males were within 100 mm SVL of the male size at maturity (500 mm SVL), and there was a steady decline in the number of males as size increased.

The overall sex ratio of 1.25:1 males to females for _N_. _taxispilota_ from Virginia was not significantly different from the expected 1:1 ratio. Burton (1970) reported that, in Oklahoma, *N. rhombifera* did not differ significantly from a 1:1 ratio but that *N. erythrogaster* showed a predominance of females. He qualified his results on *N. erythrogaster* by saying that the bias toward females was due to small sample size. Fitch (1965) suggested a predominance of females (1M: 1.58 F) for *Thamnophis sirtalis* caught in spring and summer. The proportional increase of males to females from spring to fall may be a reflection of the difference in decreasing rates of relative abundance between the sexes, i.e., the increasing ratio of males to females was a simple consequence of the widening gap between male and female abundance. Feaver (1977) also noticed an overall decrease in relative abundance as time progressed. He attributed high abundance of adults in spring and summer to mating and feeding and low relative abundance of females to males in the fall to parturition and hibernation. Actual mating and parturition were not observed in the present study, and instances of recent feeding were too few to establish a trend; however, these activities are suggested as possible explanations of seasonal abundance in light of the similar results found in this study and that of Feaver (1977). The scarcity of adult females in July is apparently due to the different areas sampled rather than relative seasonal abundance. The area sampled in 1978 (a four-mile stretch of the Appomattox River near its confluence with the James River at Hopewell) was more productive in terms of mature females caught than the area sampled in 1979 (Swift Creek--a tributary of the Appomattox River 8 to 11 km from Hopewell, and a short section of the Appomattox River 8-10 km from Hopewell). Seventeen of the 27 total adult females caught were taken on six trips from May through June, and August through September, 1978. Only nine adult females were caught during the same period in 1979 although nine trips were made. The monthly catch of adult females was higher in 1978 than 1979 for May, August, and September, and equal for the month of June. Comparative data for July were not available as sampling was done only in 1979; however, the catch for that month was similar to May, August, and September of that year. There is no assignable reason for the predominance of mature females in the lower Appomattox River in 1978 nor for the frequent occurrence of immature females upstream and in the tributaries in 1979. Comparative investigation of the two areas as to habitat differences, size of fish prey, predator abundance, and protective cover could provide possible explanations.

That males in this study had longer tails than females agrees with the findings of Kaufman and Gibbons (1975) where males of all 13 species tested had longer tails than females. In five species, including *N. taxispilota*, the difference was statistically significant. Analysis of data from my study indicate that mean tail ratio of males was significantly greater than that of females at the P=.001 level.

Regression lines for tail ratios of each sex were not parallel, a finding that agrees with the results of Zug et al. (1979), who found that the slope of the regression line for male tail ratios was greater than that for female tail ratios in all three species tested (*Coniophanes fissidens*, *Dipsas catesbyi*, *Imantodes cenchoa*). Possible reasons for the proportionally longer tail of males may be found in the summarization of Kaufman and Gibbons (1975). They were: containment of reproductive organs at the base of the tail in males; more space acquired in the female body cavity for the containment of eggs; and an enhanced grasping ability for males in mating. As mature females were generally larger and longer than most males, it was not possible to ascertain whether females had acquired any proportional increase in body cavity for the containment of eggs, at least at the expense of tail length (reason two). The first and third reasons appear the most reasonable. Assuming that all anatomical features grow in size as body size increases, the additional space in the tail of males for incorporation of the hemipenes retractor muscles would continue to increase along with continued caudal growth. A longer tail would provide enhanced grasping ability and would be advantageous in the natricine type of mating. As mating is promiscuous, the male with the longer tail may have a competitive edge in the melee of males simultaneously attempting to mate with a female.

Tail breakage in N. taxispilota (23 of 106, 22%) was considered substantial when compared with data for neotropical species given by Zug et al. (1979) who considered 10% low and 30% high. The frequency of incomplete tails did not differ significantly between the sexes in the present study nor in that of Zug et al. (1979). The steady increase in tail breakage with increasing SVL would be expected as older individuals would probably have had more chance encounters with predators. The interpretation of tail breakage being limited almost entirely to adults is that, even though natricines are overall defensively poor against predators, larger more experienced adults survive predator encounters with only a few battle scars. Less experienced juveniles are more vulnerable: they either escape detection or they suffer fatality if attacked. Data from Feaver (1977) on *N. sipedon* support this idea. Adult annual survivorship was low (30%) but survivorship of juveniles was even lower (18%), and Feaver suggested larger size of adults afforded some protection against predation since adult survivorship was higher. In the present study, lack of predator awareness among young snakes was demonstrated when a newborn male was captured simply by gliding the canoe up to its basking branch close enough to remove it by hand. Furthermore, it did not begin to struggle until several seconds after it had been seized. It should be noted that older juveniles and adults usually remained motionless on their basking branches until grasped by the Pillstrom tongs. Once any disturbance was made, the targeted snake, unless captured, quickly dropped into the water and was rarely seen again. The method of predator avoidance in *N. taxispilota* is therefore apparently passive: remaining motionless until danger is imminent. *Nerodia sipedon*, a sympatric species, exhibited a more active predator avoidance, usually taking to the water as soon as the canoe approached.

Male Reproductive Cycle

The seasonal nature of the testicular cycle in *N. taxispilota* is similar to that of other natricines (Fox, 1952; Fitch, 1965; Srivastava and Thapliyal, 1965; Bauman and Metter, 1977) other colubrids (Fitch, 1963b; Prieto, 1975) and iguanid lizards (Fox, 1958; Mayhew, 1963, 1966; Saynal and Prasad, 1967). The pattern of seasonal change is also alike: Testes small in spring, recrudescence and spermatogenesis in summer and involution in fall and winter. Only the gross morphology of testicular changes was considered in my study because histological investigation was not thought to be necessary as Fox (1952) stated that macroscopic fluctuations reflected corresponding histological changes.

Correlation between morphology and histology was also demonstrated by Prieto (1975), Hawley and Aleksiuk (1976), and Bauman and Metter (1977).

In the present study, testis length, weight, and volume were measured and divided by SVL. Seasonal alteration in testis length in _N. taxispilota_ showed a slight time lag when compared with weight and volume measurements, i.e., testis length began to increase and decrease after such changes occurred in weight and volume. The use of SVL, a linear measurement, as the denominator in the ratio formulae has been proved statistically valid for weight and length (Burton, 1970; Hawley and Aleksiuk, 1976). As volume is a function of length ($lg.^3$) it was also used (vol./SVL) as a check on length where testis length was distorted (periphery convoluted). No comparative volume data were found; however, ratios of testis lg./SVL or testis wt./SVL were used by other authors (Fox, 1952; Prieto, 1975; Hawley and Aleksiuk, 1976; Shine, 1977a).

There has been some question in the literature as to which parameter, testis length or weight, is the more valid in interpreting testicular changes. Zug et al. (1979) reported that length was ineffectual due to the poor preservation of the museum specimens used for his study, and he suggested weight or volume may have been more indicative. Conversely, Shine (1977a), studying fresh specimens, used testis length rather than weight because he thought high testis weights were correlated with the pressure of abundant spermatozoa. In the final analysis, he found that trends for length and weight showed the same degree of change.

The decrease in amount of sperm in the vas deferens of N. taxispilota in late June and July corresponded to the observations made on other natricines by Fitch (1965), Hawley and Aleksiuk (1976), Bauman and Metter (1977), and Feaver (1977). Bauman and Metter (1977) stated that the vas deferens is the principle organ of sperm storage in Nerodia. They and other authors agreed that spermatogenesis begins in mid-April and early May and mature sperm are produced by July and August, when testis size is at its maximum. Spermatozoa are moved to the vas deferens in fall and winter and stored there until the following spring. Thus, males emerging in spring possess mature sperm for mating at a time when testes are small and inactive. The decrease in amount of sperm present in mid-summer is the result of the sperm supply being used in spring mating and not replenished until the fall. It should be emphasized that, whereas the amount decreases, most males retain some sperm in the vas deferens throughout the year. I found only one male in July to be aspermic. All the rest had some sperm in the vas deferens although the amount was less than in males caught in spring or fall.

An exception to the winter storage of sperm in the vas deferens was found in the study by Srivastava and Thapliyal (1965) on *Natrix* *piscator* (*Sinonatrix piscator*--Rossman and Eberle, 1977) in India. This species breeds in the fall and therefore does not retain sperm in the vas deferens beyond that time. Fitch (1970) indicated that *Nerodia* species, as a rule, breed only in spring. Results from the present study support this as there was no evidence of fall mating in *N*. *taxispilota*. All mature males caught in the fall possessed abundant quantities of sperm in the vas deferens (i.e., no mature males were caught in the fall with low or nil amounts of sperm).

Female Reproductive Cycle

The separation of developing follicles and embryos into three size classes was based on the description of comparative vitellogenesis for crotalids and colubrids by Aldridge (1979). He described egg development in terms of two stages, primary and secondary vitellogenesis. Primary vitellogenic follicles are small, white, "non-yolking" follicles that consist mostly of protein and lipid and are present in the ovary year around. Size ranges from microscopic to about 6-10 mm depending on the species. At that point, development stops until the initiation of secondary vitellogenesis. Secondary vitellogenic follicles are the enlarged, yellow, "yolking follicles" destined for development that season. Aldridge (1979) recognized two types of secondary vitellogenesis: type 1) spring vitellogenesis and type 2) summer, fall and following spring vitellogenesis. Data for _N. taxispilota_ concur with the statement by Aldridge (1979) that _Natrix_ (_Nerodia_) fits the first type of secondary vitellogenesis, i.e., follicles are yolked in the spring of the year that they develop. Other authors have categorized follicle development into classes. Betz (1963) divided follicles arbitrarily into four size classes whereas Zug et al. (1979) recognized five follicle size classes plus oviductal eggs, based on physiological development. Class I follicles in the present study correspond to I and II of Betz (1963) and I, II, III, of Zug et al. (1979). Class II follicles are equivalent to III and IV of Betz (1963) and IV and V of Zug et al. (1979). Class III oviductal eggs correspond to the "egg" category of Zug et al. (1979).

That yolking follicles were found in ovaries of N. *taxispilota* in Virginia in mid-June and eggs in the oviducts by late June in 1978 and 1979 is supportive evidence for the assumption that ovulation occurs during this period. Ovulation for the same time of year is also reported by Bauman and Metter (1977) for N. *sipedon* in Missouri. Betz (1963) however gave 15 May-15 June as the time of ovulation for N. *rhombifera* in Missouri. In the absence of additional specific data or ovulation in *Nerodia*, it is not clear whether the earlier dates are species or latitudinally related.

The positive correlation of number of young with increasing female SVL is commonly observed in most species of snakes (Fitch, 1970). This has been well documented for the natricine species N. *taxispilota* (Herrington and Batson, 1979), N. *sipedon* (Bauman and Metter, 1977; Feaver, 1977), N. *rhombifera* (Cagle, 1937);

Burton, 1970), *N. erythrogaster* (Burton, 1970), *T. sirtalis* (Fitch, 1965) and *T. sauritus proximus* (Tinkle, 1957).

The actual number of yolking follicles of embryos for the 22 gravid females from my study ($\bar{x}$=33.9) was within the figure (av. 30-40 young) given by Franklin (1944) and slightly greater than that of Herrington and Batson (1979) ($\bar{x}$=27.3). Considering only the five females with well-developed embryos the mean size of 28.0/female approximated that of Herrington and Batson (1979). A mean of 28.0 may be more accurate than a mean of 33.9 as Fitch (1965) stated that brood size often decreased as development proceeded, i.e. the final number of viable young was usually less than the original count of yolking follicles or oviductal eggs. Some eggs are not transferred to the oviduct, some oviductal eggs are not fertilized, and some embryos are lethally malformed. Betz (1963) stated that any yolking follicles not ovulated undergo atresia, with the yolks being resorbed by the female. This would account for a descrepancy between the number of follicles originally yolked and the actual number ovulated. He also stated that atresia accounts for the decrease in number of follicles as they mature. The decline in number of eggs or embryos as development proceeds was also illutrated by Cagle (1937) for *N. rhombifera*. The mean number of embryos for 12 females was 30; however, the mean size of three actual broods was 16.

The longer, more productive right ovary of *N. taxispilota* is like that reported for *N. rhombifera* (Betz, 1963), *N. sipedon* (Bauman and Metter, 1977), and other colubrid (Tinkle, 1957), crotalid (Wharton, 1966); Aldridge, 1979), and elapid (Shine, 1977b) species. The percentage of eggs contributed by right and left ovaries for *N. taxispilota* (R, 58.5%; L, 41.5%) was close to that reported by Betz (1963) for *N. rhombifera* (R, 60%; L, 40%), Bauman and Metter (1977) for *N. sipedon* (R, 64%; L, 36%) and Wharton (1966) for *Agkistrodon piscivorous* (R, 60.7%; L, 39.3%).

The high occurrence of females with atretic follicles in June as opposed to May and August supports the statement by Betz (1963) that it is not uncommon to find mature ovarian follicles undergoing atresia in early pregnancy. Apparently, a sizable part of the decrease in number of eggs completing development occurs at or near the time of ovulation. Perhaps it is at this time that energy reserves of the female determine the number of yolking follicles that can complete development. The energy from yolk masses undergoing resorption could be recycled to the remaining developing embryos.

The female cycle in *N. taxispilota* is apparently annual, as it is similar to the seasonal pattern of vitellogenesis and embryo development reported for related species with confirmed annual cycles (Betz, 1963; Bauman and Metter, 1977; Feaver, 1977). The yolking of follicles only in spring (May-June) and possession of well-developed embryos only in late August by gravid females of this study is indicative of a three-month summer gestation period. This is the typical pattern for annually reproducing temperate zone North American colubrids (Fitch, 1970). Aldridge (1979) stated that most temperate zone snakes are potentially annual breeders but that availability of energy, either as stored fat or from spring foraging success determines whether a female reproduces during a particular year. Another reason for assuming an annual cycle for *N. taxispilota* is that over 80% of mature females were gravid for both years sampled. Feaver (1977) assumed an annual cycle for *N. sipedon* because, as he stated, over 80% (83%) of the mature females of his study were gravid.

Although four of the five non-gravid mature females were caught at a time when a post-partum condition was possible (late August, early September), all were considered non-reproductive for that season after examination of their oviducts. Oviducts of post-partum females leave alternating regions of stretching (embryo attachment areas) and constriction. The oviducts of all five females had a uniform appearance along their entire length and showed no evidence of stretching.

It was not possible to compare the embryonic development of _N_. _taxispilota_ with other species as similar studies were not located in the literature. The decrease in mean size of eggs from mid-June to late June and early July can be explained by the fact that, upon ovulation, yolk masses change in shape from elliptical to spherical. Although linear measurement decreases with the change, there is no apparent change in volume.

Parturition is assumed to be from early to mid-September as the embryos of all three gravid females caught 23 August appeared completely developed. One female had embryos with no yolk remaining, an indication that parturition was imminent. The embryos of the other two females had some yolk left and parturition was probably a few weeks away. These data agree with laboratory birthdates of early to mid-September for *N. taxispilota* in this area (pers. comm. Dr. Charles Blem, assoc. prof. of biology, Virginia Commonwealth University). Mean length of embryos from the three gravid females caught 23 August (185 mm SVL) was consistent with the figure given by Conant (1975) for *N. taxispilota* at birth (190-330 mm total lg.). Late August and early September are reported as the times of parturition for *N. taxispilota* (Semlitch and Gibbons, 1978; Herrington and Batson, 1979) as well as *N. rhombifera* (Betz, 1963; Burton, 1970) and *N. sipedon* (Bauman and Metter, 1977; Feaver, 1977).

It appears that the seasonal sexual cycles of male and female *N. taxispilota* from Virginia and Georgia are essentially alike and similar to other species of *Nerodia*, and, in fact, to most other North American colubrids. Further studies of the life history and ecology of *N. taxispilota* are needed to demonstrate its relationship with _N_. _sipedon_ and _A_. _p_. _piscivorous_ from the same area. Before conclusions can be reached concerning the reproductive behavior of _N_. _taxispilota_ throughout its range, it will be necessary to study populations between the extremes.

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Table 1. Seasonal distribution and sex ratios of mature and immature specimens of <u>Nerodia taxispilota</u> (1978 and 1979 samples combined).

	Season	Males	Females	Ratio	Chi Square
All Snakes	Spring	8	9	1:1.1	0.059
	Summer	41	34	1.2:1	0.654
	Fall	10	4	2.5:1	2.570
	Total	59	47	1.25:1	1.350
Mature Snakes	Spring	7	5	1.4:1	0.333
	Summer	38	20	1.9:1	5.586
	Fall	6	2	3:1	2.000
	Total	51	27	1.88:1	7.380
Immature Snakes	Spring	1	4	1:4	1.800
	Summer	3	14	1:3.5	7.118
	Fall	4	2	2:1	0.666
	Total	8	20	1:2.5	5.142

Table 2. Mean values of three indices used in evaluating seasonality of the testis cycle of Nerodia taxispilota. Numbers in ( ) indicate sample size.

	May	Jun	Jul	Aug	Sep	Oct	Nov
Testis	(7)	(19)	(9)	(10)	(4)	(1)	(1)
$\bar{x}$ lg.	4.3	4.1	5.6	6.1	6.2	5.0	5.9
$\bar{x}$ wt.	4.0	4.8	18.2	33.5	21.5	15.8	16.8
$\bar{x}$ vol.	0.4	0.5	2.0	3.7	2.4	2.0	2.0

Table 3. Seasonal variation in concentration of spermatozoa in the vas deferens of male Nerodia taxispilota. N=sample size.

Month	N	Abundant	Numerous	Sparse	None
May	7	7	-	-	-
Jun	19	12	3	4	-
Jul	9	-	7	1	1
Aug	10	8	1	1	-
Sep	4	3	1	-	-
Oct	1	1	-	-	-
Nov	1	1	-	-	-

Fig. 1. Distribution of *Nerodia taxispilota* in Virginia.
✹ indicates area sampled in present study.
● indicates collection records.

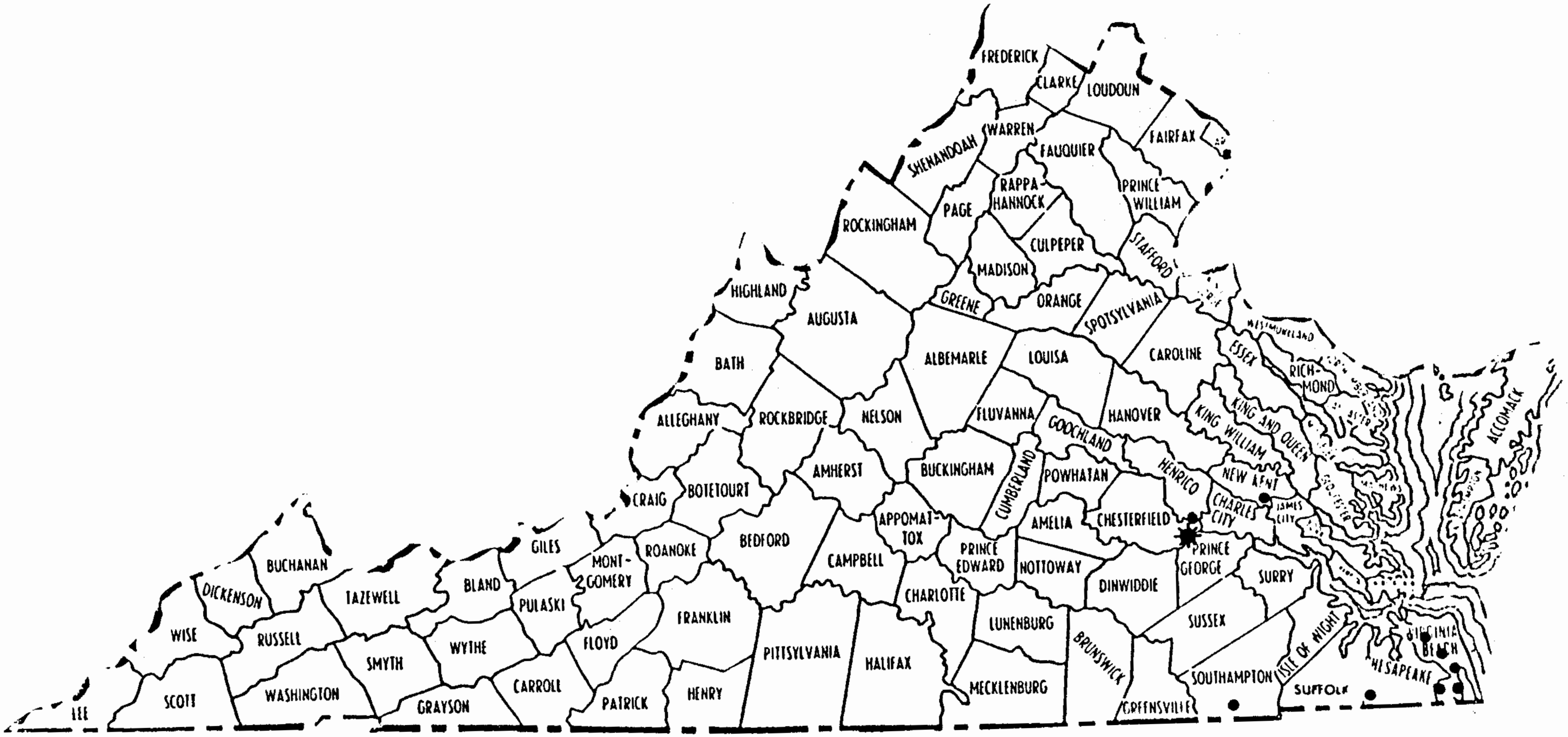
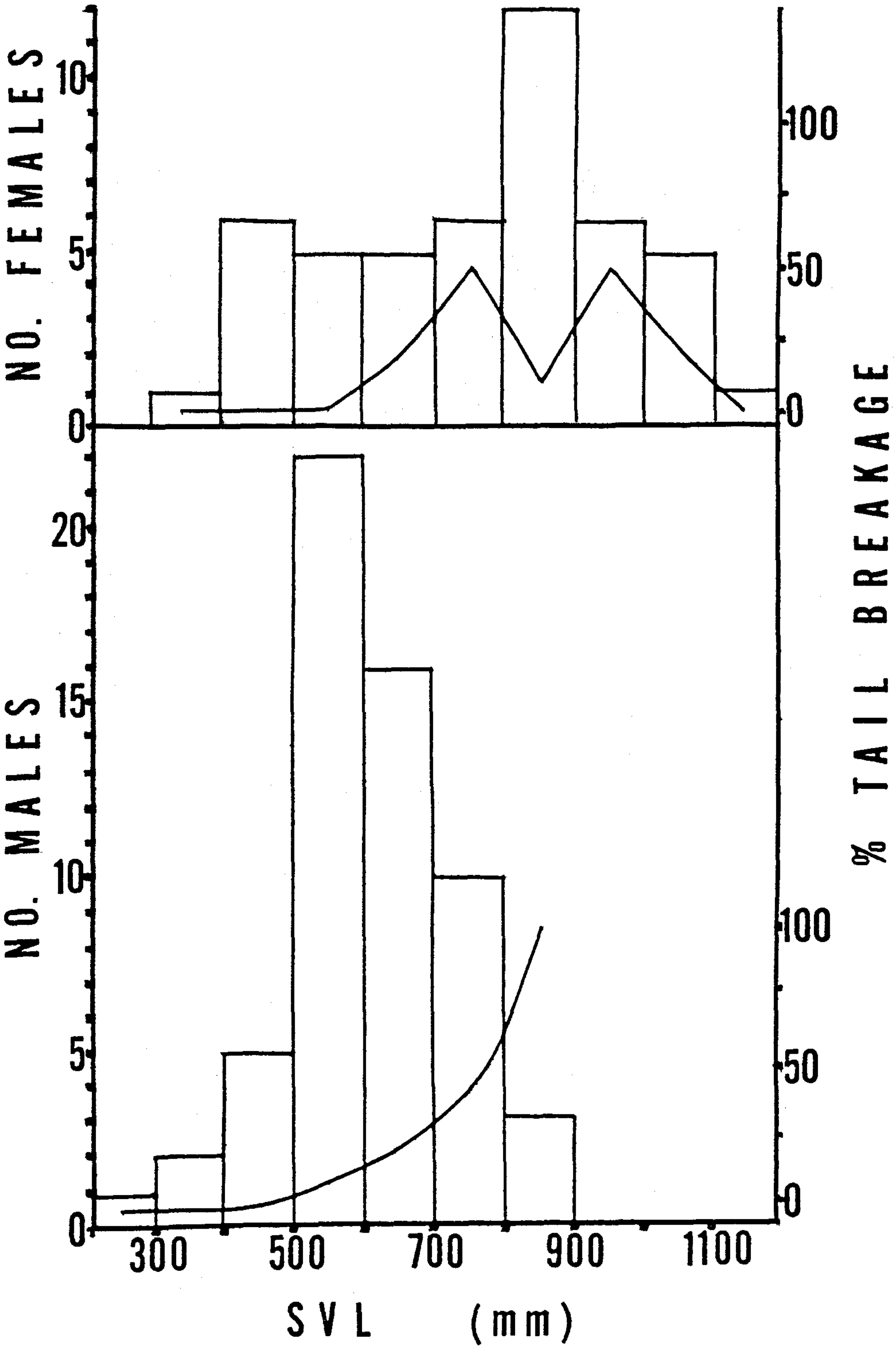

FREDERICK
CLARKE
LOUDOUN
FAIRFAX
SHENANDOAH
WARREN
FAUQUIER
PRINCE WILLIAM
RAPPAHANNOCK
PAGE
ROCKINGHAM
CULPEPER
STAFFORD
MADISON
HIGHLAND
GREENE
ORANGE
AUGUSTA
SPOTSYLVANIA
WESTMORELAND
ALBEMARLE
LOUISA
CAROLINE
ESSEX
BATH
RICHMOND
ACCOMACK
ALLEGHANY
ROCKBRIDGE
NELSON
FLUVANNA
HANOVER
KING AND QUEEN
KING WILLIAM
GOOCHLAND
AMHERST
BUCKINGHAM
CUMBERLAND
POWHATAN
HENRICO
NEW KENT
CRAIG
BOTETOURT
CHARLES CITY
JAMES CITY
APPOMATTOX
AMELIA
CHESTERFIELD
BUCHANAN
GILES
ROANOKE
BEDFORD
PRINCE EDWARD
PRINCE GEORGE
MONTGOMERY
CAMPBELL
NOTTOWAY
DICKENSON
BLAND
DINWIDDIE
TAZEWELL
SURRY
PULASKI
CHARLOTTE
FRANKLIN
LUNENBURG
SUSSEX
WISE
RUSSELL
WYTHE
VIRGINIA BEACH
FLOYD
BRUNSWICK
SMYTH
ISLE OF WIGHT
PITTSYLVANIA
HALIFAX
HESAPEAKE
SOUTHAMPTON
CARROLL
WASHINGTON
MECKLENBURG
SUFFOLK
SCOTT
HENRY
PATRICK
GRAYSON
GREENSVILLE
LEE

Fig. 2. Size-frequency histogram of male and female *Nerodia taxispilota* with corresponding percent of tail breakage among individuals of each 100 mm size class.



NO. FEMALES
10
5
0
100
50
0
NO. MALES
20
15
10
5
0
100
50
0
% TAIL BREAKAGE
300
500
700
900
1100
SVL (mm)

Fig. 3. Relationship of tail length to SVL of male and female *Nerodia taxispilota* (• - males, ✧ - females). Regression equations are: for males, $y=13.99 + 0.31x$, $r^2=0.92$; for females, $y=16.17 + 0.27x$, $r^2=0.96$.

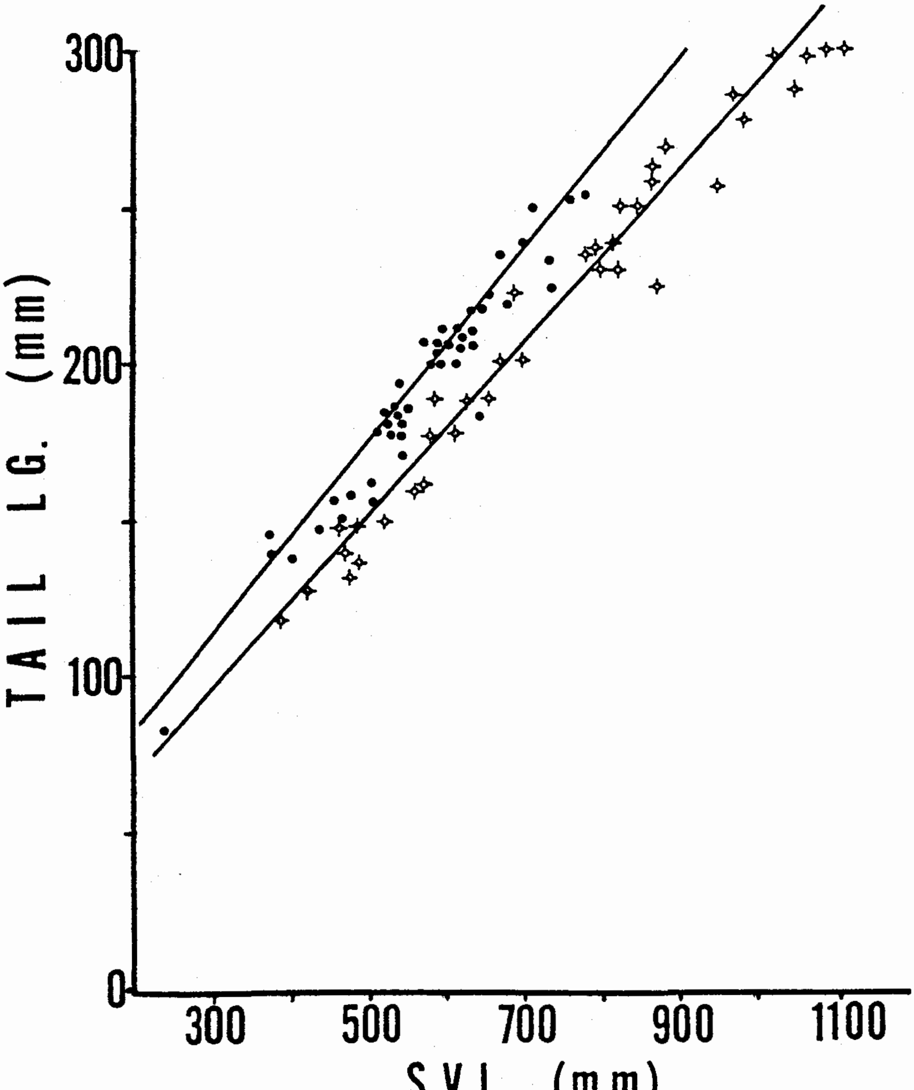

300
200
100
0
TAIL LG. (mm)
300
500
700
900
1100
SVL (mm)

Fig. 4. Monthly variation in testis weight of *Nerodia taxispilota*. "Testis wt. index" refers to testis weight divided by SVL and multiplied by 100.

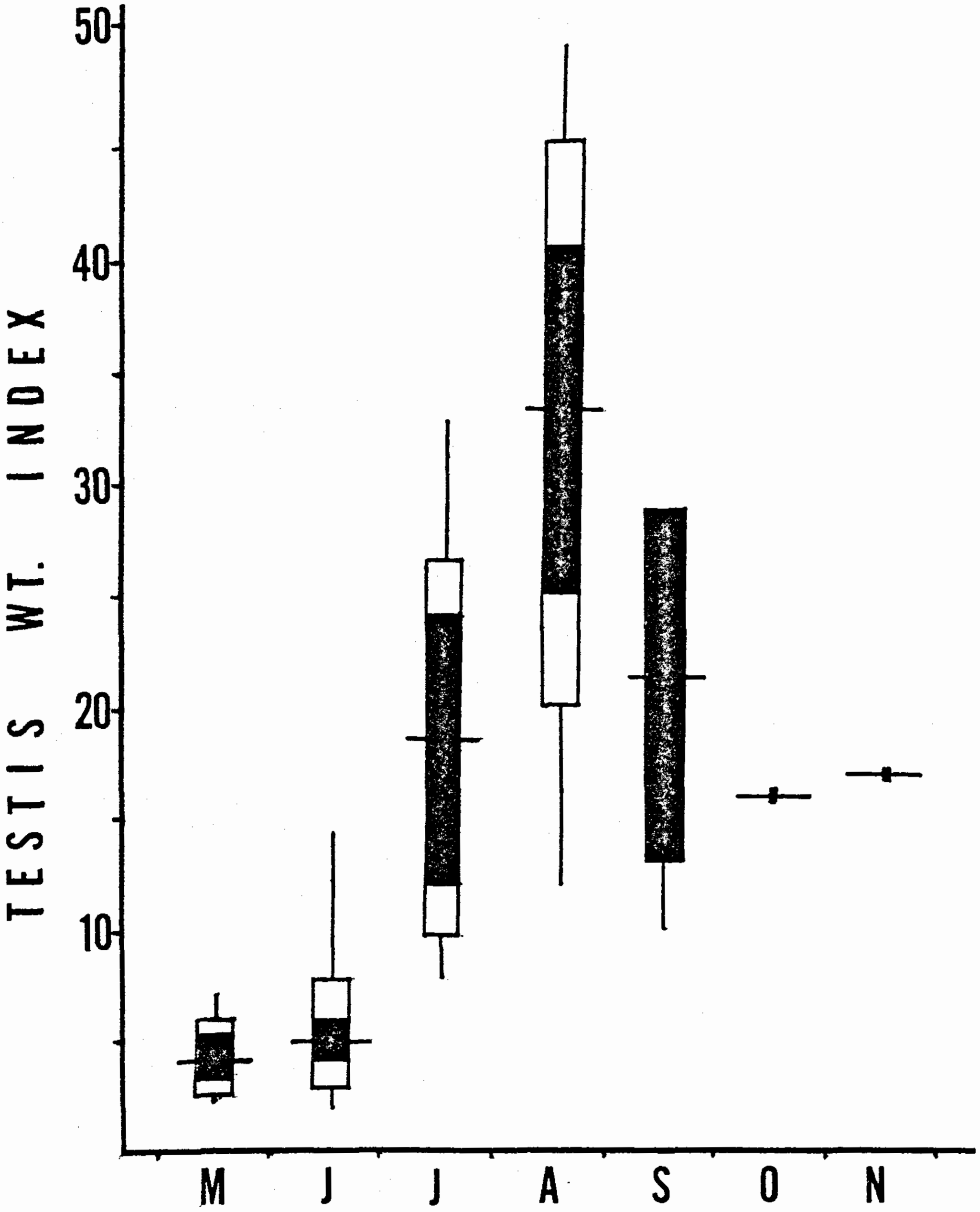

50
40
30
20
10
TESTIS WT. INDEX
M
J
J
A
S
O
N

Fig. 5. Monthly variation in testis volume of *Nerodia taxispilota*. "Testis vol. index" refers to testis volume divided by SVL and multiplied by 1000.

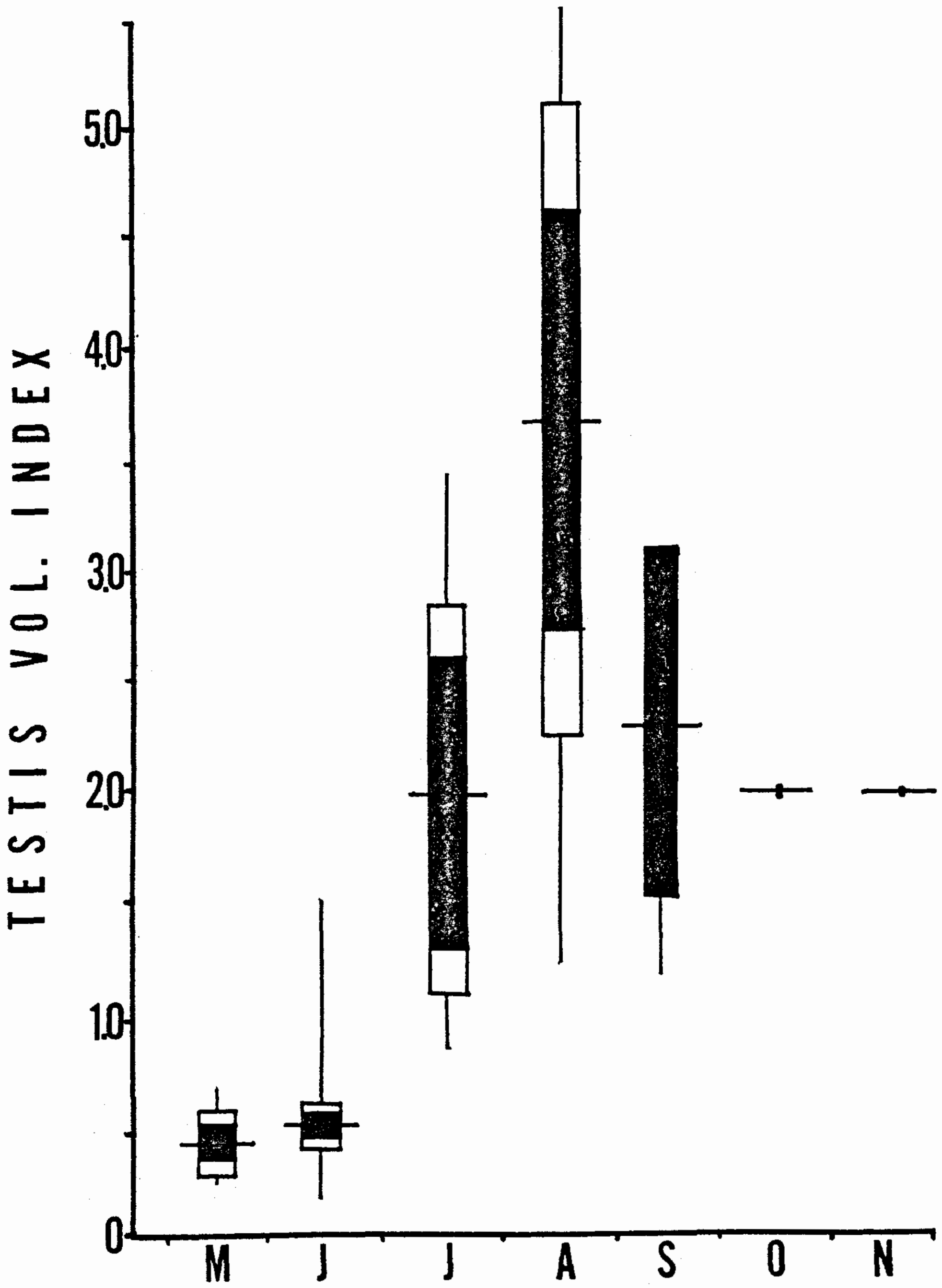

TESTIS VOL. INDEX
5.0
4.0
3.0
2.0
1.0
0
M
J
J
A
S
O
N

Fig. 6. Monthly variation in testis length of *Nerodia taxispilota*. "Testis lg. index" refers to testis length divided by SVL and multiplied by 100.

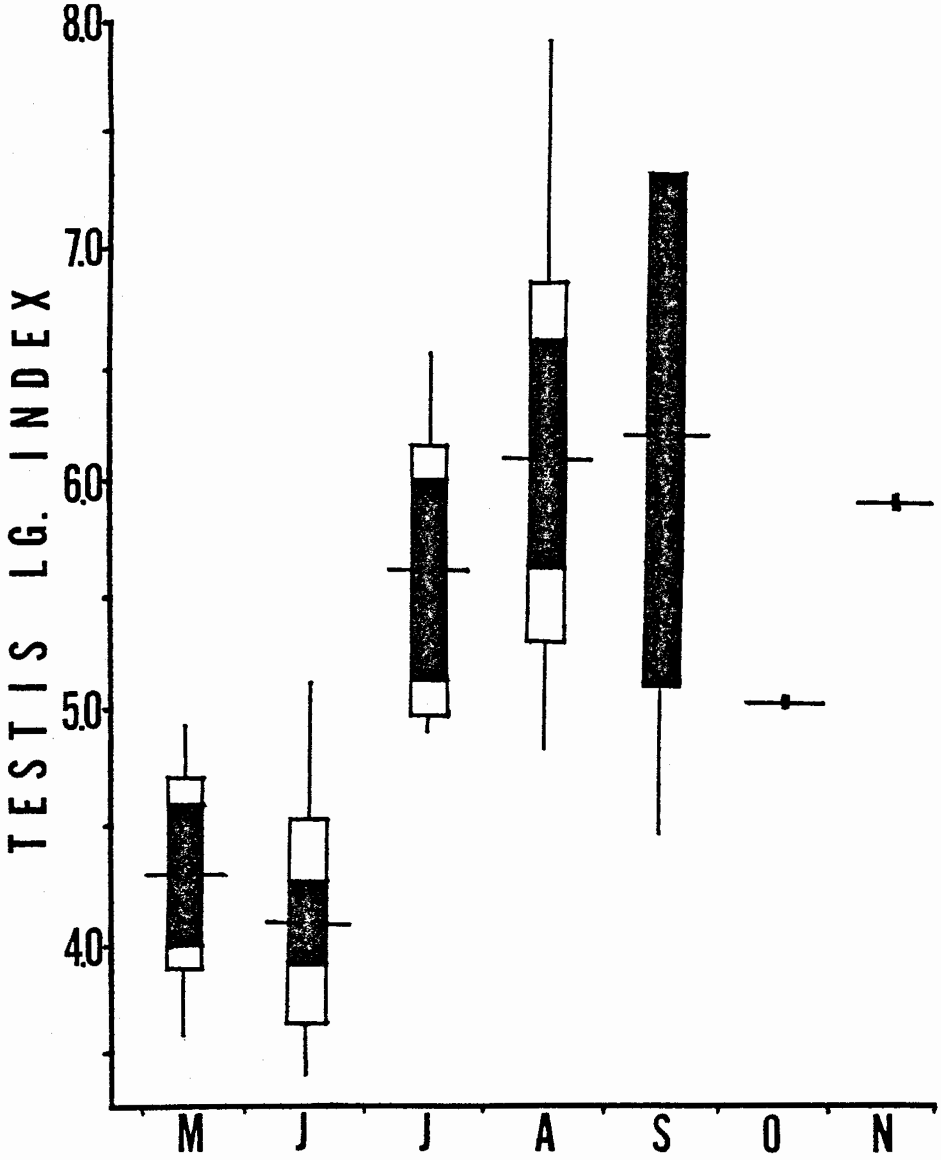

TESTIS LG. INDEX
8.0
7.0
6.0
5.0
4.0
M
J
J
A
S
O
N

Fig. 7. Distribution of follicle size-classes by month and female SVL for *Nerodia taxispilota*. + - class I, ●-class II. ○-class III. Each female is represented by the symbol corresponding to the most advanced type of follicle she possesses.

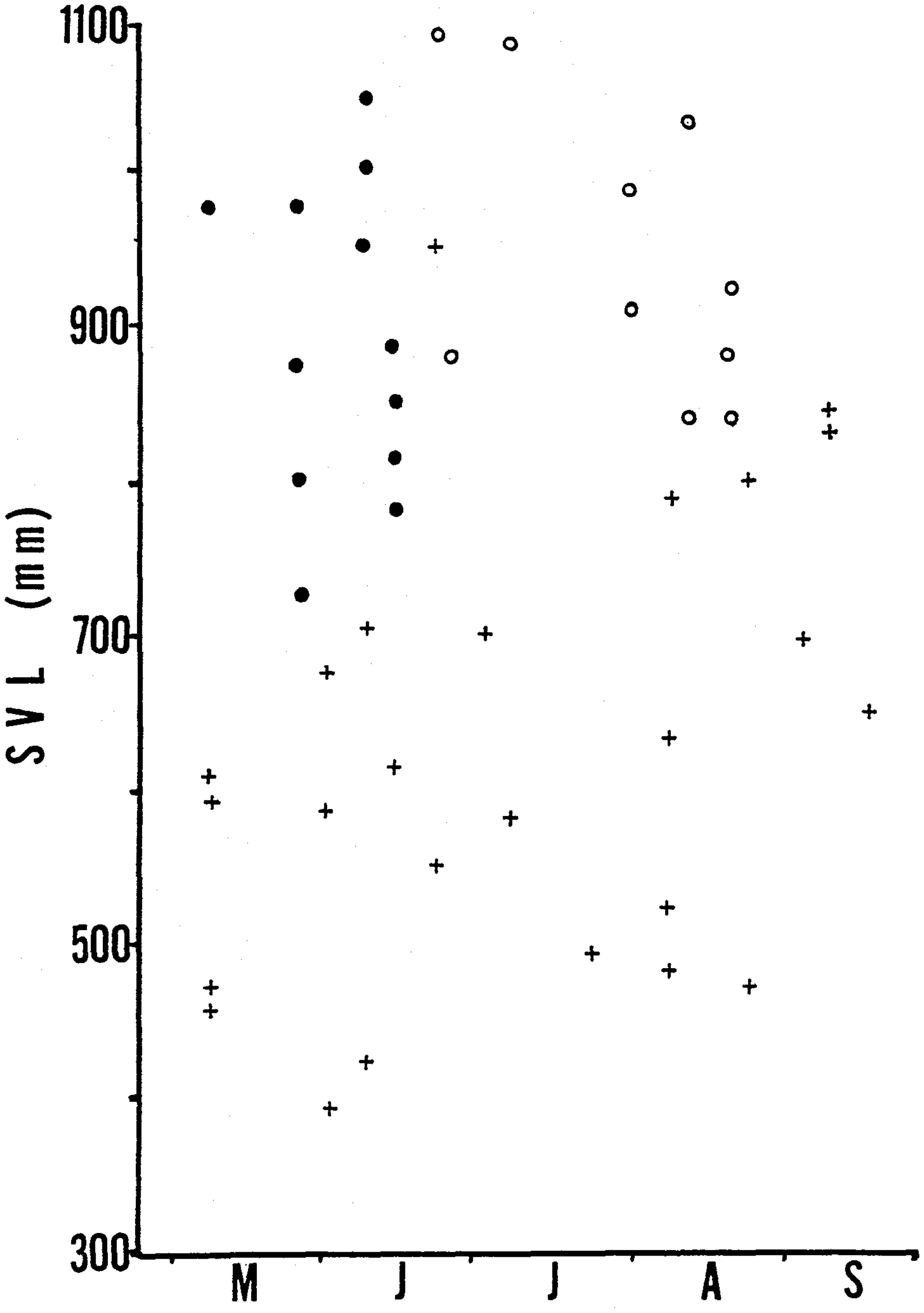

1100
900
700
500
300
SVL (mm)
M
J
J
A
S

Fig. 8. Monthly increase in mean size (diameter) of yolking follicles or oviductal eggs for _Nerodia taxispilota_. Each dot represents mean clutch size for that particular female.

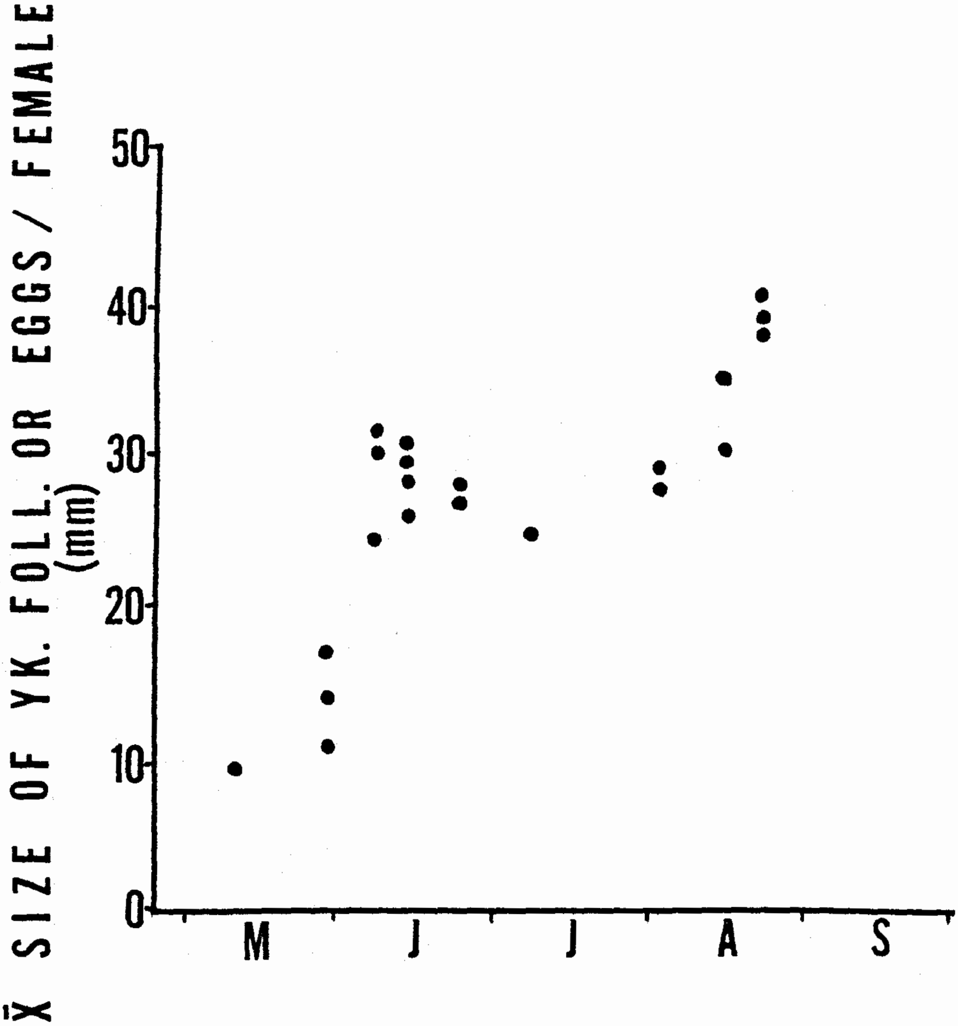
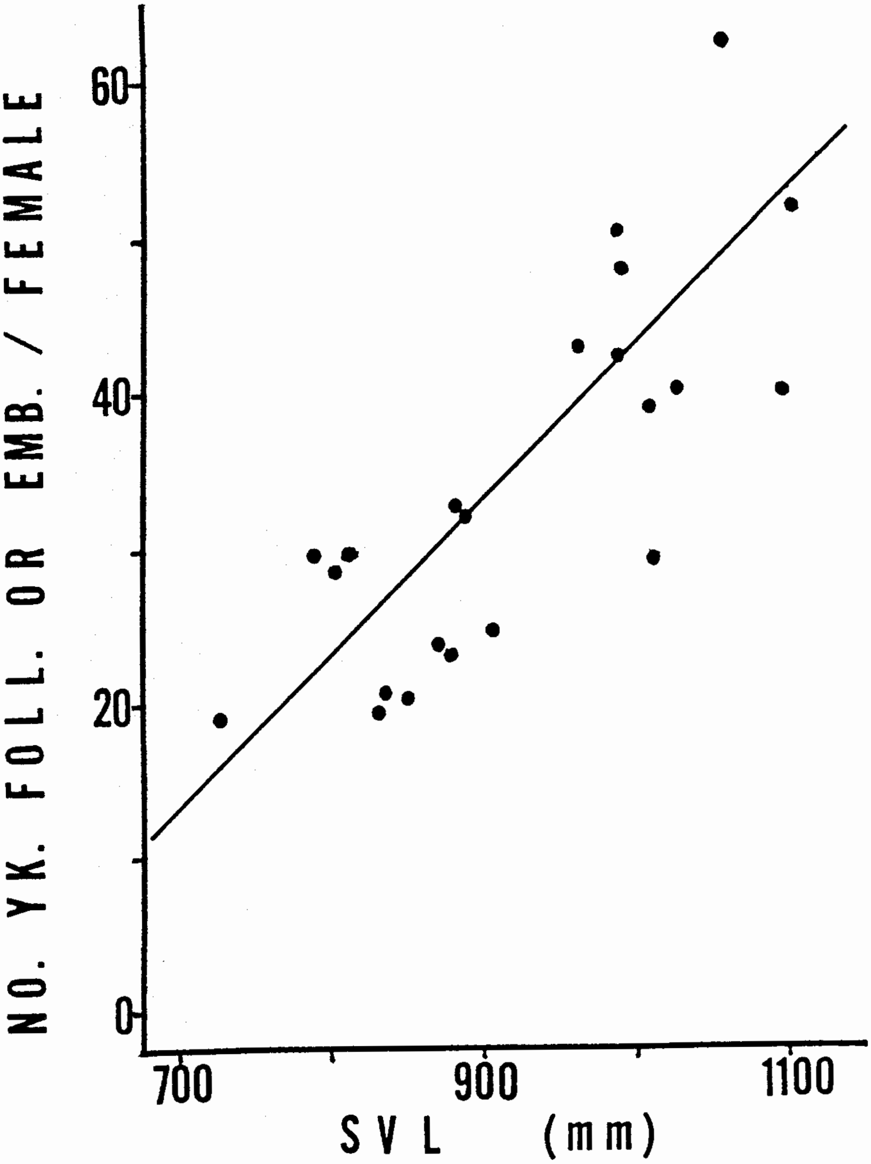

X̄ SIZE OF YK. FOLL. OR EGGS / FEMALE
(mm)
50
40
30
20
10
0
M
J
J
A
S

Fig. 9. Relationship between number of yolking follicles or embryos and female SVL for *Nerodia taxispilota*. Regression equation is $y=-53 + 0.09x$, $r^2=0.96$.


NO. YK. FOLL. OR EMB. / FEMALE
60
40
20
0
700
900
1100
S V L (mm)

Vita

David R. White was born 9 September 1954, in Baltimore, Maryland. He attended elementary school in Richmond, Virginia, and was graduated from Douglas S. Freeman High School in 1972. He began undergraduate study at University of Richmond in 1972 and, while attending there, majored in Biology. He was elected into membership of Beta Beta Beta Biological Honor Society in his senior year and was graduated from the University in May, 1976, with a Bachelor of Arts degree. After graduation, he began graduate work at the University of Richmond and served as a laboratory assistant for several General Biology sections. He received a Master of Science in Biology in August, 1980. At this writing he is currently employed with the Zoology Department at Kings Dominion. His work there includes the care and management of exotic animals.