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GROWTH AND MATURITY IN GREEN SNAKES (*OPHEODRYS AESTIVUS*)

MICHAEL V. PLUMMER

ABSTRACT: I studied growth and maturity by mark-recapture in a central Arkansas population of *Opheodrys aestivus*. Growth rate was a decreasing linear function of body size and differed according to sex. Females grew faster than males and reached a greater size. Mean body sizes of first year cohorts, size plots of known age snakes, and mean body sizes of the largest snakes were in agreement with size-age curves developed from growth rate equations. Males first bred in the spring at 21 mo of age. About half of the females first bred in the spring at 21 mo of age and half the following spring at 33 mo. Growth and age at maturity were similar to other colubrid and elapid species of similar size.

Key words: Reptilia; Colubridae; Growth; Maturity; Mark-recapture; Age; Life history

A KNOWLEDGE of growth can be a valuable and useful aid in understanding a species' ecology. For example, growth rates may reflect resource levels among populations or temporal resource levels within populations. An increase in growth with food supplementation suggests that a population is food limited. Genetic differences, sex, thermal environment, social environment, attainment of sexual maturity, and adaptations to particular life styles may be reflected in growth rates (Andrews, 1982). Demographic studies require that individuals be aged, and for many species, including snakes, a thorough knowledge of growth rates may be the only method of aging (Caughley, 1977; Gibbons, 1976).

In this paper, I describe growth in a population of rough green snakes (*Opheodrys aestivus*), an arboreal, insectivorous species inhabiting the forest edge surrounding a lake in central Arkansas. Tin-

kle (1960) and Morris (1982) estimated growth and age of maturity of *O. aestivus* based on size frequency distributions composed of individuals collected in widely different years and/or different localities. However, the variability in time of hatching and the potential for highly variable growth rates (Andrews, 1982; Case, 1978) could obscure growth estimates based on size frequency distributions, especially those from temporally and spatially mixed samples. It is therefore desirable to study growth of individuals based on mark-recapture in a single population within a restricted time.

My hypothesis is that growth in *O. aestivus* can be described by the Von Bertalanffy growth model which predicts that growth rate in length is a decreasing linear function of length:

$$GR = a - bSVL, \quad (1)$$

where GR is the growth rate, a is the ini-

tial growth rate, b is the growth constant, and SVL is the snout-vent length (Andrews, 1982). The model will then be used to age snakes and thereby provide a useful demographic tool.

METHODS

The study area (Bald Knob Lake, White County, Arkansas) was described previously (Plummer, 1981). On initial capture, I measured the SVL of snakes to the nearest millimeter, weighed snakes to the nearest gram using a Pesola spring scale, sexed, and then gave each a unique mark by clipping the ventrals, using the method of Brown and Parker (1976). On recapture, I remeasured snake SVL's. I computed growth rates as the difference between the two SVL measurements divided by the interval in days between observations. I then fitted these data to the Von Bertalanffy growth model using the finite difference approximation form to the differential equation (Andrews, 1982), and appropriate linear regression procedures (Nie et al., 1975). Because I measured growth rates over finite periods, I regressed growth rate on mean SVL to avoid underestimating or overestimating instantaneous growth rates if initial or final SVL's, respectively, were used. Because measurement error was large relative to growth for small amounts of growth, only data with a minimum of 60 days between captures were included in the analysis. The growth season was the 5 mo from May-September. Data were collected from August 1977-September 1979.

RESULTS

Growth rate was a decreasing linear function of mean SVL (Fig. 1). Analysis of covariance (ANCOVA), using SVL as the covariate, revealed a significant difference ($P < 0.01$) in the regression lines for males and females; therefore growth rates were treated separately for the two sexes. The regression of GR on mean SVL explained 81% of the variance in males and 77% in females. Logarithmic transformations (\log_{10} or \log_e) of the mean SVL

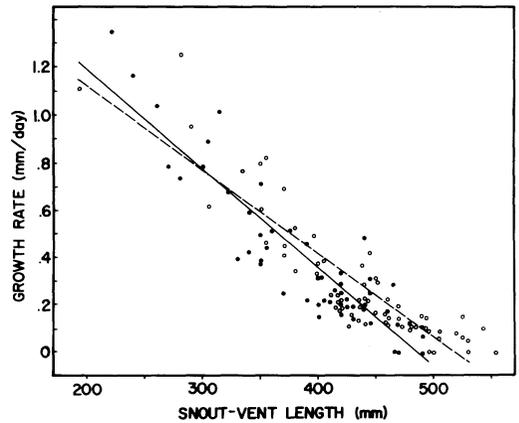


FIG. 1.—Growth rate as a function of mean SVL in *Ophedrys aestivus*. The closed circles and solid line represent males; the open circles and dashed line represent females. For males, $GR = 2.008 - 0.00416SVL$ ($n = 53$, $r = 0.90$); for females, $GR = 1.830 - 0.00355SVL$ ($n = 65$, $r = 0.88$). For both sexes, the regressions are highly significant ($P < 0.001$). Data were determined from within-season (May-September) growth records.

and/or the GR data did not result in an increase in the amount of explained variance in the regressions.

Following Van Devender (1978), the growth rate equation (1) was expressed as a differential equation:

$$\frac{dSVL}{dt} = a - bSVL, \quad (2)$$

which was integrated to yield an equation that related age and SVL

$$Age(t) = (1/b)\ln(a + bSVL) + c. \quad (3)$$

The constant of integration, c , could be calculated if age at any body size is known. Mean SVL's at hatching (age 0) were 139 mm for males and 140 mm for females (Plummer, 1984). Figure 2 shows the size-age curve generated for each sex from equation 3. In order to test the validity of the curves, plots of known-age snakes were superimposed. Overall, the fit of known-age snakes to the predicted curves was good. On the lower end, the curve slightly overestimated size and, for males, the upper end appeared to slightly overestimate

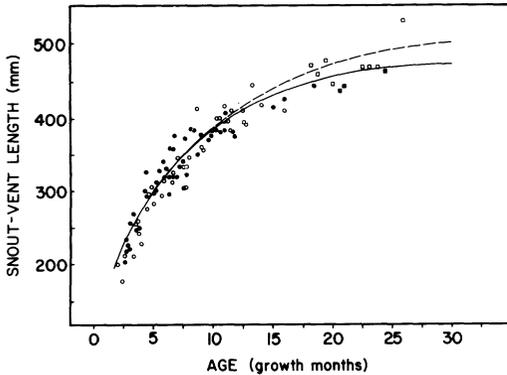


FIG. 2.—Body size as a function of age (post-hatching growth months) in *Opeodryas aestivus*. The closed symbols and solid line represent males; the open symbols and dashed line represent females. The curves are plots of equation 2 for males [$\text{age} = (-240)\ln(2.008 - 0.00416\text{SVL}) + 86$] and for females [$\text{age} = (-282)\ln(1.830 - 0.00355\text{SVL}) + 81$]. Circles are plots of known-age snakes that were marked in their first year. Squares are plots of known-age snakes that were first marked in their second year. A growth period of 1 mo after hatching (late August) is assumed before the first hibernation. To convert growth age to chronological age (months since hatching), add 7 mo (inactive) to growth ages 2–6, 14 mo to ages 7–11, 21 mo to 12–16, 28 mo to 17–21, etc. (e.g., growth age 4 = chronological age 11; growth age 14 = chronological age 35). All ages in the text are chronological ages.

size. Another independent test was to compare the mean SVL's of first year cohorts measured at various times of the year to sizes predicted by the equations of Fig. 2 (Table 1). Again, the equations slightly overestimated sizes at the lowest ages, but by July–August of the first year, there was close agreement between predicted and measured SVL's. A test of the upper end of the size-age curves was to compare mean size of the largest snakes in the population to the asymptotic sizes predicted by the growth rate equations. The mean ± 1 SE SVL of the 25 largest males was 468 ± 3.4 mm and was 522 ± 4.3 mm for females. These values compared favorably with the predicted 483 mm for males and 515 mm for females. Individual growth did in fact become asymptotic. One male (485 mm) did not grow for 1

TABLE 1.—SVL's ($\bar{x} \pm 1$ SE mm) of cohorts of small snakes that seemed to be in their first full year of growth. Predicted SVL's (mm) are determined from the equations in the legend of Fig. 2.

Month	Measured SVL from throughout month (n)	Growth age at mid-month	Predicted SVL at mid-month
May	185 ± 3.6 (13)	1.5	196
June	221 ± 5.4 (20)	2.5	229
July	254 ± 6.5 (18)	3.5	258
August	289 ± 4.7 (25)	4.5	285

yr. Five females (485–550 mm) did not show signs of growth for periods of 1–3 yr.

There was a strong ($r = 0.99$) relationship between body mass and SVL (Fig. 3). ANCOVA revealed that female mass was significantly ($P < 0.001$) greater than male mass even if adult snakes in the same size range were compared (males, mass = $1.29 \times 10^{-5}\text{SVL}^{2.33}$, $r = 0.99$; females, mass = $1.12 \times 10^{-6}\text{SVL}^{2.76}$, $r = 0.99$). If the functions relating mass and SVL in Fig. 3 were substituted into equation 3, then maximal change in mass for *O. aestivus* would occur at 26.5% of asymptotic mass for males and 27.7% for females. The Von Bertalanffy growth model predicted that growth in mass will be maximal at 30% of the asymptotic mass (Andrews, 1982).

DISCUSSION

As in many other species of reptiles (Andrews, 1982), growth in *O. aestivus* appears to fit the Von Bertalanffy model. Thus, the model can be used to predict age of snakes at any given size. However, as all methods that rely on morphological characters that vary continuously with age (Caughley, 1977), this method is subject to error. Examination of Fig. 2 shows that the probability of error increases toward the asymptote. In approximately the first 2 yr, individual snakes can be aged with confidence. In later years, samples of adequate size are needed so that errors will be compensating.

Demographically, an important life history attribute is the age at which maturity

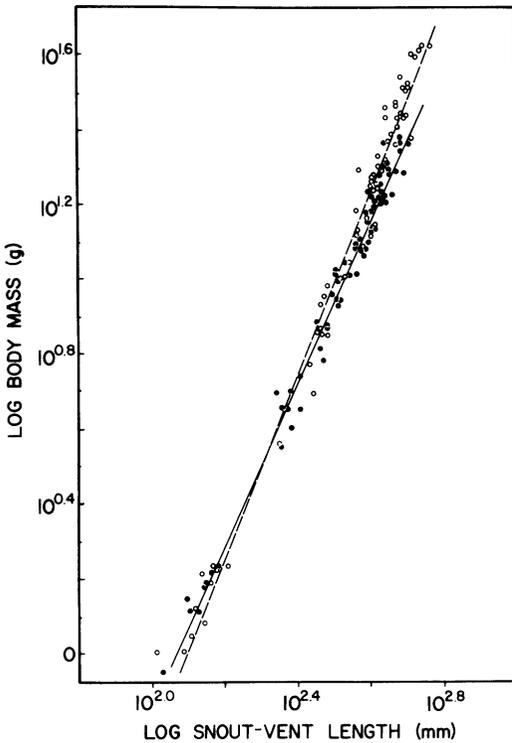


FIG. 3.—Body mass as a function of body length in *Ophedrys aestivus*. The closed circles and solid line represent males; the open circles and dashed line represent females. For females, mass = $6.5 \times 10^{-6} \text{SVL}^{2.47}$ ($n = 65$, $r = 0.99$); for males, mass = $3.0 \times 10^{-5} \text{SVL}^{2.19}$ ($n = 71$, $r = 0.99$). For both sexes, the regressions are highly significant ($P < 0.001$).

is attained. In this population, the majority of females were mature at 360–400 mm SVL and the smallest reproductive female found was a 335 mm SVL snake that contained oviductal eggs on 16 June (Plummer, 1984). Since eggs hatch in August, this individual probably was in its 22nd month after hatching (Fig. 2). In June–July, two of five females ranging 350–365 mm (22–23 mo old) and all 19 females ranging 375–395 mm were reproductive. Because of the differences in time of hatching and variation in individual growth rates, it is likely that these 19 snakes were either 22–23 or 34–35 mo old, on the average (Fig. 2). Thus, about half of the females in the population first breed

at approximately 21 mo of age and half at approximately 33 mo. Young will be produced at 24 and 36 mo of age, respectively. Intra-populational variation in the age of maturity of female snakes has been reported previously (discussed by Turner, 1977). For males, active cloacal sperm are present in the spring in the majority of snakes of about 300 mm (Plummer, unpublished data). In the fall, males of this size or slightly smaller have active testicular sperm not yet descended into the vas deferens (J. J. Greenhaw, personal communication). Thus, males mature in their first year after hatching and first breed the following spring at about 20–21 mo of age (Fig. 2).

The above estimates for age at maturity are in agreement with those made by Tinkle (1960) and Morris (1982) based on population size distributions in Louisiana and Illinois. Fall mating apparently occurs in some populations (Richmond, 1956). If the maturity schedule in this population was the same as the Arkansas population, then males could potentially first breed at 12–13 mo and females at 24–25 mo. However, because ovulation is limited to spring, fertilization would still not occur until the following spring (33–34 mo).

In order to compare roughly the first year growth rate (mm/day) of *O. aestivus* with those of other similarly-sized species, I divided the difference between the SVL's of one-year olds and hatchlings by 365 days. This procedure was necessary because growth rate constants (r), as calculated in this study, were not available for other species. The calculated finite rates were then rendered comparable by dividing each by the respective hatchling length. Hatchling length is highly correlated with adult length in snakes ($r = 0.89$; Andrews, 1982) and thus is a good indicator of size. The calculated rate for *O. aestivus* (0.0033) compared favorably with those of other small species with hatchling lengths between 100–150 mm, such as the colubrids *Carphophis amoenus* (0.0026; Clark, 1970) and *Diadophis punctatus*

(0.0030; Fitch, 1975), and the elapids *Unechis gouldii* (0.0024; Shine, 1978), *Austrelaps superbis* (0.0050; Shine, 1978), *Cacophis krefftii* (0.0022; Shine, 1980), and *Furina diadema* (0.0018; Shine, 1981). In comparison to snakes of all sizes, the growth rate of *O. aestivus* clustered predictably according to hatchling length in Fig. 9 of Andrews (1982). Except for *Unechis*, which first breeds at age 1 (Shine, 1978), ages at maturity for females were similar in the above species to *Ophedryx*. *Furina*, *Austrelaps* and *Carphophis* first breed at age 2 (Clark, 1970; Shine, 1978, 1981) and *Diadophis* and two species of *Cacophis* first breed at age 3 (Fitch, 1975; Shine, 1980). As *Ophedryx*, some *Cacophis harriettae* first breed at age 2 and others at age 3 (Shine, 1980).

Growth is a manifestation of the overall energy budget of a species. Thus, differences in timing and quantity of ingestion could be reflected in growth. For example, whereas the basic feeding mechanism of snakes results in the ingestion of large prey at infrequent intervals (Gans, 1961), some advanced snakes eat relatively small prey at frequent intervals (Greene, 1983). Thus, on one end of the spectrum are the viperids, which may take a substantial portion of their annual energy requirement in a single meal (Pough and Groves, 1983), and on the other end are insectivorous species like *O. aestivus* which feed more or less continuously. In the study population, more than 85% of the diet consisted of caterpillars, spiders, grasshoppers and crickets, and odonates. The mean number of prey in stomachs was 3.1 and more than 80% of snakes contained food in their guts (Plummer, 1981). There are potentially interesting ecological, behavioral and physiological differences between species that manifest these divergent patterns of energy intake (Pough and Groves, 1983). Whether patterns of growth differ between the two groups is unknown. Because fitted growth constants (r) in asymptotic models are directly comparable among species (Andrews, 1982), the approach taken in this paper would

be useful in elucidating potential differences between these two groups.

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MALE REPRODUCTIVE CYCLE OF THE LINED SNAKE (*TROPIDACLONION LINEATUM*)

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ABSTRACT: Forty-eight adult and 17 immature male lined snakes (*Tropidoclonion lineatum*) were collected in St. Louis, Missouri, during the active seasons of 1978-1980. Testis mass was lowest in early spring and reached a peak in late July. In early spring, seminiferous tubule diameter was smallest and spermatogonia were the most prevalent cell type. Tubule diameter increased during the summer and reached a maximum size by late July, corresponding to peak spermatogenesis. The most prevalent cell types at this time were spermatids and spermatozoa. Spermiation began in mid-July, with mating in late August. Seminiferous tubule diameter and rate of spermatogenesis decreased significantly by September. Sperm was stored in the ductus deferens throughout the winter and early spring, indicating a possibility of spring mating. By mid-June, sperm was absent from the ductus deferens. The diameter of the tubules within the sexual segment of the kidney increased significantly from May to September with a reduction in tubule diameter by late September. Males born in August showed advanced spermatogenesis by September with some spermiation in early October. This, however, was considered to be abortive. All male lined snakes began spermatogenesis in the spring. Therefore, males are capable of mating at 1 yr of age. Coelomic fat mass increased significantly in early spring, reached a maximum by mid-June, and remained at this level throughout the summer.

Key words: Reptilia; Serpentes; *Tropidoclonion lineatum*; Reproduction; Sexual segment; Maturation; Growth; Spermatogenesis

TROPIDACLONION LINEATUM, the lined snake, is a small burrowing snake found in the central United States. Little is known about the reproduction and ecology of this species, although feeding behavior (Ramsey, 1947) and activity periods (Force, 1931) have been reported. Blanchard and Force (1930) attempted to determine age at sexual maturity through analysis of growth rates. Ramsey (1946) observed fall mating in captive lined

snakes with birth occurring in the following fall. The object of this study is to describe the male reproductive cycle of the lined snake and to add to the data base for analysis of the evolution of snake reproductive cycles.

MATERIALS AND METHODS

We collected 65 male lined snakes during daylight hours between 8 May 1978 and 30 September 1980 in south St. Louis,