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Author(s): J. Malcolm Macartney, Patrick T. Gregory and M. Brent Charland

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(PAM) DEPARTMENT OF VERTEBRATE PALEONTOLOGY, AMERICAN MUSEUM OF NATURAL HISTORY, CENTRAL PARK WEST AT 79TH ST., NEW YORK, NEW YORK 10024; (BSW, RCW) DIVISION OF SCIENCE AND MATHEMATICS, STOCKTON STATE COLLEGE, POMONA, NEW JERSEY 08240. PRESENT ADDRESS (PAM): DEPARTMENT OF BIOLOGY, UNIVERSITY OF SOUTH FLORIDA, TAMPA, FLORIDA 33620. Accepted 15 April 1989.

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Growth and Sexual Maturity of the Western Rattlesnake, *Crotalus viridis*, in British Columbia

J. MALCOLM MACARTNEY, PATRICK T. GREGORY AND
M. BRENT CHARLAND

Variations in body size and growth rate underlie many patterns of variation in life history features, and their analysis in diverse populations of widely-distributed reptile species should be especially rewarding. We used mark-recapture to study growth rates, annual variation in growth, sexual maturation, and patterns of ecdysis in a population of the western rattlesnake, *Crotalus viridis*, in southern British Columbia, in the northern part of the species' range. Annual growth is highly variable in juvenile rattlesnakes but decreases relatively in magnitude and variability with increasing body size. Males have slightly more rapid growth than females and mature at a smaller size and earlier age (535 mm SVL, 3-4 yr in males vs 650 mm SVL, 5-7 yr in females). Growth rate varies among years, possibly in relation to annual differences in weather. A review of published literature on growth in this wide-ranging species shows a clear trend for annual growth in juvenile *C. viridis* to be reduced in populations that occur at higher latitudes or altitudes. This pattern of intraspecific geographic variation is explained in part by the shorter and cooler active seasons that snakes experience at northern or high elevation sites.

THE ideal demographic study would include knowledge of the ages of all individuals sampled. This unfortunately is not possible for most species of snakes because they carry no external markers of age. In rattlesnakes, the number of segments on the rattle is a potential indicator of age, but it requires intact rattles and knowledge of frequency of ecdysis. We, therefore, usually use an imperfect correlate of

age, body size, in most population studies of snakes. This is probably a reasonable approach because life history features of many species vary with body size; a number of recent models of population dynamics explicitly recognize this (Sauer and Slade, 1987). Furthermore, knowledge of the size-specific growth rates of animals may sometimes be used to make estimates about ages, especially if information on growth of very

young animals is available (Parker and Plummer, 1987).

Growth rates and cohort classes have been inferred from temporal changes in size-frequency distributions of snake populations (Carpenter, 1952; Gregory, 1977; Shine, 1978) or from a single size-frequency distribution for an entire population (Klauber, 1972; Gannon and Secoy, 1984). These methods are subjective and provide only a rough estimate of growth rates. The best method is to obtain repeated measurements on many individuals at various points in their lives (Parker and Plummer, 1987). This approach is seldom feasible, especially when the time frame of a study is short relative to the longevity of individuals in the population; however, it has been used in some studies (Fitch, 1949; Madsen, 1983). The advantages and disadvantages of these and other methods frequently employed by herpetologists to estimate growth have been reviewed recently by Halliday and Verrell (1988). In this paper we summarize patterns of growth, annual variation in growth, ecdysis, and attainment of sexual maturity of the northern Pacific rattlesnake (*Crotalus viridis oregonus*), based on a 6 yr mark-recapture study in south-central British Columbia.

A further objective of this study was to evaluate geographic variation in growth of juvenile *C. viridis*. A trend for reduced annual growth and delayed sexual maturation with declining length and warmth of the active season (increase in latitude) has been observed in turtles (Christiansen and Moll, 1973) and lizards (Ferguson and Brockman, 1980). This pattern is also expected for snakes; however, there are relatively few snake species for which comparative information is available. Growth has been studied in a number of *C. viridis* populations throughout its broad geographic distribution (Fitch and Glading, 1947; Fitch, 1949; Parker and Brown, 1974; Diller and Wallace, 1984; Gannon and Secoy, 1984). Intraspecific geographic differences in growth rates of *C. viridis* have been reported by Gannon and Secoy (1984); however, their results suggested a pattern that is opposite to that found in other wide-ranging reptile species. We critically review the literature on growth in this species in order to obtain an understanding of this discordance.

METHODS

This study was carried out at four closely adjacent sites (<15 km apart) in the Okanagan

Valley of south-central British Columbia (50°N, 119°W, 425 m elevation), near the northern limit of the species' range (Gregory and Campbell, 1984). The region experiences warm, dry summers (mean maximum and minimum daily July temperatures are 27 C and 11 C, respectively), and cool, dry winters (mean daily maximum and minimum temperatures in January are -3 C and -9 C; Atmospheric Environment Service, 1982). Average annual precipitation is 41 cm and there is an average of 153 frost free days/annum.

Rattlesnakes were sampled from 24 communal hibernacula at the four sites. Most hibernacula were in metamorphic outcroppings situated along the upper reaches of steep, rocky, south-facing slopes of northeast to southwest trending mountain ridges. The number of snakes using these hibernacula ranged from 8–226 individuals/hibernaculum. In the Okanagan Valley, rattlesnakes spend, on average, 210 d in hibernation and are usually active above ground between early April and mid-Oct. (Macartney, 1985).

Rattlesnake populations were intensively sampled between Sept. 1980 and May 1983. Periodic collecting trips were made to the sites during the summer and autumn of 1983 and during the spring and autumn of 1984. Intensive sampling resumed in the spring of 1985 and continued until autumn of 1986, but on a smaller number of denning populations. Rattlesnakes were hand collected when they were active in the vicinity of hibernacula during the emergence period (early April–late May) and during ingress into hibernacula (early Sept.–late Oct.). Hibernacula were visited, on average, every second day during these periods. During the summer, the search routine varied; however, most sites were searched at least once, and often 2–5 times per week.

Rattlesnakes were handled with tongs and secured for measuring using a padded, 3 cm wide, restraining noose (Gregory et al. 1989). Each snake was sexed by Gregory's (1983) method and weighed using a Pesola spring scale. SVL was measured to the nearest 5 mm by stretching the snake along a meter stick, and the number of rattle segments was counted. Snakes were marked individually by clipping unique combinations of ventral and subcaudal scutes (Blanchard and Finster, 1933) and by applying a small amount of nail varnish to the top of the head and around the basal rattle segment.

To determine the degree of error in mea-

asuring SVL, two sub-adult rattlesnakes were measured daily over a 7 d period. Measured lengths varied between 1.4% and 1.9% of the mean SVL. Therefore, an increase of greater than 2% of the original SVL was considered to be measurable growth in an individual. Snakes measured at hibernacula in the autumn and again the following spring showed a mean increase in SVL of 0.21% (SE = 0.08%, $n = 433$, range = -7.0–4.9%). Therefore, in calculating annual growth, we considered growth during the overwintering period to be zero. Individuals measured either in the autumn or spring encompassing one overwintering period (t) and measured again the autumn or spring encompassing the next overwintering period ($t + 1$) were included in the data set. For each recaptured snake, absolute annual growth ($SVL_{t+1} - SVL_t$), relative annual growth ($(SVL_{t+1} - SVL_t) / SVL_t$), and the frequency of ecdysis (annual increment in rattle segments) were calculated. We determined body mass (M)-length (SVL) relationships for juveniles and adults, and tested for sexual dimorphism in these relationships by visual examination of the overlap of 95% confidence intervals placed around the linear regressions of $\log M$ on $\log SVL$. Relative growth, in terms of body mass, was calculated as $([M_{\text{autumn}} - M_{\text{spring}}] / M_{\text{spring}})$, to encompass only M change that occurred during the growing season. Records of annual growth of many individual snakes were obtained in more than 1 yr; each such record was treated as an independent observation.

We used annual growth measurements from the 1981–82 growing seasons to examine annual variation in growth and sexual differences in annual growth. Because the study sites were close together and differed little with respect to habitat, snakes were expected to experience active seasons of similar duration and climate, and to have access to comparable prey bases. Therefore, growth records were pooled for snakes from all sites in each of the two major study years (1981–82). Two-factor (sex, year), two level (male, female; 1981, 1982) ANOVA were performed with relative annual growth as the dependent variable to test for year-to-year and sex-related differences in growth. To compensate for lack of orthogonality due to unequal sample size, two-way ANOVA were executed using a simultaneous solution (Spinner and Gabriel, 1981). When main effects were significant, a multiple comparison of means (GT-2

method, Sokal and Rohlf, 1981) was used to identify specific differences.

Sexual maturity in males was assessed by microscopic examination for spermatozoa in fluid palpated from the vasa deferentia of males collected during late summer and early autumn. Sperm were considered to be absent if none were found after five smears were examined. The presence of vitellogenic follicles or embryos, determined by palpation in the field, indicated sexual maturity in females (Macartney and Gregory, 1988). Data on size of neonates were collected by removing near-term gravid females from the field and maintaining them in the laboratory until parturition, at which time neonates were measured (SVL), weighed, and marked. Neonates and postpartum females were returned to the females' capture sites within 48 h of parturition.

The significance level for all statistical tests was set at $\alpha = 0.05$. Means ± 1 SE are presented.

RESULTS

During this study, approx. 2175 individual rattlesnakes were marked and about 3220 recapture records were obtained. Records of annual growth numbered 519, with approximately equal representation by each sex in yearly samples (1981—80 males, 67 females; 1982—183 males, 189 females).

Neonate growth.—Neonates were born between mid-Sept.–mid-Oct. of 1981 and 1982. The mean SVL of neonates was 267 ± 2 mm for females ($n = 75$, range = 210–290 mm) and $270 \text{ mm} \pm 2$ mm for males ($n = 68$, range = 210–290 mm); the difference between sexes was not significant ($P[t_{141} > 1.2] = 0.23$). The interval between birth and the shedding of the protointegument (Duvall et al., 1985) to the button (B) stage averaged 24 ± 1 d ($n = 37$, range = 11–40 d). During this period, neonates did not feed and relative growth was negligible ($1.3 \pm 0.4\%$ increase in SVL). Neonates began hibernation 1–15 d after shedding.

Juvenile growth.—Relative annual growth was greatest and most variable among small rattlesnakes and declined in magnitude and variance with increasing body length (Fig. 1). A majority of yearling rattlesnakes (72%, $n = 47$) shed once during their first growing season; the remainder shed twice. In general, rapidly growing ju-

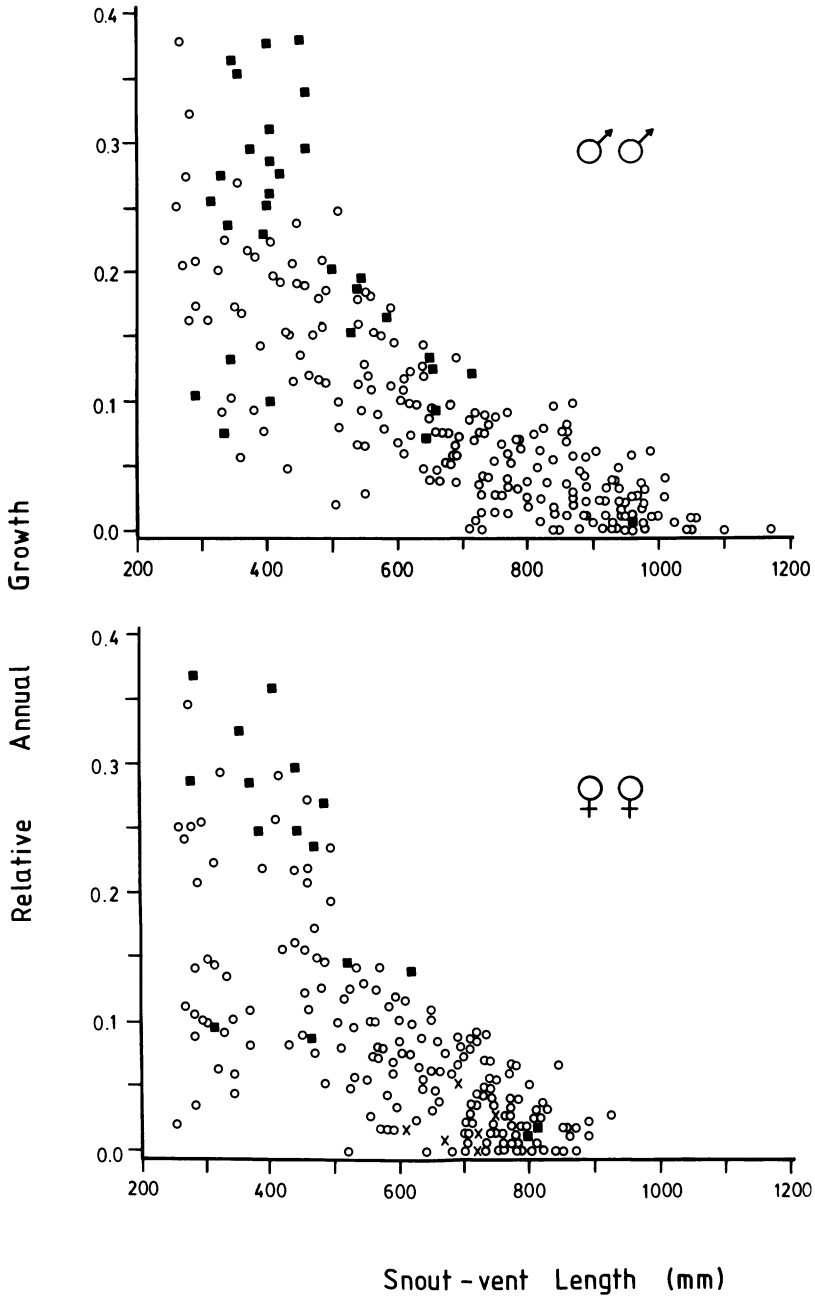


Fig. 1. Relationship between relative annual growth and SVL at the beginning of the growing season for male and female rattlesnakes, all years combined. Symbols refer to shedding frequency per annum: crosses = 0, open circles = 1, squares = 2. Hidden observations occur in each plot. n (males) = 263; n (females) = 256.

TABLE 1. SVL AND ANNUAL GROWTH DURING THE FIRST THREE GROWING SEASONS BASED ON SNAKES OF KNOWN AGE (MARKED AT B [BUTTON OR NEONATE] OR 1 + B [1 YEAR OLD] STAGES). Data combined for 1981–82 growing seasons. Means \pm 1 SE are presented. Results of t-tests to compare sexual differences in absolute and relative annual growth are shown. SVL_t = SVL at beginning of growth interval; n = sample size.

| Rattle increment class | n | SVL_t (mm) | Absolute growth (mm) | Relative growth |
|-------------------------------|----|-----------------|-------------------------------|-------------------------------|
| First year growth | | | | |
| Male | | | | |
| B to 1 + B | 10 | 282 \pm 6 | 70 \pm 6 | 0.25 \pm 0.02 |
| B to 2 + B | 3 | 295 \pm 10 | 113 \pm 40 | 0.39 \pm 0.14 |
| All males | 13 | 285 \pm 5 | 80 \pm 10 | 0.28 \pm 0.04 |
| Female | | | | |
| B to 1 + B | 17 | 285 \pm 4 | 41 \pm 5 | 0.14 \pm 0.02 |
| B to 2 + B | 8 | 276 \pm 9 | 109 \pm 11 | 0.40 \pm 0.04 |
| All females | 25 | 282 \pm 4 | 63 \pm 8 | 0.22 \pm 0.03 |
| t-test, (males vs females) | | | $t_{36} = 1.21$ $P = 0.23$ | $t_{36} = 1.15$ $P = 0.26$ |
| Second year growth | | | | |
| Male | | | | |
| 1 + B to 2 + B | 14 | 355 \pm 6 | 49 \pm 7 | 0.14 \pm 0.02 |
| 1 + B to 3 + B | 15 | 357 \pm 9 | 101 \pm 8 | 0.22 \pm 0.05 |
| 2 + B to 3 + B | 1 | 425 | 110 | 0.26 |
| All males | 30 | 358 \pm 8 | 77 \pm 7 | 0.22 \pm 0.02 |
| Female | | | | |
| 1 + B to 2 + B | 13 | 337 \pm 5 | 39 \pm 10 | 0.12 \pm 0.02 |
| 1 + B to 3 + B | 4 | 356 \pm 16 | 78 \pm 16 | 0.22 \pm 0.09 |
| 2 + B to 3 + B | 1 | 440 | 95 | 0.22 |
| 2 + B to 4 + B | 3 | 381 \pm 15 | 127 \pm 12 | 0.33 \pm 0.05 |
| All females | 21 | 352 \pm 7 | 61 \pm 7 | 0.17 \pm 0.02 |
| t-test, (males vs females) | | | $t_{49} = 1.45$ $P = 0.15$ | $t_{49} = 1.55$ $P = 0.13$ |
| Third year growth | | | | |
| Male | | | | |
| 2 + B to 3 + B | 1 | 430 | 65 | 0.15 |
| 2 + B to 4 + B | 3 | 413 \pm 25 | 115 \pm 9 | 0.28 \pm 0.01 |
| 3 + B to 4 + B | 4 | 486 \pm 8 | 86 \pm 13 | 0.18 \pm 0.02 |
| 3 + B to 5 + B | 1 | 460 | 115 | 0.34 |
| All males | 9 | 453 \pm 14 | 101 \pm 11 | 0.23 \pm 0.02 |

venile rattlesnakes tended to shed more frequently than slower growing snakes (Fig. 1, Table 1). Snakes captured at the end of their first growing season had 1 + B (read "one rattle segment plus the button") or 2 + B, whereas 2 yr old rattlesnakes had 2 + B, 3 + B or 4 + B (Table 1). Males exhibited slightly greater average absolute and relative annual growth during the first and second growing season than females, but these differences were not significantly different (Table 1). Annual growth dur-

ing the third year remained at a high level in males; comparative data were not available for females.

Estimates of mean SVL for age classes 1–6 yr that are presented in Table 2 include recaptures of rattlesnakes that were marked either shortly after birth at the B stage or at the end of their first growing season with 1 + B. The inclusion of 1 + B snakes increased the sample size of known aged snakes, but introduced a slight bias because a 1 + B snake could be identified as 1

TABLE 2. RELATIONSHIP BETWEEN AGE AND SVL OF JUVENILE MALE AND FEMALE *Crotalus viridis oreganus* BASED ON RECAPTURES FROM 1981–86 OF SNAKES THAT WERE ORIGINALLY MARKED AT BIRTH (B) OR AT 1 YR (1 + B). Mean SVL \pm 1 SE (mm) and sample size in parentheses are presented by age class, and by rattle size to illustrate the overlap in SVL and rattle size among age classes.

| Age (years) | All males | 1 + B | 2 + B | 3 + B | 4 + B | 5 + B | 6 + B | 7 + B | 8 + B |
|-------------|----------------------|----------------------|---------------------|----------------------|----------------------|---------------------|--------------------|----------------------|---------------------|
| 0 | 270 \pm 2 (68) | | | | | | | | |
| 1 | 353 \pm 3 (100) | 350 \pm 3 (95) | 402 \pm 23 (5) | | | | | | |
| 2 | 440 \pm 9 (36) | | 402 \pm 8 (15) | 467 \pm 11 (21) | | | | | |
| 3 | 552 \pm 17 (15) | | | 455 \pm 40 (2) | 549 \pm 15 (10) | 628 \pm 13 (3) | | | |
| 4 | 616 \pm 23 (7) | | | | | 603 \pm 60 (3) | 626 \pm 8 (4) | | |
| 5 | 740 \pm 5 (2) | | | | | | 740 \pm 5 (2) | | |
| 6 | 725 \pm 15 (2) | | | | | | | | 725 \pm 15 (2) |
| | All females | | | | | | | | |
| 0 | 267 \pm 2 (75) | | | | | | | | |
| 1 | 343 \pm 3 (121) | 340 \pm 3 (113) | 385 \pm 17 (8) | | | | | | |
| 2 | 423 \pm 11 (28) | | 378 \pm 6 (14) | 453 \pm 18 (9) | 493 \pm 20 (5) | | | | |
| 3 | 475 \pm 37 (6) | | | 417 \pm 42 (3) | 533 \pm 39 (3) | | | | |
| 4 | 596 \pm 28 (6) | | | | 533 \pm 13 (2) | 500 (1) | 655 \pm 5 (3) | | |
| 5 | 678 \pm 35 (6) | | | | | | 510 (1) | 711 \pm 12 (5)* | |
| 6 | 745 (1) | | | | | | | | 745 (1)** |

* Three of the five females had enlarged follicles at the end of the fifth growing season.
 ** Nongravid female.

TABLE 3. ANNUAL GROWTH OF ADULT RATTLESNAKES. Snakes were placed in the size class based on SVL at the beginning of the active season. Means \pm SE presented.

| Size class (mm) | Males | | | Nongravid females | | | Gravid females | | |
|-----------------|-------|----------------------|-------------------|-------------------|----------------------|-------------------|----------------|----------------------|--------------------|
| | n | Absolute growth (mm) | Relative growth | n | Absolute growth (mm) | Relative growth | n | Absolute growth (mm) | Relative growth |
| 650-749 | 39 | 45.1 \pm 3.6 | 0.065 \pm 0.005 | 43 | 28.1 \pm 3.3 | 0.040 \pm 0.005 | 8 | 13.1 \pm 9.9 | 0.0181 \pm 0.005 |
| 750-849 | 33 | 33.2 \pm 3.4 | 0.042 \pm 0.004 | 31 | 16.8 \pm 2.3 | 0.022 \pm 0.003 | 19 | 4.2 \pm 1.8 | 0.0054 \pm 0.002 |
| 850-949 | 24 | 22.2 \pm 4.5 | 0.025 \pm 0.005 | 4 | 13.8 \pm 5.2 | 0.016 \pm 0.006 | 4 | 8.8 \pm 5.2 | 0.0099 \pm 0.006 |
| 950-1049 | 24 | 17.1 \pm 3.5 | 0.017 \pm 0.003 | | | | | | |
| \geq 1050 | 4 | 5.0 \pm 2.9 | 0.005 \pm 0.003 | | | | | | |

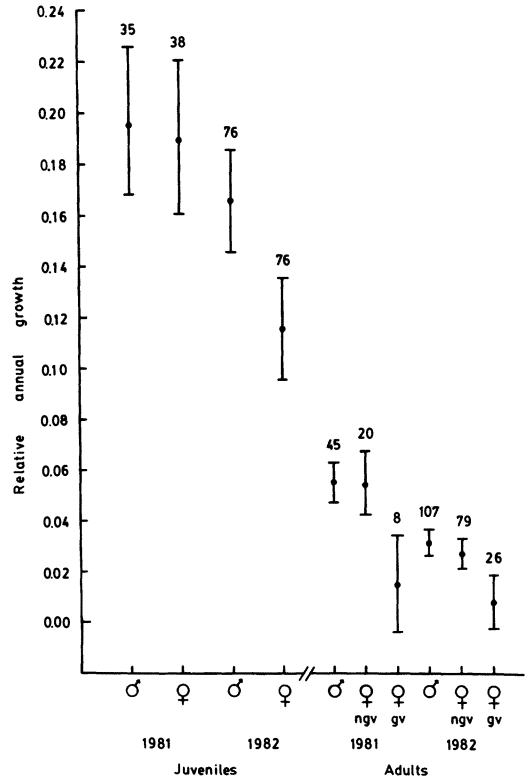


Fig. 2. Year to year variability in relative annual growth of juvenile and adult rattlesnakes. Symbols ngv = nongravid females, gv = gravid females. Vertical bars are 95% comparison intervals by the GT-2 method (Sokal and Rohlf, 1981). Within juveniles and adults, mean values whose intervals do not overlap are significantly different. Number above bar = sample size.

yr old, whereas the age of a snake first captured with 2 + B was uncertain. Unbiased estimates using only 1 yr olds marked at the B stage yielded slightly greater mean SVL values (males 364 \pm 12 mm, n = 13; females 349 \pm 8 mm, n = 25) than for all known 1 yr old snakes (Table 2). For 2 yr old rattlesnakes, unbiased estimates of mean SVL also were slightly greater (males 462 \pm 19 mm, n = 13; females 459 \pm 14 mm, n = 14) than for all known 2 yr old snakes.

There was a strong positive correlation between age and the mean SVL of individuals in an age class (males r = 0.986, females r = 0.997, n = 7, columns 1 and 2 in Table 2). Also, the average difference in mean SVL between male and female rattlesnakes in each age class was about 7% (higher in males; Table 2).

Sexual maturity.—Spermatozoa were observed in smears from 75 of 85 males examined (SVL range = 510–1050 mm) and the smallest sexually mature male in this sample was 535 mm SVL. The smallest female that possessed enlarged follicles was 650 mm SVL. Enlarged follicles were present in three of five females recaptured at the end of their fifth growing season, but not in one 6 yr old female (Table 2). Annual recaptures of adult females that were originally marked when immature (<650 mm SVL) revealed that many females did not attain sexual maturity and produce litters until they had reached between 700 and 760 mm SVL.

Adult growth.—Although males matured at a smaller SVL than females, a sudden decrease in growth did not accompany attainment of sexual maturity (Fig. 1). Therefore, when we compared differences in growth rates of adult male and female rattlesnakes, all snakes ≥ 650 mm SVL were considered to be adult. As a rule, adult rattlesnakes shed only once per annum (Fig. 1). Male rattlesnakes continued to show slightly greater average absolute and relative annual growth than nongravid females; however, the rate of decrease in annual growth with increasing SVL was about the same in both groups (Table 3). Gravid females had the lowest average annual growth; most individuals showed no measurable growth during the year in which they were gravid.

The largest rattlesnakes in the population were a 1170 mm SVL (961 g) male and a 950 mm SVL (691 g) gravid female. Large adult males typically ranged from 950–1050 mm SVL, whereas large adult females ranged from 850–900 mm SVL.

Annual and sexual differences in growth (SVL).—For juveniles (<650 mm SVL), there were significant differences in relative growth between the sexes ($F_{1,221} = 4.4$, $P = 0.037$) and between years (1981 and 1982; $F_{1,221} = 14.5$, $P < 0.001$). The interaction term was not significant ($F_{1,221} = 0.17$, $P = 0.68$). Unplanned comparisons of mean growth revealed two trends: 1) growth of juveniles was lower in 1982 than in 1981; and 2) growth rates were not significantly different between sexes in 1981, but in 1982 females grew at a lower rate than males (Fig. 2).

In the ANOVA to examine annual and sex-related differences in adults, the factor sex had three levels: males, nongravid females, and gravid females. There were significant effects

due to sex/reproductive condition ($F_{2,279} = 14.3$, $P < 0.001$) and year ($F_{1,279} = 18.8$, $P < 0.001$). The interaction term was not significant ($F_{2,279} = 1.1$, $P = 0.34$). Mean annual growth of adult males was not significantly different from nongravid females, but both showed greater annual growth than gravid females (Fig. 2). Compared across years, annual growth was significantly lower in 1982 for adult males and nongravid females.

Annual and sexual differences in growth (M).—Annual relative M increments for juveniles of both sexes approached their maximum values during the second or third growing seasons at SVL between 350–450 mm and thereafter declined with increasing SVL (Fig. 3). Relative mass changes closely paralleled relative SVL changes in juvenile rattlesnakes. There were strong positive correlations between these measures of annual growth in juvenile males ($r = 0.81$, $P < 0.001$, $n = 18$) and juvenile females ($r = 0.81$, $P < 0.001$, $n = 23$). For adult males this relationship was not quite so strong ($r = 0.74$, $P < 0.001$, $n = 37$) and relative SVL change explained only about 25% of the variation seen in relative M change in nongravid females ($r = 0.52$, $P = 0.003$, $n = 30$). Relative annual mass changes of nongravid females were nearly double those of adult males. Gravid females exhibited only small losses in M (about 6%) during gestation.

Equations describing mass-length relationships were $M = 510 \text{ SVL}^{2.85}$ for females and $M = 535 \text{ SVL}^{2.88}$ for males, where M is expressed in grams and SVL in meters. These equations were calculated from capture records for individuals from all sites and throughout the entire growing season. Confidence intervals (95%) placed around the linear regressions of log M on log SVL showed complete overlap between sexes, indicating no sexual dimorphism in this relationship, in general. Separate inspections of these relationships for different age and sex/reproductive status groups also were made. Among juveniles there was little overlap of 95% confidence intervals, and juvenile females were a slightly smaller mass at a given SVL than males (Fig. 4). Among adults, there was complete overlap between males and nongravid females; however, at a given SVL, gravid females always were heavier and postpartum females always lighter than the former adult groups (Fig. 4).

Patterns of ecdysis.—The pre-ecdysis period

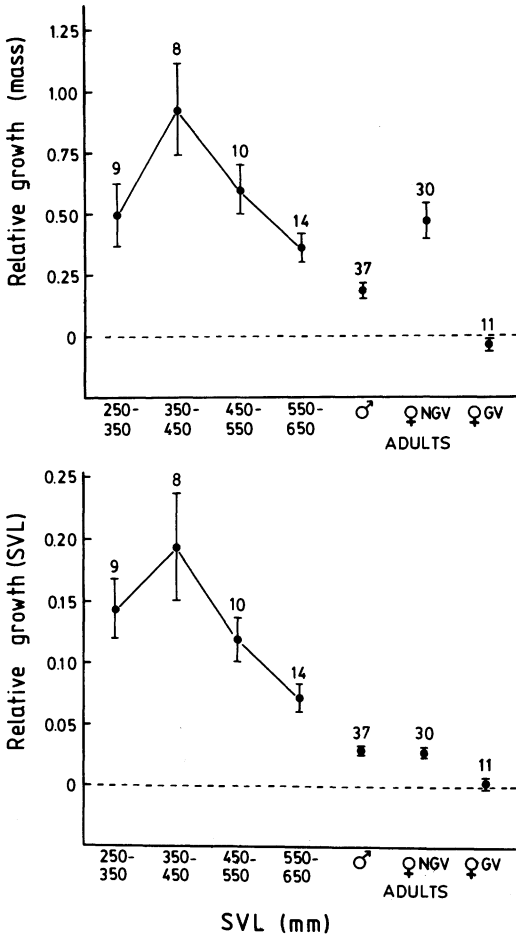


Fig. 3. Mean annual changes in relative growth (M above, SVL below) of juvenile and adult rattlesnakes. Means \pm 1 SE are shown. Gravid females include only those possessing enlarged follicles in the spring, whereas nongravid females include both postpartum females and females with anestrus follicles.

(cloudy opercular scute until sloughing) lasted 18 ± 2 d (range = 13–21 d), based on repeated field observations of seven adult rattlesnakes. The seasonal distribution of capture records of shedding snakes for different age or sex categories in the population is presented in Figure 5. Gravid females shed once per annum and earlier in the summer than most other snakes, with the exception of adult males. Some adult males underwent a second episode of ecdysis in late summer (confirmed by rattle segment number increases since their spring capture). Nongravid females generally shed 1–2 wk later than most adult males; the proportion of nongravid snakes in ecdysis peaked during the first week

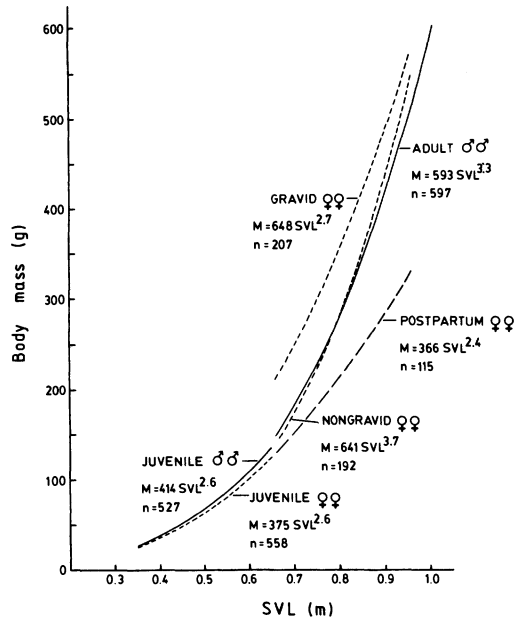


Fig. 4. M-body length curves and equations for juvenile and adult *Crotalus viridis oreganus*. Mass expressed in grams, SVL expressed in meters. The gravid female category also includes females captured in the autumn with enlarged follicles, whereas the nongravid category includes only adult females with anestrus follicles.

of August. A small number of nongravid females delayed ecdysis until late summer; others shed for a second time during late summer or early fall. The bimodal distribution of ecdysis for juveniles corresponds to a greater incidence of biannual shedding.

Geographic variation in growth.—Many studies of *C. viridis* have included information pertaining to growth rates or have presented formal analyses of growth. A summary of juvenile growth for four subspecies of *C. viridis* from seven localities supports the idea of a general trend towards slower annual growth with increasing latitude in *C. viridis* (Table 4). There are apparent exceptions to the trend, particularly the rapid growth of juvenile *C. viridis viridis* in Saskatchewan (Gannon and Secoy, 1984) and the second year growth of juvenile *C. v. oreganus* in a British Columbia population (Preston, 1964).

DISCUSSION

Rattlesnake growth usually has been analyzed by a mixture of direct and indirect methods.

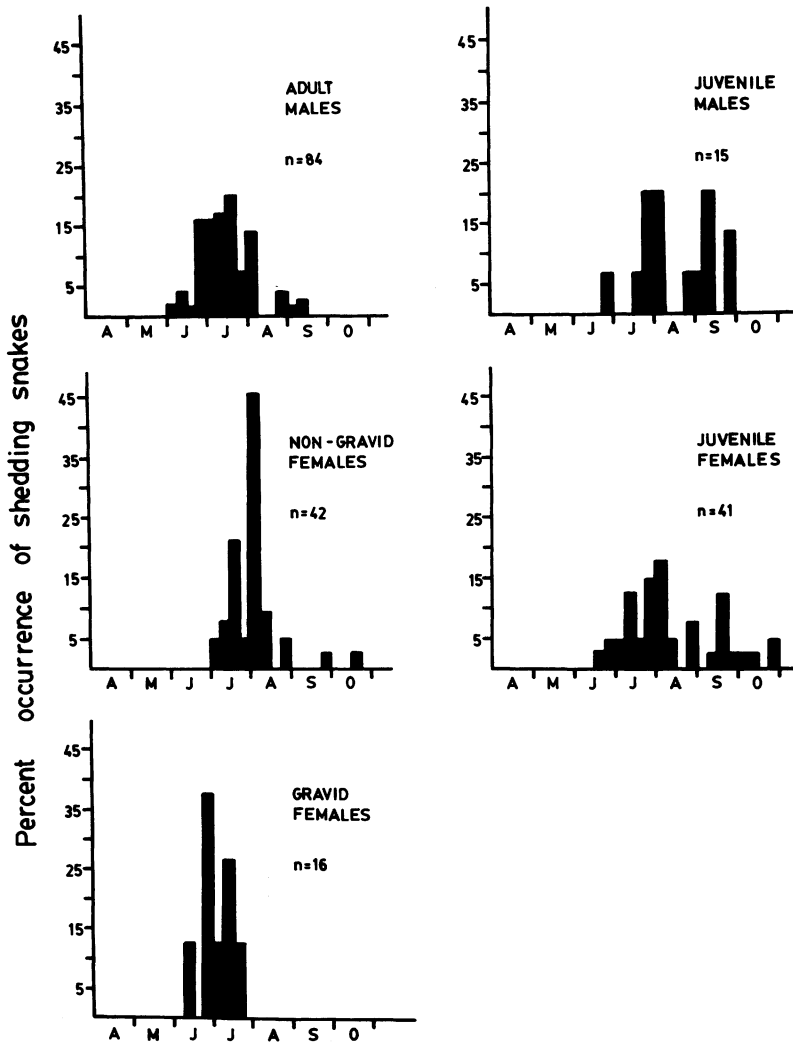


Fig. 5. Seasonal distribution of observations of ecdysis in different age and sex categories of *Crotalus viridis oreganus*, based on observations during 1981–82.

The former are based on growth measurements obtained through mark-recapture, while the latter require interpretation of size-frequency distributions (body and/or rattle size) of the population, or extrapolations based on growth rates known for a segment of the population. Klauber (1937) recognized the subjectivity and the possibility of error when using SVL or rattle class groupings to identify age classes, particularly when it is difficult to sample the entire population and when little is known about the shedding frequency of different sized individuals in the population.

We relied mainly on direct methods to estimate annual growth and to describe age/size classes in the population. Variability in juvenile growth was so great that it was not possible to distinguish non-overlapping SVL/rattle classes for consecutive age groups. Furthermore, size at birth may vary among years; Charland (1989) found that SVL of neonates from the same population in 1985 averaged 16 mm greater than those reported here. Therefore, despite a reasonable knowledge of the frequency of shedding and of growth rates in different juvenile rattle classes, we felt that extrapolation to pre-

TABLE 4. SUMMARY OF JUVENILE GROWTH FOR FOUR SUBSPECIES OF *Crotalus viridis* FROM SEVEN LOCALITIES. Average SVL (to the nearest 5 mm) and number of rattle segments (in parentheses) are presented for males where specified; otherwise sexes are combined.

| Subspecies | Locality | Lat. (°N) | Sex | Age (years) | | | Source |
|-----------------|--------------------------------|-----------|-----|-------------|----------------|----------------|--|
| | | | | 0 | 1 | 2 | |
| <i>viridis</i> | Leader, Saskatchewan | 51 | M | 250 | 590 (?) | 800 (?) | Gannon and Secoy, 1984 this study |
| | Vernon, British Columbia | 50 | M | 270 | 365 (1-2 + B) | 440 (2-4 + B) | |
| <i>oreganus</i> | Oliver, British Columbia | 49 | M | 290 | 375 (2 + B) | 560 (5 + B) | Preston, 1964 |
| <i>oreganus</i> | Nez Perce and Latah Co., Idaho | 46 | M | 280 | 395 (1-2 + B)* | 480 (3-4 + B)* | Diller and Wallace, 1984 |
| <i>lutosus</i> | Tooele Co., Utah | 41 | M | 290 | 460 (1 + B) | 560 (2-3 + B) | Heyrend and Call, 1951 Parker and Brown, 1974 |
| <i>oreganus</i> | Madera Co., California | 37 | — | 280 | 500 (3 + B) | 630 (7-8 + B) | Fitch, 1949 Fitch and Glading, 1947 |
| <i>helleri</i> | San Diego Co., California | 33 | M | 275 | 540 (3 + B) | 800 (7-8 + B) | Klauber, 1937, 1972 |

* SVL and rattle size inferred from text or calculated from data presented in source.

dict successive age/size would be too subjective. Fortunately, we could rely on mark-recapture data, although the sample size in consecutive age classes grew smaller and the estimates of mean body size were slightly biased.

In this study, growth rates were lower in 1982 than in 1981. In 1981, a cool wet spring was followed by a hot dry summer, whereas in 1982 a warm dry spring preceded a wet summer. In the Okanagan Valley, much precipitation is needed for the vegetation to flush early in the spring. The favorable conditions in 1981 may have enhanced the productivity of the ecosystem and enabled snakes to forage more effectively; however, we have no direct evidence to suggest that weather had an influence on growth rates of snakes.

Platt (1984) found a direct relationship between annual growth of bullsnakes (*Pituophis melanoleucus*) and prey availability. Prey abundance was not measured in this study; however, the proportion of rattlesnakes with stomach contents during the main feeding months (June–Aug.) was actually lower in 1981 (12.3%) than in 1982 (20.9%) (Macartney, unpubl.). It is difficult to know to what degree these data reflect differences in foraging success, prey abundance, sampling differences or a combination of these factors; therefore, annual growth may not be strongly related to this measure. Also, we do not know why growth of juvenile females was affected to a greater extent than juvenile males in 1982.

The factors affecting growth rates of *C. viridis* may be quite complex. Charland and Gregory (1989) found that postpartum females fed at a high rate in enclosures did not necessarily gain more weight than females fed at a low rate. They suggested that snakes might respond to low food levels by behaviorally maintaining a lower body temperature and thereby reducing their energy costs. Thus, weather and food supply would interact in influencing growth rates.

Male *C. viridis* attain sexual maturity in British Columbia at a minimum SVL of 535 mm, which corresponds to the third growing season. Females attain sexual maturity at a minimum SVL of 650 mm. We know from recaptures that some females in these populations have enlarged follicles at the end of their fifth growing season; these females would produce their first litter at the end of their sixth year. Other females require one or two additional growing seasons to attain sexual maturity and therefore may not produce their first litter until the end

of their seventh or eighth year. Sexual maturation occurs at a later age in British Columbia populations of *C. viridis* than in any other known conspecific population (Macartney and Gregory, 1988).

Snakes of the genus *Crotalus* exhibit a marked sexual size dimorphism in which males attain a larger body size than females in most species (Klauber, 1972). In the Okanagan Valley, average body size and annual growth of juvenile male *C. viridis* were only slightly greater than those of females in corresponding age classes. These differences in growth rates during juvenile years and the cessation of growth of females during reproductive years may be the main factors contributing to sexual size dimorphism in this species. The negligible growth of gravid females is not surprising, since they usually do not feed for the entire year in which they are gravid (Macartney and Gregory, 1988; Macartney, 1989).

Our review of geographic variation in juvenile growth among widespread populations of *C. viridis* suggests a trend of reduced annual growth of juveniles along a latitudinal gradient. Rattlesnakes are active in southern California for about 9 mo (early March–late Nov., Klauber, 1937) and for 7–8 mo in central California (Fitch and Glading, 1947). In both localities, rattlesnakes may be active above ground during occasional warm spells in winter. At high latitudes (Idaho and British Columbia) or high altitudes (Utah) there is an abbreviated active season of 5–7 mo and hibernation is continuous. Therefore, differences in growth among populations along a latitudinal gradient appear to be related in part to differences in the length and thermal regime of the active season.

An extended autumn activity period in California contributes to the rapid growth of neonates in southern California relative to neonates in British Columbia. Neonatal *C. v. helleri* in San Diego County complete their initial molt 7–14 d after birth (Klauber, 1940) and may grow as much as 45 mm during the 1–2 mo period prior to the start of hibernation at the end of Nov. (Klauber, 1937). Klauber also believed that neonates may feed before overwintering and that some growth occurs during the 3–4 mo period of hibernation, since B stage rattlesnakes had an average SVL of 350 mm upon emergence in early March. In British Columbia, neonates do not feed prior to hibernation and the lengthy overwintering period curtails growth of neonates for the first 7 mo of life. At 6 mo of age

C. v. helleri are about the same length as 1 yr old *C. v. oregonus* in British Columbia. The disparity in size at a given age between these populations increases with age. A 1 yr old from southern California is the same size as a 3 yr old from British Columbia, and at 2 yr attains a length that would be reached at about 7 yr in British Columbia.

The differences are less pronounced when annual growth of juvenile *C. v. oregonus* in British Columbia is compared with that of conspecific populations from higher latitudes. The SVL and rattle size of snakes at 1, 2 and 3 yr of age in central California (Fitch, 1949) approximate those of 3, 4 and 5 yr olds in British Columbia (Table 4). The size of *C. v. lutosus* in Utah at 1, 2 and 3 yr of age is about the same as 2, 3 and 4 yr old snakes in British Columbia.

First year growth does not vary appreciably among the three northern populations of *C. v. oregonus*. Preston's (1964) estimate of size at 2 yr suggests more rapid growth during the second year than was found in this study or than was estimated from Diller and Wallace's (1984) data. However, an inconsistency is present in Preston's data in that his 1 yr olds entered hibernation with either 1 + B or 2 + B, but the snakes he placed at the beginning of their second growing season had 3 + B. Our interpretation of his data is that snakes with 3 + B were likely beginning their third growing season and that the size of 560 mm SVL attained at 2 yr should correspond to the size attained at 3 yr. If this is correct, then there do not appear to be noticeable differences between these closely situated populations (130 km apart) in British Columbia. The average size we estimated for 1 and 2 yr old rattlesnakes from Diller and Wallace's (1984) data suggests slightly more rapid juvenile growth in Idaho; however, these values are within the range of sizes attained by rapidly growing juveniles in British Columbia.

Gannon and Secoy (1984) estimated first year growth in *C. v. viridis* from Saskatchewan to be 33.7 cm, a value higher than was previously reported for any population of *C. viridis*. This estimate was derived from a regression equation that was based on absolute growth in a small sample ($n = 6$) of adult males. Given that growth rates of juveniles are quite different from adults, we do not consider this to be an accurate method for estimating juvenile growth. Gannon and Secoy also made the assumption that a discrete, but rather broad, size class peak between neonates and adults in a single size-frequency dis-

tribution represented snakes between 12–24 mo of age. Juveniles were not well represented in the population and they provided no growth data based on recaptured juveniles to justify their assumption. Furthermore, their interpretation of the distribution peaks in their histogram as being distinct age groups is equivocal. Gaps between size distribution peaks in the juvenile segment of a population also could be due to low recruitment into the population in (a) previous year(s). Growth of Saskatchewan *C. viridis* may indeed be rapid but the data Gannon and Secoy (1984) have presented do not convincingly demonstrate this.

Fitch (1985) attempted to place *C. v. viridis* from Kansas into annual cohorts using rattle measurements, but his assignment of individuals to SVL/age class groupings was partly subjective and the data presented were not of sufficient detail for extracting growth information. However, Kansas *C. v. viridis* appear to grow at rates similar to *C. v. oregonus* from the same latitude in central California. A general trend for reduced annual growth in northern populations of *C. viridis* is supported by the majority of studies.

Neonatal rattlesnakes grow at an average rate of 13 mm/month in British Columbia, whereas in California growth during the first year is an average of 24 mm/month (Fitch, 1949). This nearly two-fold difference suggests that other factors influence growth rate. We would expect temporal and geographic differences in prey abundance to contribute to variability in growth rate among rattlesnake populations. For example, small lizards and amphibians, which make up most of the diet of juvenile *C. viridis* in California (Fitch and Twining, 1946), are scarce in our study area and juvenile rattlesnakes prey mainly on shrews and juvenile rodents (Maccartney, 1989). We have recaptured 1 yr old snakes at hibernacula that weighed less than at birth and that had grown very little. Emaciated young-of-the-year were also reported by Fitch and Twining (1946). Therefore, prey may be difficult for some neonates to find. Finally, some of the variability in growth and body size observed among populations of *C. viridis* may stem from genetic differences. Separating the effects of environment and genotype might be addressed by an experimental laboratory approach similar to that which has been used for lizards (Ferguson and Brockman, 1980). Neonatal rattlesnakes can easily be maintained in captivity and would be amenable to thermal or

dietary manipulations that would help separate these effects.

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A New Species of *Hyla* (Anura, Hylidae) from Southern Minas Gerais, Brazil

ULISSES CARAMASCHI AND RENATO N. FEIO

***Hyla ibitipoca*, a member of the *H. circumdata* species group, is described from the Parque Estadual do Ibitipoca, Lima Duarte, southern Minas Gerais, Brazil. The new species inhabits gallery forests along small creeks and is characterized by its small size, color pattern, transverse dark bars on thighs and flanks, and small tympanum.**

TREEFROGS of the *Hyla circumdata* group are characterized by a well-developed prepollex and dark vertical stripes on the posterior surface of thighs; these features distinguish this group of species from all other *Hyla* in eastern Brazil (Heyer, 1985). The species currently allocated to the *H. circumdata* group by Frost (1985) include *H. astartea*, *H. carvalhoi*, *H. circumdata*, *H. ibitiguara*, *H. izecksohni*, *H. nanuzae*, and *H. sazimai*. Heyer (1985) added *H. hylax*; we also place *H. martinsi* in the group.

During a survey of the herpetofauna of the Parque Estadual do Ibitipoca, southern Minas Gerais, Brazil, we collected specimens of a species in the *H. circumdata* group that do not agree with any of the described species. This new species is described herein.

The abbreviations used in the account are: SVL (snout-vent length), HL (head length), HW (head width), IND (internarial distance), END (eye to nostril distance), ED (eye diameter), IOD (interorbital distance), UEW (upper eyelid

width), TD (tympanum diameter), 3FD (3rd finger disk diameter), 4TD (4th toe disk diameter), THL (thigh length), and TL (tibia length). Webbing formula follows Myers and Duellman (1982). Acronyms of the collections housing specimens follow Frost (1985). All measurements are in mm.

Hyla ibitipoca n. sp.
Figs. 1–2

Holotype.—MN 4460, adult male, collected at the Parque Estadual do Ibitipoca, Lima Duarte Municipality (ca. 21°42'S, 43°53'W), State of Minas Gerais, Brazil, on 06–09 Dec. 1986, by U. Caramaschi, R. N. Feio, M. C. Britto-Pereira and H. R. Silva.

Paratopotypes.—Thirty-five adult males: MN 4453–4459, collected on 17–20 Nov. 1986, by R. N. Feio; MN 4461–4471, collected with the holotype; MN 4521–4525, collected on 16–19