



ALLEN
PRESS



Reproductive Biology of the Northern Pacific Rattlesnake (*Crotalus viridis oregonus*) in Northern Idaho

Author(s): Lowell V. Diller and Richard L. Wallace

Source: *Herpetologica*, Jun., 1984, Vol. 40, No. 2 (Jun., 1984), pp. 182-193

Published by: Allen Press on behalf of the Herpetologists' League

Stable URL: <https://www.jstor.org/stable/3892075>

REFERENCES

Linked references are available on JSTOR for this article:

https://www.jstor.org/stable/3892075?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <https://about.jstor.org/terms>



Allen Press and Herpetologists' League are collaborating with JSTOR to digitize, preserve and extend access to *Herpetologica*

JSTOR

REPRODUCTIVE BIOLOGY OF THE NORTHERN PACIFIC RATTLESNAKE (*CROTALUS VIRIDIS OREGANUS*) IN NORTHERN IDAHO

LOWELL V. DILLER AND RICHARD L. WALLACE

ABSTRACT: Reproductive biology of the northern Pacific rattlesnake (*Crotalus viridis oregonus*) was studied in snakes from three hibernacula in northern Idaho from 1978 to 1981. More females than males were captured, but an analysis of unbiased samples showed a 1:1 sex ratio. Mature males captured from late March to October carried spermatozoa in at least the distal portion of the vas deferens. Upon first emergence, reproductive females had large yolked ova, up to 35 mm in length. Ovulation occurred from mid-May to mid-June. Parturition occurred over a 30-day period beginning in early September. Males longer than 52 cm snout-vent length (SVL) and with four or more rattles were sexually mature. Most females larger than 55 cm SVL and with five or more rattles were sexually mature. Mean clutch size was 5.5, and clutch size was significantly correlated with female body size. The mean proportion of females reproducing annually varied from 54–77% in the three populations of snakes. Reproductive females had the greatest percentage body fat, followed by nonreproductive females and males. The population of snakes with the highest mean proportion of females reproducing annually (77%) also had significantly larger fat bodies. We concluded that nutrition, as evidenced by the size of fat bodies, is the major factor controlling the frequency of reproduction in females.

Key words: Reptilia; Serpentes; Viperidae; *Crotalus*; Reproduction; Fat bodies

THE northern Pacific rattlesnake, *Crotalus viridis oregonus*, is distributed from central California northward through much of Oregon, eastern Washington and northcentral Idaho to southern British Columbia (Stebbins, 1966). In general, western rattlesnakes (*Crotalus viridis*) have been rather extensively studied (Aldridge, 1979a; Diller, 1981; Fitch, 1949; Fitch and Glading, 1947; Kaluber, 1956; Rahn, 1942; Woodbury, 1951). However, the field study done by Fitch in the 1940's of *C. viridis oregonus* in central California near the southern limit of its range is the only major work done on this subspecies.

One objective of this study was to determine certain key aspects of the life history of *C. viridis oregonus* in northern Idaho near the northern limits of its range and compare these results with similar data from populations occurring in more southern regions. In particular, we compared clutch size, frequency of reproduction in females, timing of seasonal reproductive events, and fat body cycles. We worked with three populations of snakes to determine also how these same life his-

tory features might vary among sites in the same general locality.

STUDY AREA

All collections came from sites located in northern Idaho, in Nez Perce and southern Latah counties. These counties are in the eastern portion of the Columbia Plateau Province of the Pacific Northwest. Nez Perce County is bisected by the Clearwater River canyon, which separates the Palouse Hills section to the north from the Craig Mountain section to the south. There is considerable dry land farming in the region. Elevation varies from 225 m at the mouth of the Clearwater River to > 1120 m in the Craig Mountain area.

The climate of the area can be characterized as modified temperate continental, with precipitation mostly in the winter. The mean number of frost free days varies locally from 150–170 per year. Annual precipitation varies from 38–60 cm. Mean annual snow fall is about 100 cm. The average annual temperature is about 10 C. The mean maximum temperature in January is about 3 C and the mean min-

imum temperature is near -5 C. In July, the mean maximum and minimum temperatures are about 30 C and 12 C, respectively.

Hibernacula in the general study area are usually located in talus on southerly exposed grassy slopes, similar to those described by Klauber (1956) for *C. v. oreganus* in the Pacific Northwest. These rock slides can be very extensive, but most are <1 ha. We found most snakes at the upper edge of rock slides, where a layer of dirt and smaller rock covered the larger talus. We seldom found rattlesnakes in the lower half of slides, where larger rocks (20–40 cm) accumulated.

Most of our field work was concentrated at three hibernacula: Tammany Creek (TC) was located about 18 km south of Lewiston, Nez Perce County, at about 760 m in elevation, Wally's Den (WD) 9 km northeast of Kendrick, Latah County, at an elevation of 610 m, and Kendrick Den (KD) about 3 km north of Kendrick, Latah County, at an elevation of 520 m. Other hibernacula were visited during the course of the study, but they contributed only minor numbers of snakes.

METHODS AND MATERIALS

A total of 387 *C. v. oreganus* was collected over a 4-yr period from 1978–1981. The majority of snakes were collected during searches through the talus at appropriate times of day. Almost 70% of the rattlesnakes were collected in the spring with the remaining captures occurring throughout summer and fall. All captures of snakes that were found active at or near hibernacula were considered to be biased samples relative to sex ratios. Only two collections of snakes were considered unbiased relative to sex ratios. The first was 66 snakes that were excavated from a hibernaculum prior to spring emergence. The second sample considered unbiased came from a collection of 23 snakes captured in drift fences during fall reentry into one hibernaculum in 1980. All captured snakes were taken to the laboratory and immediately frozen, except for 21 ju-

venile snakes that were marked and released.

The following data were recorded for each snake: sex, snout–vent length (SVL), total body mass, number of rattles (counts excluded the proximal segment), fat body mass, and reproductive condition. Abdominal fat bodies were extracted, weighed and expressed as a percent of total body mass. Males were judged sexually mature based on the presence of spermatozoa in the vas deferens (mature males had spermatozoa in the vas deferens at all times of the year that they were collected). Females were judged sexually mature if they would have produced young the year of capture or if the snake previously had young. In the early spring, females were identified as reproductive by the presence of conspicuously yolked ova. We were able to determine that many females collected in the early spring had young the previous year by the presence of “incubation chambers” in the oviducts (Rahn, 1942). The following additional data were recorded for most females: number of yolked ova, ova size (length \times width), position of ova (ovarian or oviducal), ova mass and condition of the oviducts when appropriate. Clutch size was considered the number of ova ovulated.

Estimates of reproductive effort were patterned after Tinkle and Hadley (1973), who calculated reproductive effort in *Sceloporus jarrovi* as “the total energy content of eggs compared with that of the whole body.” Our estimates of reproductive effort were calculated in two ways: (1) mean caloric content of a clutch of recently ovulated eggs divided by the mean caloric content of the whole body of mature females, and (2) mean caloric content of a clutch of neonates divided by the mean caloric content of females. Caloric content of eggs, neonates and female whole bodies was estimated from wet weights using the conversions proposed by Vitt (1978). Neonate caloric content was calculated using the conversion for total body calories, since Vitt did not propose a separate conversion for neonates.

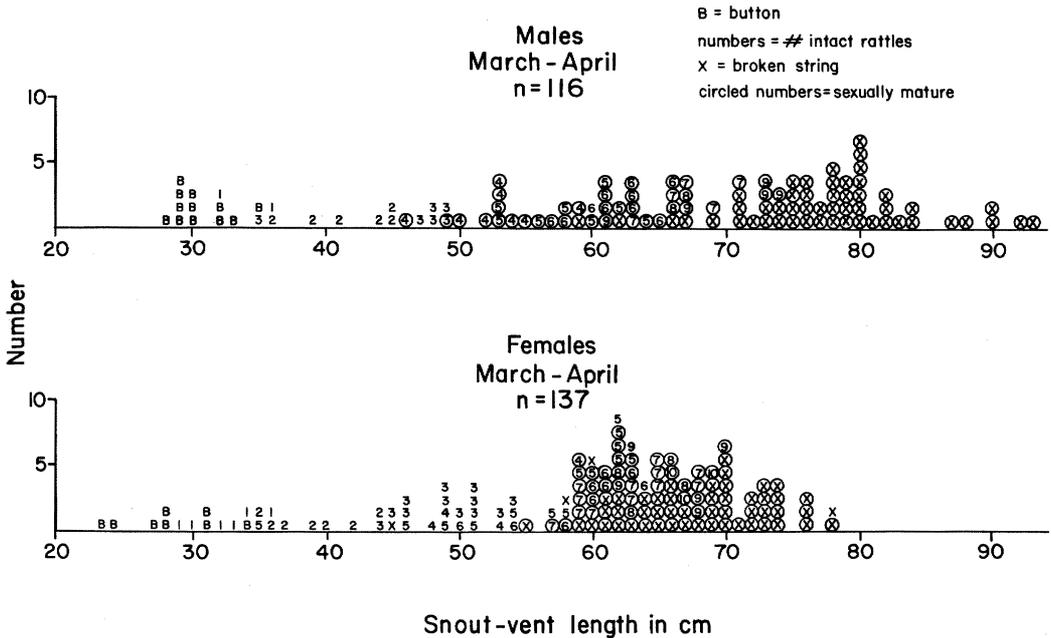


FIG. 1.—Length frequency, number of rattles, and sexual maturity of *Crotalus viridus oregonus* captured in early spring.

Student's *t*-tests were used for comparisons of mean length of males and females when variances were equal. If the variances were unequal, we used the Behren-Fisher *t*-test, *t'*, with the degrees of freedom estimated using the Satterthwaite approximation. Data on percent body fat (percent of total body mass) were treated by ARCSIN transformation. These data were then analyzed by a completely random ANOVA, 3 × 4 factorial design (three locations, four reproductive conditions of snakes).

RESULTS

Activity

First emergence of *C. viridus* from their hibernacula occurred from late March to mid-April depending on the vagaries of weather and exposure of a particular hibernaculum. The latest capture of a snake in the fall occurred on 16 November, but most snakes had reentered hibernacula by early October.

Detailed observations were not made on daily activity of snakes. However, during a typical sunny day snakes began sunning about 1000 h and all snakes were under some type of shelter by early afternoon. A second period of daily activity typically occurred in the late afternoon and evening, but it was less predictable and extensive than the morning activity period.

Population Structure and Growth Rates

Distinct size or age classes were difficult to identify based on length-frequency data or rattle formation (Fig. 1). Snakes with only a button were probably all born the previous fall and were entering their first summer of growth, but additional age classes cannot be clearly identified. The length-frequency distribution appears to be a continuum with no discrete size classes. The frequency of rattle numbers also cannot be separated into discrete groups. In the spring, only two males were

found with just one rattle and only four females had four rattles, but all other rattle numbers were approximately proportional until the higher numbers were reached where many rattle strings were broken.

Growth rates were not directly measured, but the highly variable nature of growth in these snakes is illustrated by Fig. 1. Snakes of the same length can vary 100% or more in the number of intact rattles they possess and, thus, the number of times they have shed during their lives. This apparent variation in growth was most conspicuous in females. Females with five rattles varied in size from 35–63 cm SVL. Although it was not quantified, the apparent differences in growth rates were also indicated by the difference in the taper of intact strings of rattles. Snakes that were relatively large for a given number of rattles, and apparently growing rapidly, had a very sharp taper in their rattles (each succeeding rattle was conspicuously larger than the previous one), while snakes that were relatively small for a given number of rattles, and probably growing slowly, had a very slight taper to their string of rattles.

The mean SVL of mature males was significantly greater than that of females ($t' = 3.7$, $df = 129$, $P < 0.001$). Sexually mature males (Fig. 1) had a mean SVL of 70.6 cm ($n = 90$, $SD = 10.85$), while sexually mature females averaged 65.9 cm ($n = 84$, $SD = 5.19$). Mean body masses were 230.2 g ($SD = 99.28$) and 191.9 g ($SD = 71.05$), respectively, for these same males and females. There was no significant difference in the SVL of male and female *C. v. oregonus* at birth ($t = 1.08$, $df = 19$, $P > 0.29$).

Total captures of snakes strongly favored females (240 females:147 males). However, an unequal sex ratio was not proposed, because our collecting efforts were biased toward females. Combined unbiased samples (48 females:41 males, $\chi^2 = 0.55$, $P > 0.4$) indicated that the population had a 1:1 sex ratio. Based on four clutches (eight females:11 males, $\chi^2 =$

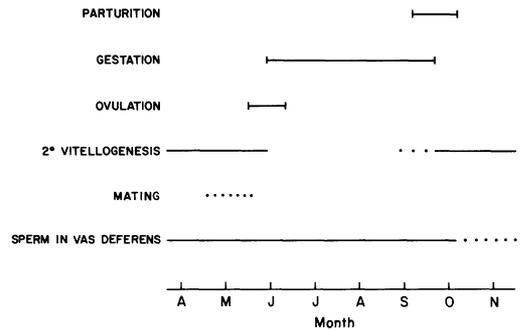


FIG. 2.—Reproductive cycle of *Crotalus viridis oregonus* in northern Idaho. Period of mating is based on estimates from other studies.

0.24, $P > 0.6$), the primary sex ratio was also equal.

Reproduction

The annual timing of reproductive events for *C. v. oregonus* in northern Idaho is summarized in Fig. 2. At all times when mature males were captured (late March–early October), spermatozoa were present in at least the distal portion of the vas deferens. Mating activity was never observed, so it can only be surmised that breeding occurred in the spring as has been reported for other *C. v. oregonus* (Fitch and Glading, 1947; Klauber, 1956).

Secondary vitellogenesis (Aldridge, 1979a) began shortly after parturition in the fall in those females that would reproduce in the succeeding year. Upon first emergence in the spring, reproductive females already carried large yolked ova up to 35 mm in length. Secondary vitellogenesis was completed and ovulation occurred by mid-May to mid-June depending on annual and individual differences. On the average, gestation extended from early June to late September (about 110 days). Parturition occurred during about a 30-day period from early September to early October. Eliminating annual variation by just considering 1980, when we had the best samples, ovulation occurred during a 3-wk period (3 June–24 June), while parturition occurred during a 4-wk period (6 September–5 October).

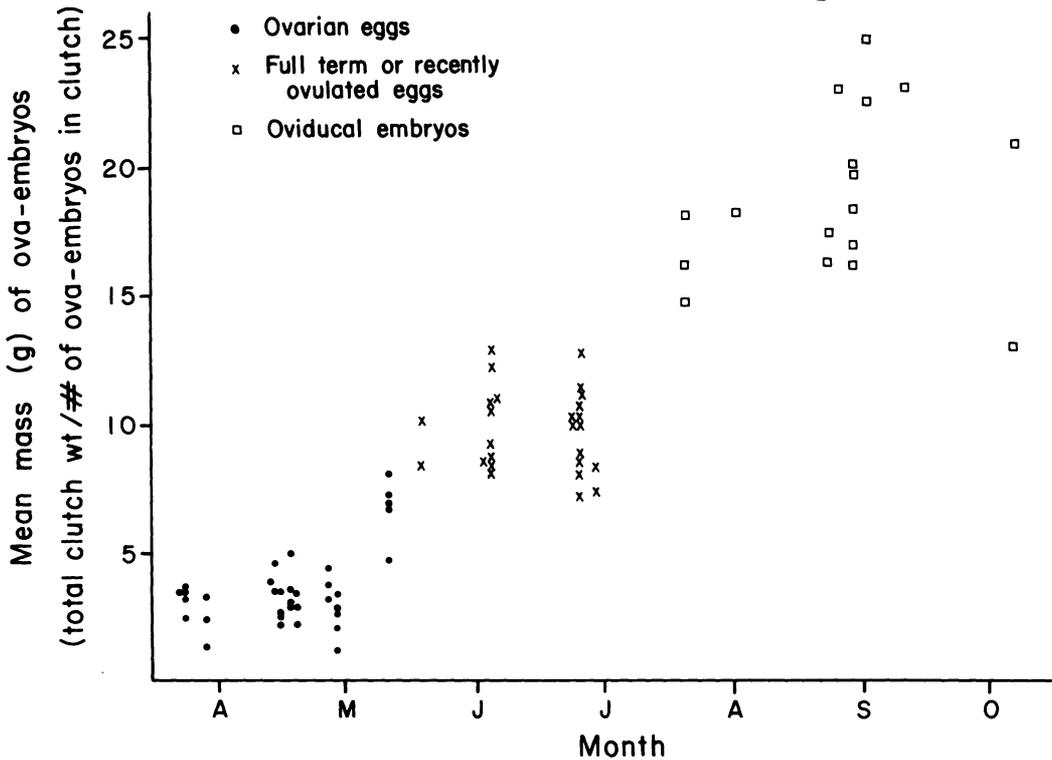


FIG. 3.—Seasonal change in mean mass of ova and embryos of gravid *Crotalus viridis oregonus*.

Ova weighed from 2–4 g each when reproductive females first emerged in the spring (Fig. 3). At ovulation, the mean mass of ova was 9.8 g (based on 26 clutches, $SD = 1.58$). At birth, the young weighed 18.1 g ($n = 22$, $SD = 2.21$).

The smallest sexually mature male was 46 cm SVL and had four rattles. Another male at 49 cm with just three rattles was sexually mature. With only one exception, all males over 52 cm in SVL and with four or more rattles were sexually mature. The smallest sexually mature female was 55 cm SVL but had a broken string of rattles. The female with the fewest rattles when sexually mature was 59 cm SVL with only four rattles. Of the females >55 cm SVL and with five rattles, six of nine were sexually mature. Excluding one obviously aberrant female, the largest females not sexually mature were a female at 63 cm

with nine rattles and another one at 64 cm with six rattles.

There was a significant correlation between clutch size and female SVL in all three populations of *C. v. oregonus* (linear regression; TC, $F_{1,26} = 30.25$, $P \leq 0.0001$; WD, $F_{1,51} = 49.48$, $P \leq 0.0001$; KD, $F_{1,34} = 16.59$, $P \leq 0.0001$). Although the slopes of these three regressions (Fig. 4) were not significantly different (ANCOVA, $F_{2,111} = 1.28$, $P > 0.10$), the regression from TC produced the greatest slope ($b = 0.22$), followed by WD ($b = 0.20$) and KD ($b = 0.14$). R -squared values showed the same pattern with TC having the highest value ($R^2 = 0.54$) followed by R^2 values of 0.49 and 0.33, respectively, for the regressions from WD and KD.

The mean clutch size was 5.5 ($n = 117$, $SD = 1.35$) based on counts of developing ova and oviducal eggs/fetuses (including

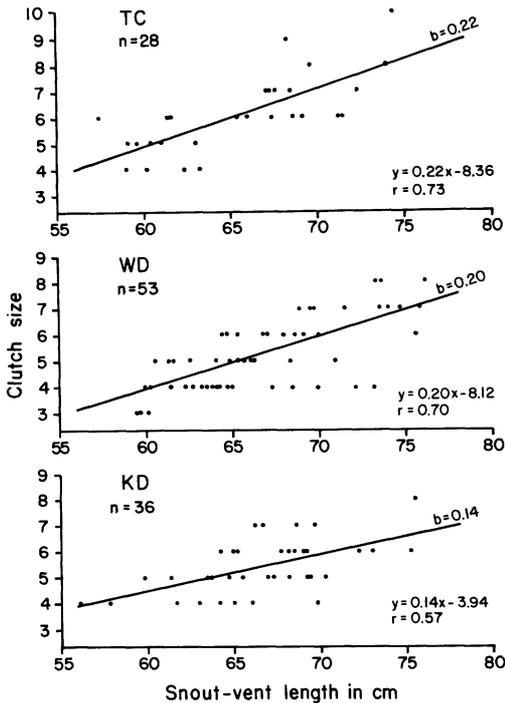


FIG. 4.—Regression of clutch size on snout-vent length in three populations of *Crotalus viridis oreganus*.

nonviable ones). There was a significant difference in clutch size adjusted for female SVL among locations (ANCOVA, $F_{2,113} = 12.48$, $P \leq 0.0001$). Females from TC had a significantly greater clutch size ($\bar{x} = 6.1$, $n = 28$, $SD = 1.47$) than those from WD or KD ($\bar{x} = 5.2$, $n = 53$, $SD = 1.34$ and $\bar{x} = 5.4$, $n = 36$, $SD = 1.35$, respectively; LSMEANS, $P < 0.01$). However, of 197 developing fetuses, 24 were not viable due to either egg infertility or fetal death. Thus, the realized fecundity was 12.2% less than mean clutch size based on ovarian and oviducal egg counts.

The proportion of females reproducing annually varied among sites. At each site, there was also annual variation in the proportion of females reproducing, but sample sizes were too small each year to make meaningful comparisons. The frequency of gravid females captured in the spring was 30 of 39 (77%) at TC, 23 of 40 (58%)

at WD, and 6 of 11 (54%) at KD. Thus, a significantly higher proportion ($\chi^2 = 3.94$, $P = 0.047$) of females reproduced annually at TC as compared to WD and KD combined.

Two estimates of reproductive effort were calculated due to the difference in mean mass of recently ovulated eggs versus neonates. This difference gave estimates of 87.3 kcal for a clutch of recently ovulated eggs, while a clutch of neonates was estimated to contain 191.0 kcal. Mature female bodies contained an estimated 379.6 kcal. Thus, reproductive effort, defined as the mean caloric content of a clutch of recently ovulated eggs divided by the mean caloric content of the whole body of a mature female, was 0.23. However, if reproductive effort is defined as the mean caloric content of a clutch of neonates divided by the mean caloric content of a sexually mature female, then its value was 0.50.

Fat Bodies

Reproductive females had the highest percentage of body fat followed by immature females, nonreproductive females and males (Table 1). Since there was no significant interaction between location and reproductive condition (ANOVA, $F_{6,203} = 0.71$, $P = 0.64$), we could combine locations to analyze percent fat of snakes in various reproductive conditions, and combine reproductive conditions to analyze percent fat of snakes at the three locations. There was a significant difference in percent fat among reproductive conditions (ANOVA, $F_{2,203} = 32.37$, $P \leq 0.0001$). Reproductive females and immature females had significantly more body fat than non-reproductive females or mature males (LSMEANS, $P \leq 0.0001$). There was a significant difference in percent body fat among locations (ANOVA, $F_{2,203} = 12.08$, $P \leq 0.0001$). Snakes from TC had a significantly greater amount of body fat than did snakes from WD or KD (LSMEANS, $P < 0.001$).

The seasonal fat body cycle of reproductive females was indicated by plotting

TABLE 1.—Mean fat body mass (percent of total body mass) in four classes of rattlesnakes from three locations, 1978–1981. All samples were collected in the spring, March through 18 May.

Reproductive condition	TC			WD			KD			Totals		
	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
Reproductive females	30	9.5	1.93	28	7.1	2.06	6	7.6	1.60	64	8.29**	2.27
Non-reproductive females	9	6.0	3.59	17	4.6	2.56	7	3.6	2.79	33	4.74	2.95
Immature females	10	8.4	2.40	9	7.5	2.41	13	6.5	2.61	32	7.38**	2.54
Mature males	29	5.6	1.96	33	4.5	1.63	24	3.7	1.59	86	4.66	1.88
Totals	78	7.5*	2.85	87	5.6	2.43	50	4.9	2.57			

* Significantly different (ANOVA, $F_{3,300} = 12.08$, $P \leq 0.0001$; LSMEANS, $P < 0.001$) from totals at other locations.

** Significantly different (ANOVA, $F_{3,300} = 32.37$, $P \leq 0.0001$; LSMEANS, $P \leq 0.0001$) from other totals.

percent body fat of reproductive females captured at various times throughout their activity period (Fig. 5). Although there was considerable individual variation, the figure indicates a decrease in body fat during the spring and little change throughout the summer and fall. Few nonreproductive females could be collected throughout the summer and fall. However, even with limited data, there is evidence that non-reproductive females increased in body fat throughout the summer and fall (Fig. 5). Similar plots of fat body cycles for mature males indicate considerable individual variation, and no obvious seasonal cycle could be identified (Fig. 5).

DISCUSSION

Sexual size dimorphism (males larger than females) has been reported in *C. viridis* and most other species of Crotalidae (Shine, 1978a). He suggested that this results from a breeding advantage enjoyed by larger males where male-male combat occurs. Although we did not observe male-male combat, Klauber (1956) reported that it does occur in *C. viridis*.

It is difficult to know if unequal numbers of males and females in a sample indicate an unequal sex ratio in the population, since differences in behavior and activity between the sexes often bias capture success. The sex ratio of snakes captured during this study strongly favored females, but this was due to an apparent

difference in behavior between the sexes and not to a numerical difference. Almost all of our collecting efforts occurred at or near hibernacula, since collecting in other areas was unproductive. In the early spring, when snakes were first emerging, and in the fall, when they were returning to their hibernacula, captures of males and females were essentially equal. However, during the summer months (June, July and August), almost all snakes captured (49 of 50) were gravid females. This strongly suggests that immature and nongravid females plus all males disperse from the hibernaculum, while at least some and perhaps all gravid females remain near the hibernaculum. By excluding summer captures, we conclude that the sex ratio is equal in the populations we studied.

Most field studies of *C. viridis* report a sex ratio favoring males (Fitch, 1949; Julian, 1951; Parker and Brown, 1973), which is interpreted to result from a higher mortality rate in females. Since our primary sex ratio was not significantly different from 1:1, it would appear that mortality rates for males and females in the study populations were equal.

Seasonal testicular events were not monitored, but the presence of spermatozoa in the vas deferens at all times of the year when snakes were collected indicates that the male reproductive cycle of *C. viridis* in northern Idaho is the "aestival type" as described by Saint Girons (1982). Aldridge (1979b) described this same male reproductive cycle for *C. vir-*

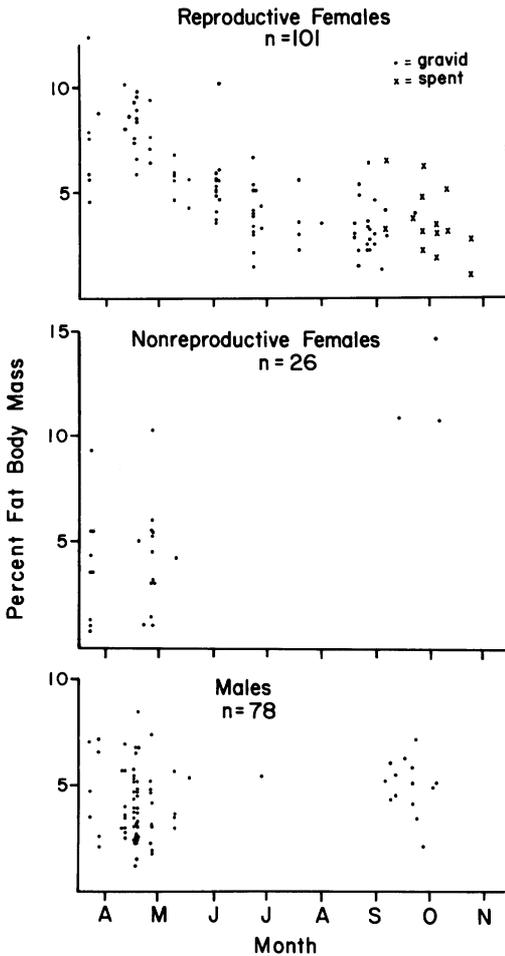


FIG. 5.—Seasonal fat body cycles of reproductive female, nonreproductive female, and mature male *Crotalus viridis oregonus*. (Snakes from TC were not included because of limited mid-summer and fall collections.)

idis in New Mexico, where spermatogenesis occurs during the summer months, but spermatozoa are stored in the vas deferens throughout the winter. Thus, males are capable of breeding in the spring before the onset of summer spermatogenesis.

The female reproductive cycle for *C. viridis* in northern Idaho fits the pattern of a "Type II cycle" as described by Aldridge (1979a). This cycle has been described for all Crotalidae that have been studied (Aldridge, 1979a; Gibbons, 1972;

Rahn, 1942; Tinkle, 1962; Warton, 1966).

There are few studies that have attempted to determine the age structure of a snake population because of the difficulty in aging snakes. Although it is enticing to try to use length-frequency data to establish size and age classes, the highly variable growth rates of these snakes makes such calculations too arbitrary to be meaningful.

If the frequency of sheddings were known, this could be used to estimate the age of snakes. Klauber (1956) discussed various studies where the frequency of shedding in at least subadult rattlesnakes was estimated by showing that rattle numbers of unbroken strings occurred in discrete modal classes. For example, Fitch (1949) found that *C. v. oregonus* in central California had a modal rattle number of four after their first year of growth, while most snakes had six or seven rattles after their second year. From these types of data, Klauber concluded that juvenile rattlesnakes in the wild "... shed from 2 to 4 times in their first full growing season, and from 1 to 4 times their second, and that the number of sheddings depends on the duration of the season of activity." Klauber indicated that adult rattlesnakes typically shed once a year where the climate allows only about 6 mo of activity per year.

Rattle numbers did not occur in discrete modal classes in snakes from this study, which suggests that at least part of the snakes were shedding annually. If juvenile snakes were shedding two to four times during their first season of growth, then snakes emerging in the spring with one rattle should be absent in the population and most juveniles should have three rattles. Since few male snakes were found with one rattle and there were no modal classes of any rattle number, it appears that most juvenile males shed twice in their first year. Females with even one rattle are well represented, which suggests that many females may shed only once even in their first year of growth. Unpublished data from a mark-recapture study by the

authors indicates that most mature rattlesnakes shed once per year.

It is well known that the frequency of shedding varies with the rate of growth (Fitch, 1949; Klauber, 1956). Since we suspect highly variable growth rates, we would expect that frequency of sheddings was also quite variable in this population of snakes. However, we believe that rattle numbers allow one to tentatively estimate the age at sexual maturity for most snakes from this study. Since one of six males with three rattles and all males with four rattles were sexually mature, we believe that most males reach sexual maturity in 2–3 yr. This estimate for males is consistent with other estimates of temperate zone snakes (Diller, 1981; Fitch and Gladding, 1947; Parker, 1974; Shine, 1981). The age at sexual maturity appeared more variable for females. One of four with four rattles, six of 14 with five rattles, six of nine with six rattles and all females with seven or eight rattles were sexually mature, but one female with nine rattles was still not sexually mature. This would suggest that age at sexual maturity could vary from 4–6 yr or even more in rare cases. Most estimates of age at sexual maturity of females ranged from 3–5 yr for temperate zone snakes (Diller, 1981; Keenlyne, 1978; Klauber, 1956; Parker, 1974; Shine, 1980; Volsøe, 1944), except for the estimate of 6 yr reported for female *C. horridus* (Gibbons, 1972). Although the magnitude may be tentative, this study and most studies listed above indicate a delayed maturity for females relative to males.

Mean clutch size of 5.5 reported here for *C. viridis oregonus* in northern Idaho is much less than the mean clutch size of 9.9 reported for *C. viridis oregonus* in central California (Fitch, 1949) and 8.3 for *C. viridis lutosus* in southern Idaho (Diller, 1981). Glismeyer (1951) reported a mean clutch of 5.5 for *C. viridis lutosus* in Utah, but this was based on palpation counts that we consider unreliable. The small clutch size of *C. viridis oregonus* in

northern Idaho initially suggests a low reproductive effort, but it is explained simply by their smaller body size. Fitch (1949) reported females typically weighing between 300–400 g with one individual weighing >600 g and Diller (1981) reported a mean of >400 g for mature females. Mature females in this study averaged only 192 g. Instead of a low reproductive effort superficially suggested by a small clutch size, the calculation of reproductive effort for females in this study is higher (0.5 versus 0.4) than the same calculation for *C. viridis lutosus* in southern Idaho (Diller, 1981). No calculation of reproductive effort is available for *C. viridis oregonus* in central California (Fitch, 1949).

Comparing our results with Fitch's (1949) study in central California indicates that there is a decrease in clutch size with increases in latitude in *C. viridis oregonus* due in part to a smaller body size in northern populations. Using Klauber (1956) as a source, Fitch (1980) reported that *C. viridis* shows an increase in clutch size with latitude. However, his comparison was among several subspecies of *C. viridis* which may be genetically dissimilar. Klauber (1956) reported that, in general, rattlesnakes show a decrease in size with increases in latitude, although local feeding conditions may reverse this trend. Since larger females tend to have larger clutches, it seems most likely that rattlesnakes have smaller clutches at northern latitudes as evidenced by this study.

The calculated increase in caloric content of neonates relative to recently ovulated eggs and the concomitant increase in estimates of reproductive effort suggest a maternal-fetal exchange of nutrients in *C. v. oregonus*. This same phenomenon was also noted for *C. v. lutosus* in southwestern Idaho (Diller, 1981). Some form of placentation with nutritive exchange has been suggested for several snake species with intra-uterine embryonic development including several species of *Thamnophis* (Hoffman, 1970) and *Vipera*

berus (Bellairs et al., 1955). We know of no such work demonstrating placentation for a Crotalidae.

The strong correlation between expected fecundity and female size indicates that reproductive potential increases with age. Both the increased reproductive potential with age and the high reproductive effort of females result in delayed sexual maturity of females relative to males. By delaying reproduction with its associated risks and energy costs, until the body size has increased, females theoretically can increase their life-time reproductive potential (Bull and Shine, 1979). Reproduction for males presumably does not entail the high risks and energy costs required of females, so selection does not favor delaying sexual maturity in males (Shine, 1978*b*).

Historically, researchers have assumed an innate biennial reproductive cycle for female rattlesnakes whenever collections indicated that, on the average, approximately one half of the mature females were gravid during any one year (Fitch, 1949; Glissmeyer, 1951; Klauber, 1956; Rahn, 1942). Our data could be interpreted to indicate that females in two populations (WD and KD) have a biennial reproductive cycle, while females from the third population (TC) are genetically either annual or biennial reproducers. However, there was evidence that some females reproduce annually in all three populations. Certain females collected in early spring after they have recently emerged from hibernation contained remnants of incubation chambers in the oviducts from the previous years' litter and had conspicuously enlarging ova indicating that they will reproduce in two consecutive years. A total of 11 of 23 (47.8%) females at TC, 12 of 35 (34.3%) females at WD and two of nine (22.2%) females at KD showed evidence of annual reproduction. (Their numbers were not used in calculating frequencies of reproduction, because evidence of brood chambers is rapidly lost in the spring and it was not

always possible to distinguish between females that had not reproduced the previous year and those in which all remnants of brood chambers had simply disappeared.)

We believe that the best explanation of our data on the proportion of females reproducing annually is supplied by Aldridge (1979*a*). He postulated that all temperate zone snakes are potentially annual breeders and that energy requirements determine the actual percentage of females breeding in a given year. Possibly rattlesnakes at TC had a "better" prey base (qualitatively or quantitatively) than those at either WD or KD, so that a higher percentage of the females at TC could meet the energy requirements to reproduce annually.

There were additional data that would support the conclusion that snakes at TC had an increased reproductive capacity due to a better food supply. The mean clutch size was significantly higher at TC than either WD or KD, even though there was no difference in mean SVL of females among sites. Also, the regression of clutch size on SVL produced a higher slope at TC than the other two sites. Although these differences in slopes were not statistically significant ($P = 0.14$) due to high individual variation, we believe that females of a given size are able to produce more young at TC. It could be postulated that these are genetic differences, except that all three populations occur within 40 km of each other, and there are continuous populations of snakes between the sites to facilitate gene flow.

Total lipid stores in a snake have been shown to be accurately reflected by the weight of abdominal fat bodies (Cale and Gibbons, 1972). The primary function of these fat bodies is believed to be related to either overwintering or reproduction. If females have proportionately larger fat bodies than males, and there is a decrease in fat body size during times of high reproductive demands, then fat bodies are believed to be utilized primarily for re-

production (Derickson, 1976; Hahn and Tinkle, 1965).

Our data indicate that fat bodies are used primarily for reproduction in *C. viridis* in northern Idaho, since reproductive females have larger fat bodies than males, and the size of fat bodies decrease throughout the spring and early summer in gravid females. The same conclusion was reached for several other species of rattlesnakes (Gibbons, 1972; Kennlyne, 1972; Tinkle, 1962). Based on the relatively large fat bodies of reproductive females in the spring as compared to non-reproductive females (nearly twice as large on the average), it seems likely that insufficient lipid reserves inhibit vitellogenesis and prevent reproduction in a similar fashion to that reported by Hahn and Tinkle (1965). They excised fat bodies from the lizard *Uta stansburiana* and vitellogenesis was inhibited. The critical time is probably immediately after parturition, when females with ample fat bodies were observed to immediately begin secondary vitellogenesis, while ovaries of emaciated females would remain quiescent.

Vipera berus is reported to reproduce strictly on a biennial cycle in southern England because fat reserves are depleted following parturition, and there is not time for females to feed before hibernation (Prestt, 1971). Although our graphs of fat body cycles of reproductive and non-reproductive females (Fig. 5) appear to be quite similar to that reported for *V. berus* by Prestt (1971), there is a much greater range of individual variation in fat body size in *C. viridis*. Thus, females with the greater amounts of fat reserves are able to reproduce in successive years. It is difficult to explain how *C. viridis* in northern Idaho could obtain adequate energy reserves to reproduce in successive years when *V. berus* in southern England cannot. The two species have similar ecologies and are active for almost exactly the same period of time during the year. It is also interesting to speculate whether certain female *C. viridis* in northern Idaho can reproduce annually for several suc-

cessive years, or if they only reproduce annually for 2 yr in a row after a period of exceptional feeding success.

Larger fat bodies combined with greater reproductive rates at TC in comparison to the other two sites provides indirect evidence that food supply influences reproductive rate and that adequate energy reserves are essential for annual reproduction in *C. viridis* in northern Idaho. Based on the variation seen among sites in the same locality, and the fact that biennial reproductive cycles have been identified in rattlesnakes in southern localities (Gibbons, 1972; Tinkle, 1962), it appears that the frequency of reproduction in female rattlesnakes is more dependent on food supply than latitude.

Acknowledgments.—We thank James Howard, Michael Pate, Jeffery Pate and James Lynch for help in collecting specimens. Donald R. Johnson reviewed the manuscript and made helpful suggestions.

LITERATURE CITED

- ALDRIDGE, R. D. 1979a. Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis*. *Herpetologica* 35:256–261.
- . 1979b. Seasonal spermatogenesis in sympatric *Crotalus viridis* and *Arizona elegans* in New Mexico. *J. Herpetol.* 13:187–192.
- BELLAIRS, R., I. GRIFFITHS, AND A. BELLAIRS. 1955. Placentation in the adder *Vipera berus*. *Nature* 176:657–658.
- BULL, J. J., AND R. SHINE. 1979. Iteroparous animals that skip opportunities for reproduction. *Am. Nat.* 114:296–316.
- CALE, W. G., AND J. W. GIBBONS. 1972. Relationship between body size, size of the fat bodies, and total lipid content in the canebrake rattlesnake (*Crotalus horridus*) and the black racer (*Coluber constrictor*). *Herpetologica* 28:51–53.
- DERICKSON, W. K. 1976. Lipid storage and utilization in reptiles. *Am. Zool.* 16:711–723.
- DILLER, L. V. 1981. Comparative ecology of Great Basin rattlesnakes (*Crotalus viridis lutosus*) and Great Basin gopher snakes (*Pituophis melanoleucus deserticola*) and their impact on small mammal populations in the Snake River Birds of Prey Natural Area. Ph.D. Dissertation, University of Idaho.
- FITCH, H. S. 1949. Study of snake populations in central California. *Am. Midl. Nat.* 41:513–579.
- . 1980. Reproductive strategies of reptiles. Pp. 25–31. In J. B. Murphy and J. T. Collins (Eds.), *Reproductive Biology and Diseases of Captive*

- Reptiles. Soc. Study Amph. Rept. Contri. Herpetol. 1.
- FITCH, H. S., AND B. GLADING. 1947. A field study of a rattlesnake population. *California Fish Game* 33:103-123.
- GIBBONS, J. W. 1972. Reproduction, growth, and sexual dimorphism in the canebrake rattlesnake (*Crotalus horridus atricaudatus*). *Copeia* 1972:222-226.
- GLISSMEYER, H. R. 1951. Egg production in the Great Basin rattlesnake. In A. M. Woodbury, Symposium—A snake den in Tooele County, Utah. *Herpetologica* 7:24-27.
- HAHN, W. E., AND D. W. TINKLE. 1965. Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *J. Exp. Zool.* 158:79-86.
- HOFFMAN, L. H. 1970. Placentation in the garter snake, *Thamnophis sirtalis*. *J. Morphol.* 131:57-88.
- JULIAN, G. 1951. Sex ratios of the winter populations. In A. M. Woodbury, Symposium—A snake den in Tooele County, Utah. *Herpetologica* 7:21-24.
- KEENLYNE, K. D. 1972. Sexual differences in feeding habits of *Crotalus horridus horridus*. *J. Herpetol.* 6:234-237.
- . 1978. Reproductive cycles in two species of rattlesnakes. *Am. Midl. Nat.* 100:368-375.
- KLAUBER, L. M. 1956. *Rattlesnakes: Their Habits, Life History and Influence on Mankind*. University of California Press, Berkeley.
- PARKER, W. S. 1974. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* and *Pituophis melanoleucus deserticola*. Ph.D. Dissertation, University of Utah.
- PARKER, W. S., AND W. S. BROWN. 1973. Species composition and population changes in two complexes of snake hibernacula in northern Utah. *Herpetologica* 29:319-326.
- PRESTT, I. 1971. An ecological study of the viper *Vipera berus* in southern Britain. *J. Zool. London* 164:373-418.
- RAHN, H. 1942. The reproductive cycle of the prairie rattler. *Copeia* 1942:233-240.
- SAINT GIRONS, H. 1982. Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* 38:5-16.
- SHINE, R. 1978a. Sexual size dimorphism and male combat in snakes. *Oecologia* 33:269-278.
- . 1978b. Growth rates and sexual maturation in six species of Australian elapid snakes. *Herpetologica* 34:73-79.
- . 1980. Ecology of the Australian death adder *Acanthophis antarcticus* (Elapidae): evidence for convergence with the Viperidae. *Herpetologica* 36:281-289.
- . 1981. Venomous snakes in cold climates: ecology of the Australian genus *Drysdalia* (Serpentes, Elapidae). *Copeia* 1981:14-25.
- STEBBINS, R. C. 1966. *A Field Guide to Western Reptiles and Amphibians*. Houghton Mifflin Co., Boston.
- TINKLE, D. W. 1962. Reproductive potential and cycles in female *Crotalus atrox* from northwestern Texas. *Copeia* 1962:306-313.
- TINKLE, D. W., AND N. F. HADLEY. 1973. Reproductive effort and winter activity in the viviparous montane lizard *Sceloporus jarrovi*. *Copeia* 1973:272-277.
- VITT, L. J. 1978. Caloric content of lizard and snake (Reptilia) eggs and bodies and the conversion of weight to caloric data. *J. Herpetol.* 12:65-72.
- VOLSØE, H. 1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L.). *Spolia Zool. Mus. Hauniensis* 5:1-157.
- WARTON, C. 1966. Reproduction and growth in the cottonmouth, *Agkistrodon piscivorus*, of Cedar Keys, Florida. *Copeia* 1966:149-161.
- WOODBURY, A. W. 1951. Symposium—A snake den in Tooele County, Utah. *Herpetologica* 7:1-14.

Accepted: 12 September 1983
Associate Editor: James Spotila

Department of Biological Sciences,
University of Idaho, Moscow, ID 83843,
USA (PRESENT ADDRESS OF LVD: Department of Biology, Frostburg State College, Frostburg, MD 21532, USA)