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Source: *Copeia*, Feb. 5, 1988, Vol. 1988, No. 1 (Feb. 5, 1988), pp. 47–57

Published by: American Society of Ichthyologists and Herpetologists (ASIH)

Stable URL: https://www.jstor.org/stable/1445921

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ESTACION DE BIOLOGIA TROPICAL "LOS TUXTLAS," INSTITUTO DE BIOLOGIA, UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO, APT. POST. 94, SAN ANDRES TUXTLA, VERACRUZ, MEXICO. Accepted 28 May 1987.

# Reproductive Biology of Female Rattlesnakes (*Crotalus viridis*) in British Columbia

J. MALCOLM MACARTNEY AND PATRICK T. GREGORY

Age at sexual maturity, mating behavior, reproductive cycles, and litter characteristics of female northern Pacific rattlesnakes (*Crotalus viridis oreganus*) were documented in a 3 yr mark-recapture study of populations in British Columbia near the northern limits of the species' range. Sexual maturity was attained at 5–7 yr and first litters were produced at 6–8 yr. Mating occurred during late summer and follicles of mated females underwent vitellogenesis prior to hibernation. Ovulation occurred in June and parturition followed in Sept. or early Oct. Mean litter size was 4.6 and relative clutch mass averaged 0.37. Females generally did not feed during the year they were gravid and fat body reserves were low at the time of parturition. The frequency of reproduction depended on a female's ability to regain body mass during nongravid years. Postpartum females that were able to double their body mass in one active season reproduced biennially; however, most females (74%) followed a triennial or longer cycle. Extended female reproductive cycles in these northern populations are viewed as a manifestation of the combined constraints of phylogeny (large size of neonates) and an active season that is cooler and shorter than that experienced by conspecific southern populations.

FEW species of North American snakes have been studied as intensively as the western rattlesnake, *Crotalus viridis* (Rahn, 1942; Fitch, 1949; Klauber, 1972; Parker and Brown, 1974; Duvall et al., 1985), and yet only recently has information been acquired for a sufficient number of populations over the range of this species to enable an examination of geographic variation in life history traits (Diller and Wallace, 1984; Gannon and Secoy, 1984; Fitch, 1985). Intraspecific comparisons of geographically separated populations is a potentially productive means of examining the relationship between life history attributes and environmental variation, since phylogenetic effects are minimal. Reproductive traits such as age at sexual maturity, clutch size, and reproductive frequency should be particularly susceptible to adjustment by local environmental conditions because each is affected, in varying degrees, by the annual amount of energy that can be acquired.

Climatic conditions during the active season influence growth rates and female reproductive cycles of reptiles by determining the amount of time that is available for foraging and growth. Assuming that food is not limiting, individuals from populations at high latitudes or high elevations experience a shorter and cooler active season and therefore are expected to have lower annual growth rates and to attain sexual maturity at a later age than conspecifics inhabiting areas where growing seasons are longer and warmer. In addition, a short active season may curtail completion of embryonic development and reduce a female's ability to provide energy stores for future reproduction, thereby reducing reproductive frequency.

Another factor that contributes to geographic variation in reproductive traits is variation in prey availability among sites. Growth rate, clutch size, and the proportion of reproductive females in snake populations have been shown to vary in relation to food availability (Andrén and Nilson, 1983; Seigel and Fitch, 1985; Seigel and Ford, 1987). Prey abundance is seldom measured in snake studies, but the proportion of snakes with stomach contents is often reported and may offer an indirect means of assessing relative differences in prey availability among sites. Although we would expect there to be some differences in prey diversity and abundance among sites, there is no a priori reason to expect it to vary along a latitudinal gradient.

In British Columbia, C. viridis hibernates for 7 mo and is active only between early April and early Oct. (Macartney, 1985). In more southerly areas, C. viridis is active for 7–8 mo and rattlesnakes may emerge from overwintering sites to bask during occasional periods of warm weather (Fitch, 1949; Jacob and Painter, 1980). This contrast between environments should be accompanied by predictable differences in life history traits. This study describes age at sexual maturity, mating behavior, reproductive cycles, reproductive frequency, and litter characteristics of female northern Pacific rattlesnakes (C. viridis oreganus) from populations very near the northern limit of the species' distribution in southern British Columbia.

## STUDY AREA

This study was carried out at four sites in the Okanagan Valley of south-central British Columbia (50°N, 119°W). These sites are within 15 km distance of each other, and are situated about 100 km southeast of the northernmost record for C. v. oreganus (Gregory and Campbell, 1984). The study area typically experiences warm, dry summers (mean daily maximum and minimum July temperatures are 27 C and 11 C) and cold, dry winters (corresponding Jan. temperatures are −3 C and −9 C). Average annual precipitation is 41 cm, most of which occurs during late autumn and late spring. The months of April–Sept. contribute nearly all of the average 975 degree-days (°d) above 10 C accumulated per annum in this area (Atmospheric Environment Service, 1982).

Rattlesnakes were sampled from a total of 24 communal hibernacula on four sites (Macartney, 1985). Hibernacula were generally located within rock outcroppings situated along the upper regions of steep south-facing slopes of northeast-southwest trending mountain ridges (500–750 m elevation). Hibernacula on the two main study sites were not far apart, with nearest neighbor distances between dens ranging from 40–750 m. Each of the other study sites had only one known hibernaculum.

## METHODS

Field work was conducted mainly between Sept. 1980 and June 1983, with additional collecting trips to the sites in autumn of 1983 and spring of 1984. Intensive collections were made by hand while rattlesnakes were active in the vicinity of hibernacula during spring emergence (early April to late May) and during the period of autumnal ingress (early Sept. to mid-Oct.). Hibernacula were visited, on average, every second day during these periods. Searches were also conducted during the summer (June–Aug.); the number of visits to each site varied between 5–15 each month.

Rattlesnakes were handled with tongs and secured for processing by a padded, 3 cm wide restraining noose. Each snake was sexed by Gregory's (1983) method, its snout–vent length (SVL) was measured (stretched out along a meter stick), and the number of rattle segments was recorded. Snakes were marked individually by removing a unique combination of ventral and subcaudal scutes (Blanchard and Finster, 1933). Prey items in the stomach were palpated into the buccal cavity and either identified and returned to the gut, or removed and preserved for later identification. Fecal material was also removed, dried, and identified by guard hair

analysis. Snakes were weighed to the nearest 2 g with Pesola spring scales in the field or to 0.1 g with a digital balance in the lab. Snakes with stomach contents were not weighed.

A female's reproductive condition during a given year was assessed by abdominal palpation for follicles or embryos. Females were considered to be gravid (G) during a given year if they possessed enlarged (vitellogenic) follicles (approx. 2 cm or greater in length) in the spring, or if they contained embryos during the summer. Females were classed as nongravid (N) during a given year if they lacked enlarged follicles at any time of the year or if they contained enlarging follicles only in autumn. Postpartum females were readily distinguished by their collapsed abdomen and longitudinal skin folds.

Information on reproductive cycles was obtained largely through recapturing females whose previous reproductive condition was known. Fat body weights were determined by dissecting a small number of rattlesnakes (n = 13), mostly snakes found dead or which died as a result of handling. Also, the number, length and weight of follicles or embryos in these dissected females were recorded. Smears were taken from the uteri and examined by light microscopy for spermatozoa. Near-term G females were taken from the field and maintained in the laboratory (22–30 C, 8L:16D) until parturition. Data on litter size and the weights, SVL, and sex of neonates were recorded. Postpartum females and their litters were returned to the female's capture site within 48 h of parturition. Weight lost at parturition (including neonates, fluids, extra-embryonic membranes, dead embryos and unfertilized ova) divided by near-term G weight was used as a measure of relative clutch mass (RCM).

We used t-tests to examine sexual differences in SVL and weight of neonates and t-tests for samples of unequal variance (Snedecor and Cochran, 1967) to examine SVL differences between reproductive classes. Nested ANOVA was used to test follicle size differences among and within autumn- and spring-sampled females. The sex ratio at birth, combining different litters, was determined using a method for estimating proportions in cluster sampling (Cochran, 1963). The significance of probability values in a correlation matrix of female characteristics and litter characteristics was verified by a multistage Bonferroni statistic (Larzelere and Mulaik, 1977). Means ± 1 SE are reported. The rejection level for all tests was set at $\alpha = 0.05$.

## RESULTS

*Size and age at sexual maturity.*—In this study, 844 female rattlesnakes (including neonates) were marked and a total of 2112 captures were obtained. SVL of females ranged between 210–950 mm. The smallest female with enlarged follicles measured 650 mm SVL and weighed 233 g. Eight additional small females (650–700 mm SVL) contained enlarged follicles in autumn or spring samples (mean SVL = 681.3 ± 5.7 mm, mean weight = 227.8 ± 7.8 g). Ages of these females determined from recapture of known aged snakes and Gompertz growth models (Macartney, unpubl.) ranged from 5–7 yr. These females would produce their first litter in the following year, at ages between 6–8 yr. Consecutive annual recaptures of females which were initially captured when immature (<650 mm SVL, n = 34), provided evidence that many females did not produce their first litter until they reached 700–760 mm SVL, at probable ages of 7–9 yr. In the subsequent analyses presented in this paper we consider all females ≥650 mm SVL to be adults, thus encompassing the known range of SVL of sexually mature females in this population.

*Mating behavior.*—Bisexual aggregations (n = 29 groups), consisting of at least one adult male and one adult N female rattlesnake, were observed during July, Aug., and early Sept. (Fig. 1a). Aggregation size ranged from 2–8 individuals, but the majority (18 of 29) of aggregations consisted of pairs. The formation of aggregations appeared to be related to mating since copulation was witnessed in three groups and courtship in another. Seasonal distribution of bisexual aggregations closely overlapped the period of ecdysis for N females (Fig. 1b). Aggregations in which a N female was undergoing, or had recently completed, ecdysis comprised 80% of the observations in July and Aug. These aggregations often formed at shedding rocks used by adult males and N females. Shedding males were present in only three groups; males in most groups had shed prior to our observation as determined by rattle segment gains since their last capture. A peak of spermatogenic activity in males (Macartney, 1985) also coincided with the maximal occurrence of bisexual aggregations (Fig. 1c).

Features common to the mating and courtship groups were: 1) they occurred in late summer (Fig. 1a); 2) females had usually completed
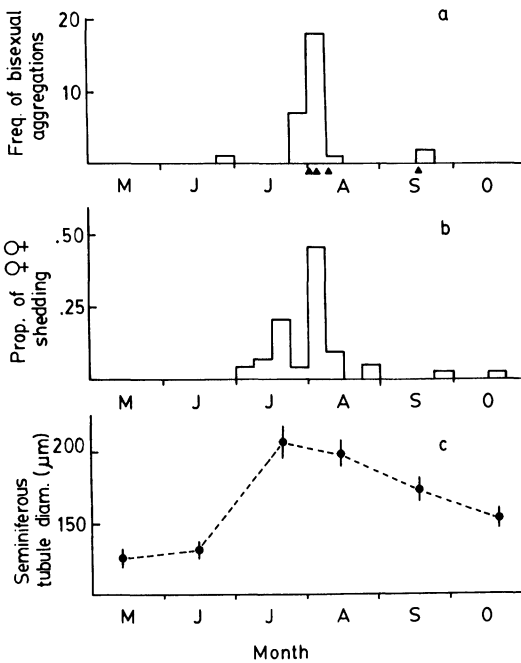
Fig. 1. Relationship between the seasonal occurrence of bisexual aggregations, ecdysis in nongravid females and spermatogenic activity in male rattlesnakes. a) Frequency of bisexual aggregations for 1981–83 combined. Triangles = mating or courtship observed. b) Proportion of shedding nongravid females in weekly intervals. Data are pooled from observations in 1981–83 (n = 42). c) Seasonal change in mean seminiferous tubule diameter (n = 40 diameters, from two snakes) in male *Crotalus viridis oreganus* (data from Macartney, 1985).

ecdysis a short time (<48 h) prior to courtship or copulation; and 3) enlarged follicles were absent in females (n = 3) at the time of observation, but were present when the same females

were recaptured at emergence from hibernacula the next spring.

*Reproductive cycles.*—A general phenology of the typical female reproductive cycles in these populations is shown in Figure 2. Adult females examined in the spring or autumn belonged to one of three reproductive classes. They either possessed enlarged follicles, lacked enlarged follicles, or were postpartum (=G in early autumn of the preceding year). Enlarged follicles and stored spermatozoa were absent from the reproductive tracts of postpartum females. Postpartum females contained previtellogenic follicles (<1.6 cm) within their ovaries and remnants of incubation chambers in their uteri. Fat bodies of two females comprised 2.2% and 4.1% of postpartum body weight.

Two groups of N females were distinguished in autumn or spring samples, based on the presence or absence of enlarged follicles. Recaptures of females that contained enlarged follicles in the autumn or spring showed that these females became G the subsequent summer. Dissections revealed the presence of stored spermatozoa in the constricted, posterior region of the uteri of each of the five females belonging to this category that were examined. Fat bodies in these females averaged 6.7 ± 0.4% of body weight (n = 8, range 5.6–8.8%).

The second group consisted of females that were clearly not postpartum, and yet did not possess enlarged follicles. Spermatozoa were absent from the uteri of the one female in this category that was available for dissection. Females lacking enlarged follicles in the autumn or spring were never G when recaptured the subsequent summer. Furthermore, vitellogenesis was not observed in these N females (or in
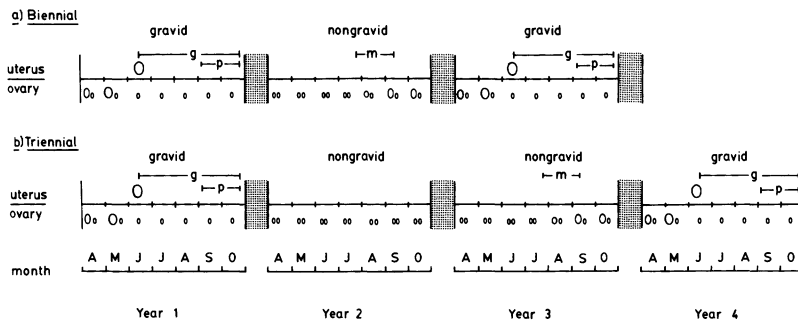


Fig. 2. Reproductive cycles of female *Crotalus viridis oreganus* in British Columbia. a) Biennial cycle. b) Triennial cycle. Shaded boxes represent the overwintering period. Symbols: o = ovulation, g = gestation, p = parturition, m = mating. Relative sizes of follicles in the ovary are shown.

TABLE 1. THE RATIO OF GRAVID (G) TO NONGRAVID (N) ADULT (≥650 MM SVL) FEMALE *Crotalus viridis oreganus* IN EACH YEAR SAMPLED.

| Year | Number of adult females captured | Ratio G:N |
|---|---|---|
| 1981 | 124 | 1:1.58 |
| 1982 | 214 | 1:2.75 |
| 1983 | 187 | 1:1.63 |
| Total | 525 | 1:1.98 |

postpartum females) until early autumn. Adult females lacking enlarged follicles for an entire active season demonstrated that they were N for more than 1 yr (i.e., certain females followed a triennial or longer reproductive cycle).

Lengths of enlarged follicles of autumn- and spring-collected females were not significantly different ($F_{(1,6)}$ = 2.2, $P$ > 0.25, n = 8), indicating that enlarged follicles undergo no detectable growth during hibernation. Ovulation probably occurred during June, judging by the early stage of development of embryos removed from a G female in mid-July and by the presence of enlarged follicles in the ovaries of a female dissected in mid-May.

During the 3–4 mo gestation period, G females resided at rock outcrops or rock piles which were located at, or within 50 m of, hibernacula. As a rule, G females did not feed during the entire active season. The average weight lost by G females between spring emergence and parturition was 6.1 ± 2.1% of spring body weight (n = 14, range −6.1–20.7%). Only eight spring-captured individuals from a total of 362 captures of G females (2.2%) had prey in their stomachs. In contrast, during June, July, and Aug. 17.1% of all captured rattlesnakes in monthly samples contained stomach or fecal material (n = 656).

Most G females gave birth at hibernacula; however, parturition also was recorded at basking rocks located short distances (<30 m) from dens. Parturition dates for 34 captive- and field-born litters ranged from 12 Sept.–23 Oct. (all years combined). There was a slight peak in parturition during the last 2 wk of Sept., a trend that was consistent among years for field-born and captive-born litters. Postpartum females usually entered hibernation within 1–10 d after having young.

*Reproductive frequency.*—N females consistently outnumbered G females in yearly samples, av-

TABLE 2. PROPORTION OF GRAVID (G) FEMALES IN THREE ADULT SIZE CLASSES. Data for 1981–83 combined.

| SVL (mm) | n | Proportion G |
|---|---|---|
| 650–739 | 172 | 0.19 |
| 740–799 | 220 | 0.39 |
| 800–950 | 133 | 0.43 |

eraging twice as many N as G females over all years (Table 1). This was not due to a sampling bias because rattlesnakes were sampled mainly during the spring and autumn at hibernacula, and at other times G females were much easier to locate in the field than N females. Some of the excess of N females probably resulted from inclusion of females that were not mature (Table 2).

Reproductive histories of 142 adult females were determined by recaptures obtained over three or four years (Table 3). No females reproduced in consecutive years. Nearly half of the marked females were N the year they were first captured, became G the following year and were N the third year. Although they followed a cycle that was at least biennial, the proportion of these females that were truly biennial or followed longer cycles could not be ascertained because further recaptures were not made. Of the remaining 81 females whose reproductive schedules were better known, 21 females (26%) were G in alternate years and 60 females (74%) exhibited triennial or longer cycles. Of the latter group, seven females were N for three consecutive years.

A closer inspection was made for differences between females that followed biennial, triennial, and longer cycles. The mean SVL of fe-

TABLE 3. REPRODUCTIVE HISTORIES OF 142 MARKED ADULT FEMALES RECAPTURED OVER PERIODS OF THREE OR FOUR YEARS. G = gravid, N = nongravid.

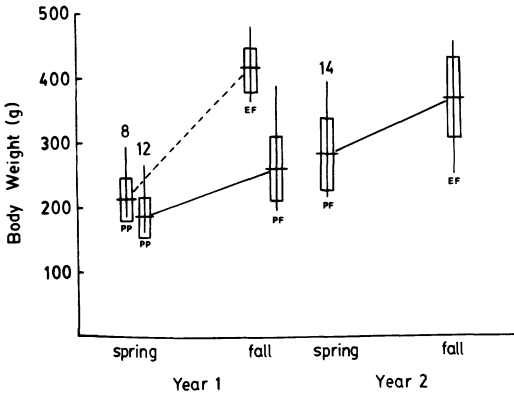| n | Reproductive condition | | | | Reproductive frequency |
|---|---|---|---|---|---|
| | Year 1 | Year 2 | Year 3 | Year 4 | |
| 61 | N | G | N | — | at least biennial |
| 21 | G | N | G | N | biennial |
| 39 either a) | G | N | N | — | at least triennial |
| or b) | N | N | G | — | at least triennial |
| 14 | G | N | N | G | triennial |
| 7 | N | N | N | — | at least quadrennial |

Fig. 3. Annual weight gains of female rattlesnakes during nongravid years in biennial (dashed line) and triennial (solid lines) reproductive cycles. Symbols: PP = postpartum, EF = enlarged follicles, PF = pre-vitellogenic follicles. Horizontal bar = mean, vertical line = range, rectangle = ±1 SD. Sample size given above each bar.



Fig. 4. Relationship between snout–vent length and percent body weight increase of postpartum females during the active season following parturition. Circles = postpartum females on a biennial cycle (n = 8), triangles = postpartum females on a triennial or longer cycle (n = 12).

males (measured when snakes were first G or postpartum) that reproduced biennially (799 ± 10.5 mm, n = 21) was greater than the SVL of triennial females (776 ± 7.6 mm, n = 14), but the difference was not significant (t = 1.8, P > 0.05).

A prominent difference between biennial and triennial females was in body weight gained during the year following parturition (Fig. 3). Mean relative increase in body weight of postpartum females that possessed enlarged follicles 1 yr after parturition (i.e., at the end of a N year in a biennial cycle) was 96.2 ± 5.1% (n = 8, range 63–125%). Postpartum females whose ovaries did not contain enlarged follicles the next autumn (the first N year of a triennial or longer cycle) increased 39.2 ± 4.6% (n = 12, range 22–70%). Another group of females for which weight changes were measured for the second year of a triennial cycle (the year of follicular enlargement) averaged 32.2 ± 3.2% increase over spring weights (n = 14, range 16–43%). Triennial females required two active seasons to gain roughly the same proportion of body mass that biennial females gained in one season (Fig. 3). There was a positive correlation between female SVL and percent weight increase in the year following parturition (n = 20, r = 0.66, P = 0.004). Two groups of females are again apparent in this analysis (Fig. 4). Records of annual weight change for females that were N for three consecutive years were available for only five females (813 ± 16 mm SVL, range
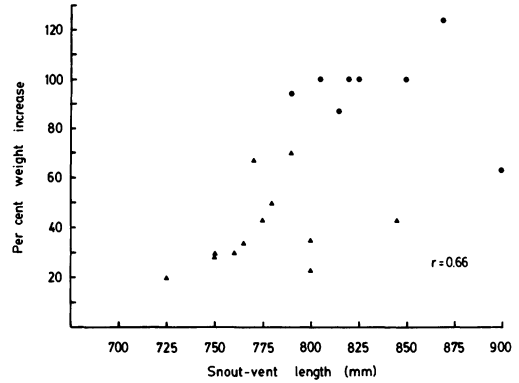
770—865 mm) in 1982. The mean gain in body mass during that year was 18.4 ± 7.6% (range 1–45%).

We also determined the change in SVL for females in each reproductive class. Relative growth of G females was negligible (0.9 ± 0.1%, n = 34), whereas during the N year in a biennial cycle relative growth of females was 3.5 ± 0.05% (n = 8). In the first and second N years of a triennial cycle, relative annual growth of females averaged 1.9 ± 0.04% (n = 12) and 2.4 ± 0.04% (n = 14) respectively.

*Litter characteristics.*—The mean litter size was 4.6 ± 0.31 (n = 28, range 2–8). Stillborn young were included in the estimate of mean litter size; however, apparently unfertilized ova were not included. Dead embryos and unfertilized ova were recorded in 32% of litters. Litter size was correlated with G weight (measured 1–2 d before parturition; r = 0.67, P < 0.001; Fig. 5) but not with female SVL (r = 0.25, P = 0.2).

The mean SVLs of neonates were 267.2 ± 1.5 mm for females (n = 75, range 210–290 mm) and 269.9 ± 1.7 mm for males (n = 68, range 210–290 mm). Mean weights of neonates were 17.2 ± 0.35 g for females (n = 75, range 5.7–23.9 g) and 17.9 ± 0.34 g for males (n = 67, range 6.7–22.0 g). In neither case was there a difference between sexes (SVL, P = 0.23; weight, P = 0.13). The sex ratio at birth, based on 28 captive-born litters and 14 field born *C. viridis* was 1:1.1 (68 male : 75 female). The estimated proportion of males among neonates

was 0.496 (SE = 0.044), not significantly different from 0.5.

Mean RCM was 0.37 ± 0.06 (n = 28, range 0.23–0.54) and the mean effort per individual progeny (RCM/litter size) was 0.089 ± 0.013 (range 0.053–0.176). RCM was correlated with litter size (r = 0.61, $P$ < 0.001), but was not correlated with female SVL (r = −0.27, $P$ = 0.15). In addition, correlations of either mean SVL or mean weights of littermates with female SVL, G weight, litter size, or RCM were not significant.

## DISCUSSION

The ages at which female *C. v. oreganus* in British Columbia attain sexual maturity and produce their first litter are greater than has been reported for most populations of *C. viridis*. Diller and Wallace (1984) estimated sexual maturity was reached at 4–6 yr and at SVL between 580 and 600 mm in *C. v. oreganus* from Idaho. In California populations, the smallest female with enlarged follicles or embryos was 720 mm SVL (Fitch and Glading, 1947). Fitch (1949) estimated that 4 yr were required for rattlesnakes to reach 800 mm SVL; if so, females mature at 3 yr in California. The younger age at sexual maturity in California is likely the result of a longer growing season and more rapid juvenile growth rates compared to British Columbia juveniles (Macartney, 1985).

The body size at which females attain sexual maturity in British Columbia is similar to that of California females, and both are much larger at maturity than are Idaho females. However, the length and temperature regimes of the active seasons, and juvenile growth rates, are nearly the same for British Columbia and Idaho rattlesnakes. Why Idaho females mature at an earlier age than females in British Columbia is not known. Age at maturity at these sites may be related to the overall smaller size of rattlesnakes in Idaho populations and may have a genetic rather than an environmental basis.

Female reproductive cycles of temperate zone viperids have been described as being primarily annual, primarily biennial, or both biennial and triennial. Biennial reproductive cycles are common to most species and populations of *Crotalus* (Fitch, 1970), and occur in many northern populations of *Vipera* (Saint Girons, 1957; Prestt, 1971; Andrén and Nilson, 1983). The occurrence of triennial cycles has been suspected in some crotaline snakes (e.g., *Agkistrodon contor-*
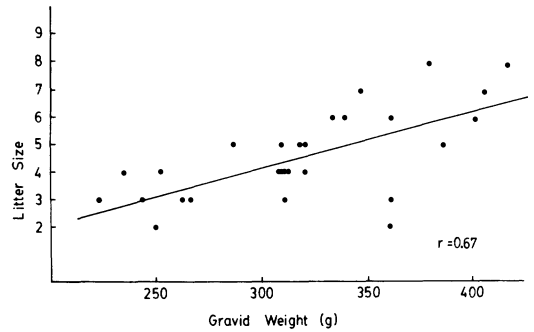


Fig. 5. Relationship between litter size and female gravid weight (measured 1–2 d before parturition, n = 28).

*trix*, Fitch, 1960 and *C. horridus*, Gibbons, 1972; Galligan and Dunson, 1979; Fitch, 1985); however, triennial or longer cycles have been confirmed only in the present study and in northern populations of *C. horridus* (W. S. Brown, pers. comm.).

A commonly employed method for assessing reproductive frequency in snakes has been to determine the ratio of G to N females in a population. Reproduction is considered to follow a biennial pattern if the G:N ratio is not markedly different from 1:1. Blem (1982) has pointed out that in many studies a statistical analysis of the G:N ratio is questionable or lacking, and Seigel and Ford (1987) further comment on the validity of this approach. There are other serious problems that may stem from wrongly interpreting this ratio. For example, if the ratio is based on dissections of females that have been collected during a single season, or from such data pooled over several years, erroneous conclusions could be reached because the ratio may more accurately reflect differences in seasonal activities or the ease of capture of the two reproductive classes, than reproductive frequency. Or, workers postulating annual reproduction based on a majority of G females in a sample, may fail to recognize (or ignore) the possibility that a biennial cycle could equally apply if the ratio were reversed in alternate years (Tinkle, 1962). Further, all females in a population may not follow the same cycle, as was evident in this study. For these reasons, studies that rely on the G:N ratio in the absence of other evidence may provide only a general indication of reproductive frequency or may be entirely misleading.

The most reliable method for accurately documenting reproductive frequency is to conduct

long-term, mark recapture studies. To our knowledge, in only a few studies of snakes has an assessment of reproductive frequency based on G:N ratios been corroborated by mark-recapture information (Saint Girons, 1957; Prestt, 1971; Gannon and Secoy, 1984). Saint Girons (1957) noted a 1:2, G:N ratio in a population of Vipera aspis in which a triennial cycle prevailed. In the present study, the yearly G:N ratios were consistently biased toward N females, and if comparable ratios are found in other populations of snakes the occurrence of extended reproductive cycles may be expected.

Fitch (1949) originally concluded that California rattlesnakes followed a biennial cycle because enlarged follicles were present in 16 of 33 females in a spring (March–June) sample. Females dissected shortly after emergence from hibernation (March–April) had only previtellogenic follicles, whereas enlarged follicles were present in most females in late spring (May–June). The inconsistency of these findings with those of Rahn (1942) on the seasonal development of follicles in a biennial cycle of C. v. viridis was brought to light by Fitch (1970). The absence of two distinct follicle size classes in early spring samples suggests that vitellogenesis begins in the spring (Type I pattern of vitellogenesis, Aldridge, 1979). Although females in California enter hibernation a few weeks after parturition (Fitch and Glading, 1947), emergence occurs in early March and females feed during the 8 wk spring mating period (Fitch and Twining, 1946). Through spring feeding, a postpartum female may be able to restore sufficient fat reserves to reproduce annually.

Aldridge (1979) determined that vitellogenesis begins in late summer in C. v. viridis from New Mexico (Type II pattern of vitellogenesis) and alluded to a potentially annual reproductive cycle in that population if females are able to initiate vitellogenesis immediately after parturition; however, he did not provide direct evidence for this. Type II vitellogenesis in an annual cycle has been reported in Idaho populations of C. v. oreganus by Diller and Wallace (1984). Some females in their early spring samples contained both enlarged follicles and remnants of incubation chambers in their uteri. These findings indicate that postpartum females with large fat reserves may initiate vitellogenesis prior to entrance into hibernation. Both annual and biennial cycles in these populations have since been confirmed by mark-recapture (R. Wallace, pers. comm.).

Type II vitellogenesis also occurs in British Columbia females but does not begin immediately following parturition. Fat reserves are low at parturition and climatic conditions generally do not allow postpartum females to forage prior to hibernation. Females rarely feed during the year they are G and must depend on fat reserves sequestered in the previous year(s) to sustain themselves and their developing embryos. Some females lessen the burden on fat reserves by feeding in early spring. Postpartum females require at least one active season to build up sufficient fat reserves to initiate vitellogenesis. Consequently, annual reproduction does not occur in these populations.

There is a trend for reproduction to become less frequent with increasing latitude in C. v. oreganus, thereby supporting the hypothesis that differences in the length of the active season may explain some of the intraspecific variation in reproductive frequency of reptiles (Fitch, 1970; Christiansen and Moll, 1973). Although length of the active season has a major influence on reproductive frequency, there are examples in the literature of viperids in which the reproductive frequency differs between closely situated populations (e.g., Vipera aspis, Saint Girons, 1957 and Crotalus viridis, Diller and Wallace, 1984) and examples of northern populations in which females reproduce more frequently than in southern populations (A. piscivorus, Wharton, 1966; Blem, 1981). These, in addition to intrapopulation variation in reproductive frequency, suggest that differences in the duration of the active season alone do not provide a satisfactory explanation of geographic variation in reproductive frequency. Differences in prey availability also may contribute to temporal and geographic variation in reproductive traits among populations (Seigel and Ford, 1987). In the case of C. v. oreganus, differences in the rate of prey consumption during June–Aug. between California (17.8% of snakes with food, n = 160, Fitch and Twining, 1946) and British Columbia populations (17.1% with food) are not evident. Although this comparison is simplistic, it is consistent with the possibility that prey availability is similar between these sites and probably therefore does not contribute significantly to the obvious differences in life history parameters between these populations.

A reduction or cessation of feeding by G females has been reported in several species of viperids and other snakes (Fitch, 1960; Prestt, 1971; Keenlyne, 1972; Saint Girons, 1979). Re-

duced feeding by G females may suggest a potential loss of energy that could otherwise be put into reproduction or growth. However, G *C. v. oreganus* greatly restrict their movements and do not actively forage, and therefore vastly reduced prey consumption may be explained simply by the fact that a G female would only rarely encounter prey. Balancing low energy intake are the low energy costs during gestation (6% loss of body mass), and that G females apparently benefit by restricting their movements because, as a group, they show higher annual survivorship than actively foraging N females (Macartney, 1985). Thus low rates of feeding and activity are not necessarily maladaptive behaviors for G females.

The rate of body mass recovery following parturition appears to be an important determinant of reproductive frequency. Females lose, on average, 6% of their weight during gestation, 37% through parturition, and an additional 6% of their postpartum weight during hibernation (Macartney, 1985). To reproduce in alternate years, a postpartum female must regain this lost mass over the next active season. Vitellogenesis does not occur in females that are unable to double (approximately) their postpartum weight during the next summer. Vitellogenesis appears to be inhibited for even longer periods if females continue to show poor weight gains, resulting in triennial or longer cycles. An apparent inhibition of vitellogenesis when fat reserves are minimal has been noted for other viperids (Saint Girons, 1957; Tinkle, 1962; Prestt, 1971).

Body size also may have an influence on reproductive frequency because the proportion of body mass gained by females during the year following parturition appears to be related, in part, to body size (Fig. 4). Similar relationships between body size, accumulation of lipid reserves, and reproductive frequency have been shown for other crotaline snakes (Tinkle, 1962; Cale and Gibbons, 1972; Seigel and Ford, 1987). In general, snakes might delay reproduction in a given year in order to grow larger and produce larger litters. This seems to be unlikely to happen in our populations because: 1) there was a weak correlation between litter size and SVL; and 2) postpartum females that reproduced triennially regained about the same proportion of body mass and increased their SVL by amounts similar to postpartum females that reproduced biennially, except that the former group took longer to do this.

In British Columbia, vitellogenesis is initiated by females that experience large weight gains during the summer. Mating occurs in late summer (coincident with the peak period of spermatogenesis in males) but also at a time when females have only previtellogenic follicles in their ovaries. As small follicles are also present in females that are not destined to produce young the next year (i.e., in females that gain little weight and do not undergo vitellogenesis) there must be a relationship between body weight gains, vitellogenesis, and female attractiveness. The onset of vitellogenesis cannot be detected by palpation. Thus, it is not clear whether females that gain weight rapidly become sexually attractive and, following mating, initiate vitellogenesis. Alternatively, females may become sexually attractive and mate after the onset of vitellogenesis. Heavy feeding induces sexual attractiveness in *Thamnophis melanogaster* (Garstka and Crews, 1982) and copulation appears to be a prerequisite to vitellogenesis in *T. sirtalis* (Bona-Gallo and Licht, 1983). These mechanisms may also operate in British Columbia populations of *C. v. oreganus*. If females produce a sexual attractiveness pheromone and if the amount of pheromone produced is correlated with body weight, then male rattlesnakes would have a means of distinguishing between females capable of reproduction and those incapable of reproduction. Apparently, ecdysis enhances female attractiveness and may stimulate courtship by male *C. v. oreganus*, as has been demonstrated in several other snakes (Kubie et al., 1978; Andrén, 1982; Burchfield, 1982). Further research is needed to gain an understanding of the differences in the two patterns of vitellogenesis, the recovery of female body mass, and in the timing of mating that exist among populations of *C. v. oreganus*.

Litter size also varies among populations of *C. v. oreganus*. Mean litter sizes, based on counts of ova, are 5.5 in Idaho (Diller and Wallace, 1984) and 9.9 in California (Fitch, 1949). Our estimate of 4.6 was based on neonates; however, if the total number of young and ova expelled at birth is used, mean litter size becomes 5.2. These data suggest a trend for smaller litter sizes in northern populations. However, because each of these estimates is based on data collected over a short time and because litter size in snakes has been shown to vary as widely among years as among populations (Seigel and Fitch, 1985), this trend may not be very meaningful. Our estimate of RCM is similar to mean

RCM in Idaho females (0.42, R. Wallace, pers. comm.). Apparently, there is only minor geographic variation in size of neonates. Neonates typically average between 270–290 mm SVL and 17–20 g in all three populations (California, Idaho, and British Columbia).

A female's foraging success, year-to-year variability in prey abundance, and the amount of time available for foraging during an active season—dictated by climatic conditions—are factors that influence reproductive frequency (Saint Girons, 1957; Wharton, 1966; Diller and Wallace, 1984). One phylogenetic constraint that may affect frequency of reproduction in this genus is the relatively large size of rattlesnake neonates. For example, the average ratio of G female mass to mean offspring mass of annually reproducing, viviparous colubrids from the same study site is 37:1 in *T. sirtalis* (n = 18) and 42:1 in *T. elegans* (n = 4), whereas in *C. v. oreganus*, the ratio is 17:1 (Macartney, unpubl. data). A long time is required for completion of vitellogenesis and embryonic development (6–7 mo), and a considerable amount of energy is required to produce each neonate (about 9% of a G female's body weight). The 5 mo active season in British Columbia results in an interrupted (at vitellogenesis) developmental period, thereby extending the reproductive cycle. The short active season also limits the time available for replenishment of energy reserves needed for future reproductive efforts. In British Columbia, a minimum biennial reproductive cycle is imposed by these constraints. Further, whether a female can reproduce this often seems to be determined chiefly by the rate and amount of body mass gained during N years.

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