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THE ECOLOGY OF THE NORTHERN PACIFIC RATTLESNAKE, *Crotalus viridis oreganus*, IN BRITISH COLUMBIA

by

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ABSTRACT

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The western rattlesnake *Crotalus viridis* occurs in arid regions from southern Canada to northern Mexico. The ecology of this species is well known from studies conducted in southern and central portions of the range, but less is known about the ecology of northern populations. Life-history parameters of the northern pacific rattlesnake *Crotalus viridis oreganus* were documented in a three year mark-recapture study of populations at 24 communal hibernacula in the Okanagan valley of south-central British Columbia. Data collected in this study facilitated an examination of geographic variation in the life-history of this wide ranging species.

Rattlesnakes in the Okanagan valley spend about seven months in communal hibernacula (September to April). The active season is short and foraging is confined mainly to the months of June, July and August. Growth rates of juveniles are lower than reported for conspecific populations from lower latitudes. Males grow more rapidly than females and sexual maturity is attained at 3 to 4 years in males and 7 to 8 years in females.

Mating occurs in late summer or early fall and vitellogenesis is initiated prior to hibernation. Ovulation occurs the subsequent spring and parturition follows in September or October. The average litter size is 4.6 young. Females are capable of reproducing on a biennial basis, but most follow triennial cycles. The frequency of reproduction is largely determined by a female's ability to accrue body mass (fat reserves) during nongravid years. The slower rate of growth, delayed sexual maturity, and less frequent reproduction in these populations, compared to more southerly populations, is due in part to a shorter active season.

Radiotelemetry was used to determine movements and activity ranges of individual snakes. Rattlesnakes disperse up to 2 km from hibernacula during the summer and may have large activity ranges (> 8 ha). Gravid females, however, remain in close proximity to dens and have small activity ranges (0.16 to 0.22 ha). Summer ranges of rattlesnakes from neighbouring dens overlap considerably, but individuals show high fidelity to hibernacula. Observations of inter-den matings suggest that den populations are not reproductively isolated demes. Population size and composition are highly variable among dens, but remain fairly stable within dens. Switching between dens is rare (mostly juveniles) and recruitment into a den population occurs mainly as a result of birth.

Annual survivorship increases with size (age) and adult males experience higher survivorship than adult females. Overwintering survivorship is high (averaging 97% for males and and 86% for females) and energetic demands during hibernation are low (weight loss averages 5 - 7%). A life table based on estimates of age-specific survivorship and fecundity suggests, tentatively, that these populations are declining (R_o = 0.50). Additional evidence, however, suggests that populations on these sites are above historical levels (1930's - 1950's).

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1.0 INTRODUCTION

By themselves, autecological studies provide little more than a catalogue of facts pertaining to the life-history of a population of organisms which have evolved under a specific set of local environmental pressures. Their value, however, lies in enabling one to compare life-histories of conspecific populations studied in various areas of a species' range (e.g. Pianka, 1970). Students of life-history theory have made numerous predictions about which combinations of traits should evolve in organisms living in specified circumstances, but tests of theoretical models lag far behind the generation of such models (Stearns, 1976, 1977). Field studies can, at best, provide correlative evidence of environmental/life-history patterns; nonetheless, they serve as an important first step towards documenting the existing patterns of variation in life-history traits both within and among species.

In this respect, the western rattlesnake, *Crotalus viridis*, is a useful study organism. It has a wide geographic distribution in western North America and there is a large body of literature from which comparative information can be extracted, particularly for populations in the central and southern areas of the range (Fig. 1). Studies on northern populations of *C. viridis* have not focussed on life-history attributes *per se* (Preston, 1961;

Gannon, 1980) and knowledge of the life-history of northern populations is needed if intraspecific comparisons are to be made. Of concern in this study are populations of the northern pacific rattlesnake, *Crotalus viridis oreganus*, located in British Columbia, near the northern limit of the species' range in western North America. Sampling of these populations is facilitated by the occurrence of communal overwintering (denning) behaviour.

The objectives of this study were:

1) To document reproductive cycles, growth rates, seasonal activities, movements, food habits, ecdysis, hibernation and other aspects of general ecology;

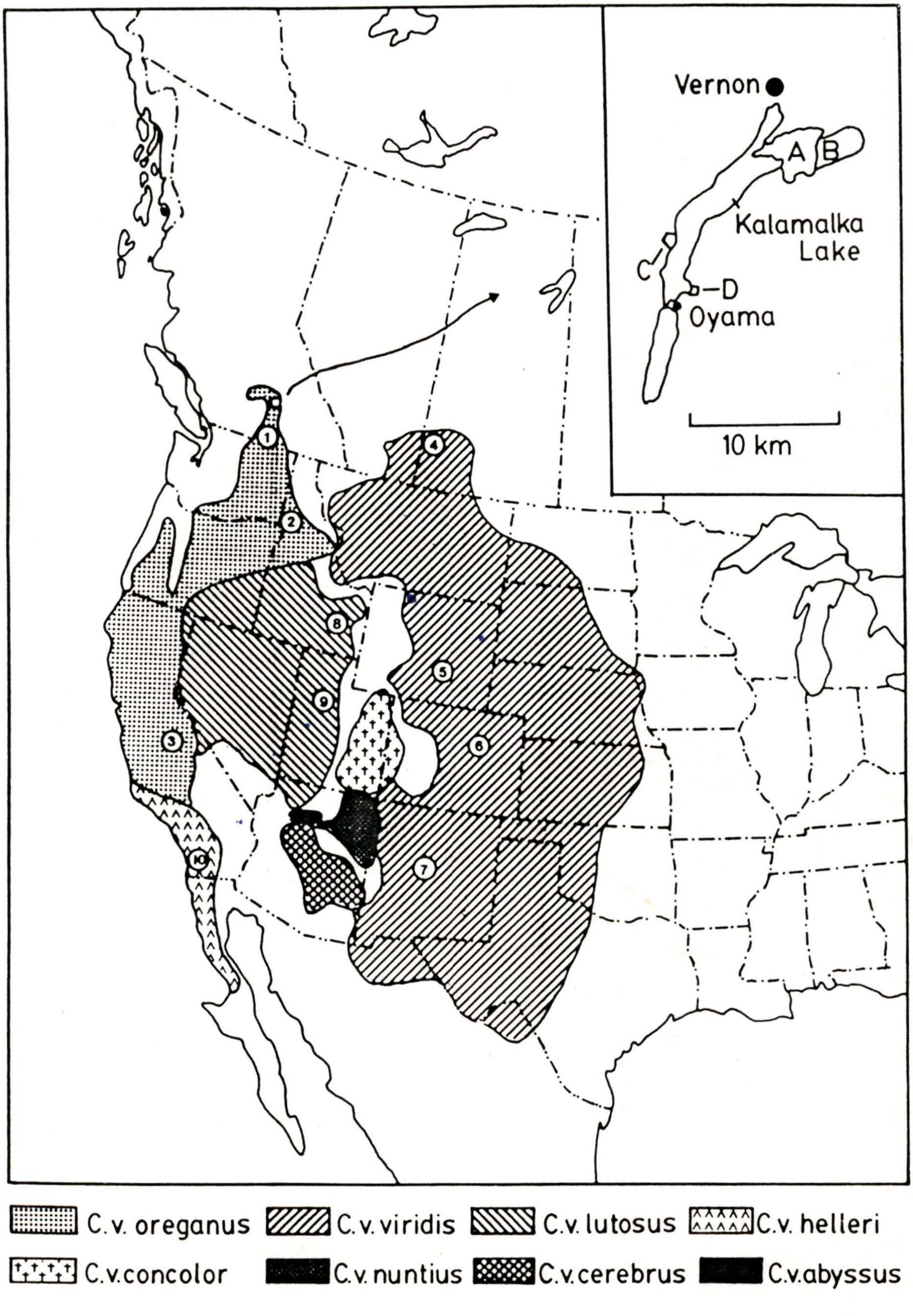
2) To determine the mean and variance of important life-history traits such as age at sexual maturity and first reproduction, litter size, size of young and reproductive frequency;

3) to provide demographic data for constructing a life table for northern populations of *C. viridis*.

I predicted that differences in life-histories would exist among populations of this species along a latitudinal gradient, if only because climatic conditions, which have a major influence on the seasonal activities of reptiles, vary geographically. At high latitudes (or high elevations) climatic conditions allow only a short period

Figure 1: The distribution of the eight subspecies of *Crotalus viridis* (based on Klauber, 1972) showing the location of previously studied populations (circled numbers) and the location of study sites in the Okanagan valley, British Columbia (inset).

C. v. oreganus: 1= Preston, 1961, 2 = Diller and Wallace, 1984, 3 = Fitch and Twining, 1946; Fitch and Glading, 1947; Fitch, 1949. *C. v. viridis*: 4 = Gannon, 1980; 5 = Duvall *et. al.*, 1985, 6 = Klauber, 1936, 1937; Ludlow, 1981, 7 = Aldridge, 1975, 1979a, 1979b; Jacob and Painter, 1980. *C. v. lutosus*: 8 = Sehman, 1977, 9 = Woodbury, 1951; Hirth, 1966a, 1966b; Parker and Brown, 1974. *C. v. helleri*: 10 = Klauber, 1937, 1940.


Vernon
A
B
Kalamalka Lake
C
D
Oyama
10 km
1
2
3
4
5
6
7
8
9
10
C.v. oreganus
C.v. viridis
C.v. lutosus
C.v. helleri
C.v.concolor
C.v. nuntius
C.v.cerebrus
C.v.abyssus

for summer activity and impose a lengthy period of winter dormancy on reptiles (Gregory, 1977, 1982). Any reduction in the period of time available for foraging during the annual active season is likely to result in reduced annual growth, delayed reproduction, and a decrease in reproductive frequency, all of which may have important demographic consequences. By studying the life-history parameters of populations occurring at the edge of a species' range it may also be possible, ultimately, to determine what factors limit the species' distribution.

1.1.1 Description of study sites

This study was carried out at four sites in the Okanagan valley, in the vicinity of Vernon, British Columbia (latitude 50°15'N, longitude 119°12'W, elevation 425 m). The two major study areas were Rattlesnake Hill in Kalamalka Lake Provicial Park (Site A) and an adjacent hillside (hereafter referred to as Deep Lake Ridge) on the Coldstream Ranch (Site B) (Fig. 1). These ridges lie in a NE-SW direction and are separated by an open grassland valley about 1.5 km in width. On these sites a total of 22 communal hibernacula were located: 15 on Site A and seven on Site B. Site C was a British Columbia Ecological Reserve situated about 15 km south of Vernon on the west side of Kalamalka Lake. A fourth site (Site D) was located on the east side of Kalamalka Lake about 3 km north of the town of Oyama. Each of the latter sites contained only one known den. The study areas were approximately 100 km southeast of the northernmost site record for *C. v. oreganus* (Carl, 1968); therefore the populations that I studied are representative of the subspecies at the extreme northern edge of its distribution in North America (Fig. 1).

The ridges on Sites A and B are similar in topography. Each has a steep, often precipitous, rocky south-facing slope which rises between 75 and 200 m above the valley floor. The north faces are gently sloped and covered with *Agropyron spicatum* (Bluebunch Wheat Grass) and *Pinus ponderosa* (Ponderosa Pine) and numerous species of shrubs. Extensive areas of open native pasture and cultivated fields characterize the north slope of Deep Lake Ridge, while the ridge top and north side of Rattlesnake Hill are more heavily forested and bordered at lower elevations by pastures, orchards and human settlements. Site C is on a steep southeast-facing slope and Site D is located on a moderately steep southwest-facing hillside.

These study sites are located at the northern end of the Okanagan Valley and lie in the rainshadow of the Cascade Range and the Thompson Plateau. Meteorological information pertaining to the study sites was obtained from an

Environment Canada climate station on the Coldstream Ranch (Site B). The average annual total precipitation is 41 cm and most of this falls during the winter and late spring. Annual snowfall averages 121 cm. The mean number of frost free days is 153 per annum. The mean annual temperature is 7.2±0.6°C (SD). In January the mean maximum temperature is -2.6°C and the mean minimum temperature is -9.4°C. In July the corresponding mean temperatures are 27.0°C and 11.2°C respectively. The months April through September contribute nearly all of the average 975 degree days above 10°C accumulated per year in this area.

1.1.2 Description of hibernacula

Rattlesnake hibernacula in this area were usually inside discrete rock outcrops or within localized regions of large continuous rock faces; the den on Site C was inside a large earth covered mound of broken rock. The number of entrances ranged from one to three; most dens had two. Most of the hibernacula on Sites A and B were situated along the upper one-third of the south-facing slope and about 25% of the dens were located in the middle or lower regions of these slopes. Areas of talus which covered portions of the southern face did not appear to be used for overwintering by rattlesnakes; however, patches of talus adjacent to dens were preferred basking areas in the spring.

Hibernacula were also used by other species of snakes but all dens were numerically dominated by rattlenakes. Small numbers of the western racer (*Coluber constrictor*) were found at 92% of the dens. About 40% of the dens were also used by small numbers of adult garter snakes (*Thamnophis sirtalis*) and about 20% were used by small numbers of gopher snakes (*Pituophis melanoleucus*). Two other species of snake (*Thamnophis elegans* and *Charina bottae*) were uncommon on all sites and were never found at rattlesnake hibernacula.

1.1.3 Structure of the thesis

The results of this research are presented in four parts. The first section includes a general methods section outlining the sampling procedures used in this study and provides a synopsis of the annual activity cycle of *C. v. oreganus* in British Columbia. The annual cycle can be roughly divided into four periods: spring emergence and dispersal from hibernacula, a summer foraging period, the return and ingress into hibernacula and hibernation. The subsequent three sections focus on growth, reproduction and population dynamics. Each section contains its own Methods section that provides details on procedures and statistical methodology. For all statistical tests a minimum significance level of $\alpha = 0.05$ was used.

2.0 ANNUAL CYCLE

2.1.0 General Methods

2.1.1 Sampling procedures

The active season was divided into spring (March 15-May 31), summer (June 1-August 31) and fall (September 1-October 31) periods. In the fall of 1980, 49 snakes were marked by P.T. Gregory at three dens on Site B (8,9 and 11) and at den 27 (Site C). Additional hibernacula were discovered and incorporated into the study as follows: spring 1981, three dens; fall 1981, four dens; spring 1982, six dens; fall 1982, one den; and spring 1983, six dens, for a total of 24 dens on the four study sites.

Intensive hand collecting was carried out while snakes were active in the vicinity of the dens in the spring and fall periods. During spring and summer 1981 dens on Sites A, B and C were visited biweekly. Between fall 1981 and the end of field work in spring 1983, visits to dens on Sites A and B were increased to every second day and and daily at den 27 (Site C). The location of dens along a fairly narrow band on the southern slopes of Sites A and B made it convenient to begin a day's sampling at one end of the hillside and work towards the opposite end, visiting each den (except the last den) once in the morning and again in the afternoon. Varying the order in which dens were sampled helped to reduce collecting bias due to the time of day that dens were visited.

On August 26, 1981, a 0.8 m tall fence was erected around the entrance to den 27 (Site C) to facilitate the capture of snakes arriving at the den. Access to the den was provided by wire mesh funnels, each fitted with a removable wire mesh cylinder which served as a trap. Funnels could be reversed such that during the fall all led inwards and during the spring all funnels led away from the den entrance. Traps were checked and emptied daily. At the end of each spring and fall period, the traps were removed to enable free movement to and from the hibernacula for late dispersing or late arriving rattlesnakes.

Total visits to dens during each fall and spring period numbered 20 to 30 for dens on sites A and B and 50-60 for den 27. For logistic reasons, den 15 (Site A) and den 28 (Site D) were visited only once or twice in each period of the active season. During the summer period, the dens were inspected periodically but most of the searching for rattlesnakes at this time was done away from dens.

2.1.2 Processing rattlesnakes

Rattlesnakes were handled with Pilstrom tongs and secured for measuring by placing a padded restraining noose over the head and clampling it firmly around the neck, just posterior to the angle of the jaw. At each capture a snake was sexed by Gregory's (1983) method, its snout-vent length (SVL) was measured to the nearest 5 mm and the number of rattle segments was counted. Each snake received an individual mark by removing a unique combination of ventral and subcaudal scutes (Blanchard and Finster, 1933). Prior to its release from the noose, each snake was palpated to determine the presence or absence of stomach and fecal material, and, in females, to ascertain the approximate size and number of embryos or follicles. In addition, individual identifying characteristics (e.g. scars, scute anomalies etc.) were noted. Fecal material was collected and any stomach contents were gently forced up towards the mouth. A snake was then released from the noose, pinned and the stomach contents were manually manoeuvered into the buccal cavity. There, they were either identified and quickly returned to the stomach, or removed from the mouth and preserved in formalin.

Measurements of body weights were not initiated until the late summer of 1981. Snakes were weighed, using either Pesola spring balances in the field or a digital top loading balance in the laboratory (necessitating up to a 48 h removal period).

The entire field procedure required about three minutes per snake to perform. Rattlesnakes seemed to tolerate handling well. In thousands of handling times, fewer than 15 individuals sustained serious injuries or died as a direct result of handling.

2.2.0 Methods - Annual cycle

Patterns of spring emergence and fall arrival of rattlesnakes at hibernacula were based on the first spring and the first fall captures of individuals. Time spent in hibernation was calculated for the interval between an individual's last fall sighting and its first spring sighting. Analysis of variance was used to test for age/sex and year-to-year differences in time spent in hibernation. To compensate for lack of orthogonality, two-way ANOVA's were performed with all possible orders of effects and a most conservative - most optimistic F table constructed for each effect (a modified hierarchical solution, see Spinner and Gabriel, 1981; Tupper and Rosenblood, 1984).

The distinction between juveniles (< 650 mm SVL) and adults (> 650 mm SVL) was based on the SVL of the smallest gravid female (see Reproduction).

Data on movements of rattlesnakes from dens on Sites A, B, and C were obtained through recaptures of marked snakes, by locating shed skins of marked snakes and by radiotracking individual snakes. Each new location was marked with flagging tape and the distance from the snake's last location (approximately a straight line) was measured to the nearest 5 m with a surveyor's topolite. Distances less than 50 m were visually estimated. When a direct line of sight was possible between two capture points the compass bearing from the old location to the new location was measured in the field to the nearest 5 degrees; otherwise, direction of travel was determined using aerial photographs.

The topography and large area of the sites made it impractical to conduct searches in a random pattern. Areas which seemed suitable for basking or shedding were intensively searched and revisited if snakes were found there on previous visits. An effort was made to cover as much area as possible and incorporate new areas in the search routine. There was admittedly a bias towards maximizing the return on search effort by visiting more frequently productive places than nonproductive areas. Site B was the most amenable to searching because of its smaller area and more open terrain; consequently, more information on summer movements was collected on this site than at other sites. The steep and rugged terrain at all sites made searches at night difficult and dangerous, and such searches were seldom conducted.

Radiotelemetry was used to provide information on movements of individual rattlesnakes. Radiotransmitters (Model SM1, AVM Instrument Co.) were potted in a 1:1 paraffin:beeswax mixture and waterproofed with two thin coats of liquid plastic (Plasti Dip, Plasti Dip International; Jansen, 1982). A potted transmitter (4 x 1.5 cm, 12-15 g, with a 35-40 cm teflon coated whip antenna) was implanted extraperitoneally into the lower abdomen following a procedure modified from Reinert and Cundall (1983).

Rattlesnakes were anesthetized with Halothane (=Fluothane B.P., Ayerst Laboratories; Bonath, 1979) supplied via a head mask using a Mark IV Halothane vapourizer. Halothane induced anesthesia in less than 30 minutes and enabled the transmitter implantation to be completed in under one hour. Consciousness was regained usually within 45 minutes of surgery, as evidenced by rattling and tongue flicking. Snakes were kept in captivity for 2-6 days to ensure that the incision was healing and that transmitters were not affecting movements adversely. Transmitters were removed (under anesthesia) by making a small incision just posterior to the initial incision and withdrawing the transmitter package with one gentle motion.

Three adult *C. v. oreganus* (one male and two gravid females) from Site A were radiotracked for periods of 8-12 weeks between June and September 1982. Rattlesnakes were located in the field using a portable receiver (LA12DS, AVM Instrument Co.) and a hand-held, three-element Yagi antenna. Snakes were located, on average, every second day. Activity ranges of radiotracked rattlesnakes were determined by the convex polygon method (Jennrich and Turner, 1969).

Population home range (PHR), defined as the total area surrounding a hibernaculum that is used as summer range by all den members, was determined by mapping the locations of all snakes from each den captured in the summers of 1981 and 1982. The PHR boundaries were then demarcated for each den population and the convex polygon area determined from scale drawings. PHR overlap for a pair of dens was calculated by employing a measurement of niche overlap given by Pianka (1973). Using this measurement, overlap is calculated by:

$$O_{jk} = \Sigma^n P_{ij} P_{ik} / \sqrt{\Sigma^n P_{ij}^2 \Sigma^n P_{ik}^2}$$

where n = number of different resources and P_i = the proportion of all resources actually used, which is made up of resource i. In a pair-wise overlap calculation three resources (areas of habitat) are considered; the area used exclusively by individuals from den j, the area used exculsively by individuals from den k, and the area which is used by members of both dens. Overlap (O_{jk}) varies from 0 (no overlap) to 1 (complete overlap) in value. The amount of overlap of PHR's provides a rough measure of the potential mixing among populations from two different dens during the summer months.

Data on food habits were collected by palpating rattlesnakes for stomach contents and fecal material. In 1981, all stomach contents were collected and preserved. Since it was felt that meal deprivation could affect growth or survivorship, in 1982 only the tail and one hind foot (of mammalian prey) were removed for identification and the rest of the prey was returned to the snakes's gut. When identification by this method proved uncertain in the field or when more than one prey item had been ingested, the entire stomach contents were kept. Keys used to identify mammalian prey were Cowan and Guiget (1965) and Maser and Storm (1970). Avian prey were relatively rare and could usually be identified only from stomach contents, and not from feathers in fecal material.

The presence of fecal material in the rectum was noted for rattlesnakes sampled in 1981, but collection of fecal material for identification by guard hair analysis did not begin until 1982. Feces were dried and prey were identified to genus with the aid of premanent slides made from guard hairs of stomach contents collected in 1981 and from a few museum specimens (British Columbia Provincial Museum) collected from the Vernon area. A key to dorsal guard hairs (Moore *et al.*, 1974) aided in the identification of some of the material. Hairs were presumed to belong to one prey item unless the presence of more than one prey item or species was obvious. Identifications based on guard hairs were confirmed in all cases when intact skulls contained within the feces were also keyed out.

The semi-digested state of most stomach contents precluded the use of prey volume or length as a measure of prey size. Instead, average skull breadth for each mammalian prey species was obtained by measuring the zygomatic width of two to ten museum skulls (B.C.P.M.) collected in the Vernon area.

Finally, information concerning predation on rattlesnakes was collected from three sources: examination of mammalian scats for rattlesnake remains; the number, size and position of scars or injuries on rattlesnakes; and rattlesnake carcasses found in the field.

2.3.0 Results

2.3.1 Summary of captures

The information presented in this study was derived from a data base of 1693 individually marked rattlesnakes and 2537 recaptures obtained between September 1980 and May 1983. Several hundred additional recapture observations which essentially provided no new information were excluded from the data set. Recapture frequencies for individuals ranged from 0 (never recaptured) to a maximum of 13 recaptures. Summaries of sample sizes of unmarked snakes caught in each season at the four study sites are presented in Tables 1 and 2. Additional snakes were marked and others recaptured during week long visits to the study sites in the summer and fall of 1983 and during the spring and fall of 1984.

2.3.2 Patterns of emergence from hibernacula

Patterns of emergence from hibernacula were documented for 1982 and 1983. In both years emergence began in the last week of March and peaked in April; by late May most snakes had emerged onto the surface (Figs. 2 and 3). The average span of emergence was 48 days in 1982 (n = 10 dens, SE = 4.6, range 28-71) and 46 days in 1983 (n = 14 dens, SE = 3.2, range 18-67). In both years, the lowest maximum temperature on days in which snakes emerged was 8°C;

Table 1: Season of capture of unmarked snakes on Site A. Italicized values are the number of snakes caught during the season in which the den was initially located. Snakes caught prior to this season were free ranging snakes which were later caught at the den. Missing values (-) indicate the den area was not searched in a season, while zeros indicate the den was visited but no new snakes were marked. Unknown means that an individual's den affiliation was not determined. Sp = spring, Sm = summer and Fa = fall.

	1980		1981			1982		1983	
Den	Fa	Sp	Sm	Fa	Sp	Sm	Fa	Sp	Den Total
4	-	*8*	0	0	4	0	5	2	19
5	-	*55*	10	29	24	3	4	8	133
7	1	*23*	7	21	15	0	13	9	89
1	-	-	2	*28*	17	1	3	3	54
2	-	-	7	*51*	20	5	13	3	99
3	-	-	6	9	*11*	8	21	28	83
14	-	-	-	-	*14*	0	20	16	50
15	-	1	4	2	*38*	2	12	10	69
20	-	-	-	-	*10*	-	-	3	13
23	-	-	-	2	*10*	4	14	8	38
24	-	-	3	0	3	1	*17*	2	26
21	-	-	-	2	0	0	1	*19*	22
22	-	-	-	3	2	3	0	*17*	22
25	-	3	-	-	-	-	-	*5*	8
26	-	-	-	-	1	1	0	*11*	13
Unknown	2	23	25	13	10	12	1	9	95
Season Total	3	113	64	160	179	40	124	153	Site Total 836

Table 2: a) Season of capture of unmarked snakes at Sites B, C and D and b) Study totals by season. Symbols as in Table 1.

a) Site B.

	1980		1981			1982		1983	
Den	Fa	Sp	Sm	Fa	Sp	Sm	Fa	Sp	Den Total
8	*6*	47	16	11	15	1	9	7	112
9	*6*	7	3	5	1	0	3	3	28
11	*21*	53	4	9	10	4	42	7	150
16	-	3	5	*30*	12	6	33	10	99
17	-	1	34	*41*	51	19	49	31	226
10	-	-	1	3	0	1	0	*11*	16
13	-	1	0	2	1	0	1	*7*	12
Unknown	1	2	6	2	1	4	0	0	16
Season Total	34	114	69	103	91	35	137	76	Site Total 659

Sites C (den 27) and Site D (den 28).

	1980		1981			1982		1983	
Den	Fa	Sp	Sm	Fa	Sp	Sm	Fa	Sp	Den Total
27	*16*	52	11	28	16	1	9	5	138
28	-	-	-	-	*40*	1	8	11	60

b) Totals number of rattlesnakes marked during the study by season.

1980		1981			1982		1983	
Fa	Sp	Sm	Fa	Sp	Sm	Fa	Sp	Study Total
53	279	144	291	326	77	278	245	1693

however, emergence was not common except on days when maximum air temperature exceeded 10°C. Days of peak emergence were those with air temperatures above 15°C.

Snow melt occurred two weeks earlier in spring 1983 and the first period of warm weather arrived 7-10 days earlier than in 1982. This is reflected by the earlier first emergence peak in 1983 (Figs. 2 and 3).

A tendency for adult females to emerge from hibernation earlier than adult males was observed at most dens in both years. Mann-Whitney U-tests (individuals ranked by order of emergence from a den) were performed separately for adults and juveniles to test the hypothesis of no diifference in the timing of emergence of males and females. For four of eight dens in 1982 and five of ten dens in 1983, the null hypothesis was rejected for adults ($P < 0.05$). Postpartum and gravid females (enlarged follicles) emerged earlier than most adult males (Figs. 2 and 3). At seven of eight dens in 1982 and all of nine dens in 1983 there were no significant differences in emergence times of juvenile males and females.

In early spring, rattlesnakes were observed to spend the first few days after emergence basking near den entrances during the day and retreating into the dens by late afternoon. Later in the spring more snakes moved directly to talus patches or rocky areas adjacent the den, spending

Figure 2: Patterns of emergence of rattlesnakes from three dens in spring 1982 in relation to air temperature and precipitation. Triangle denote days on which the dens were visited but no new snakes (marked or unmarked) were caught. Den 5, n=70; Den 27, n=83; Den 11, n=27.

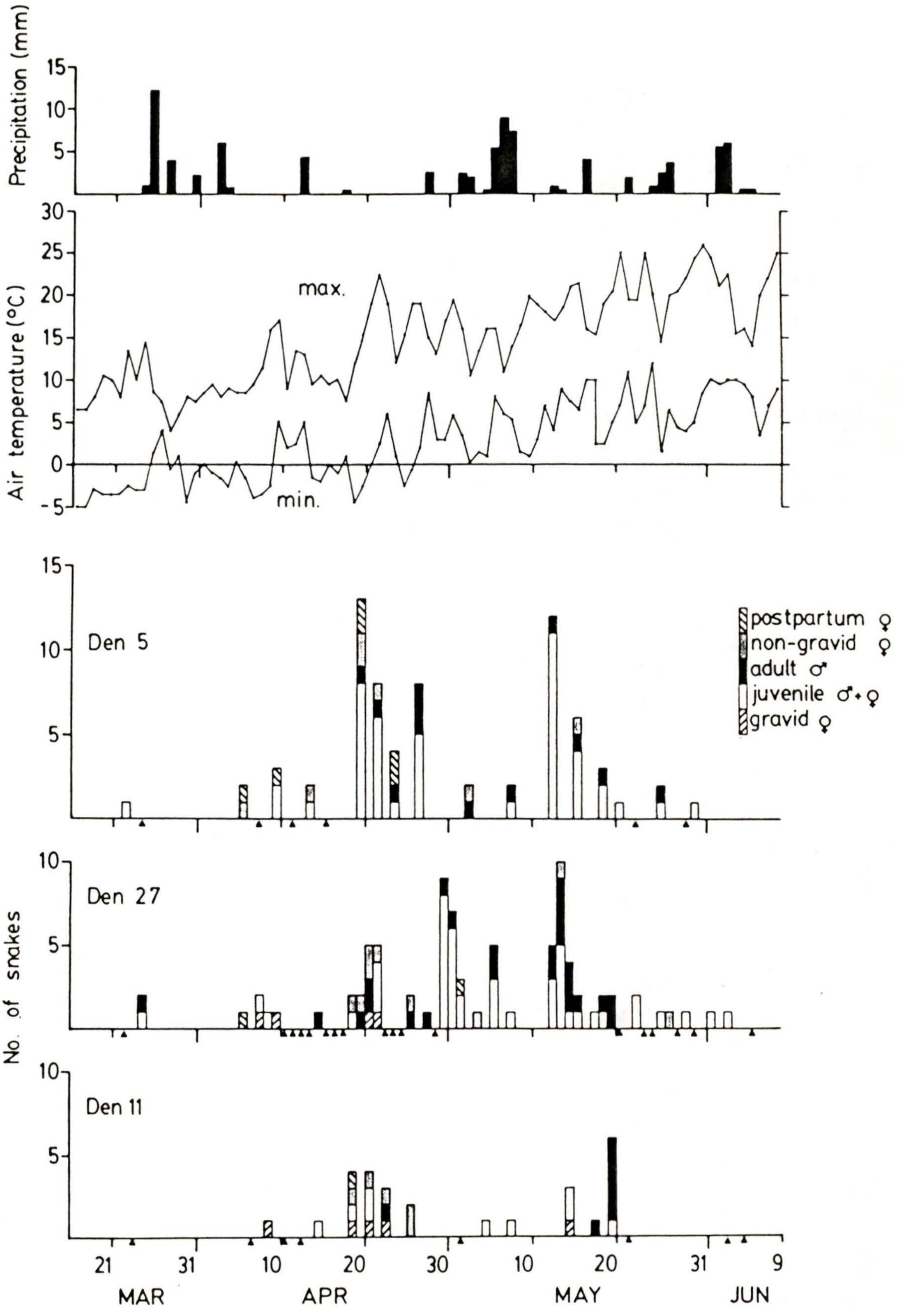
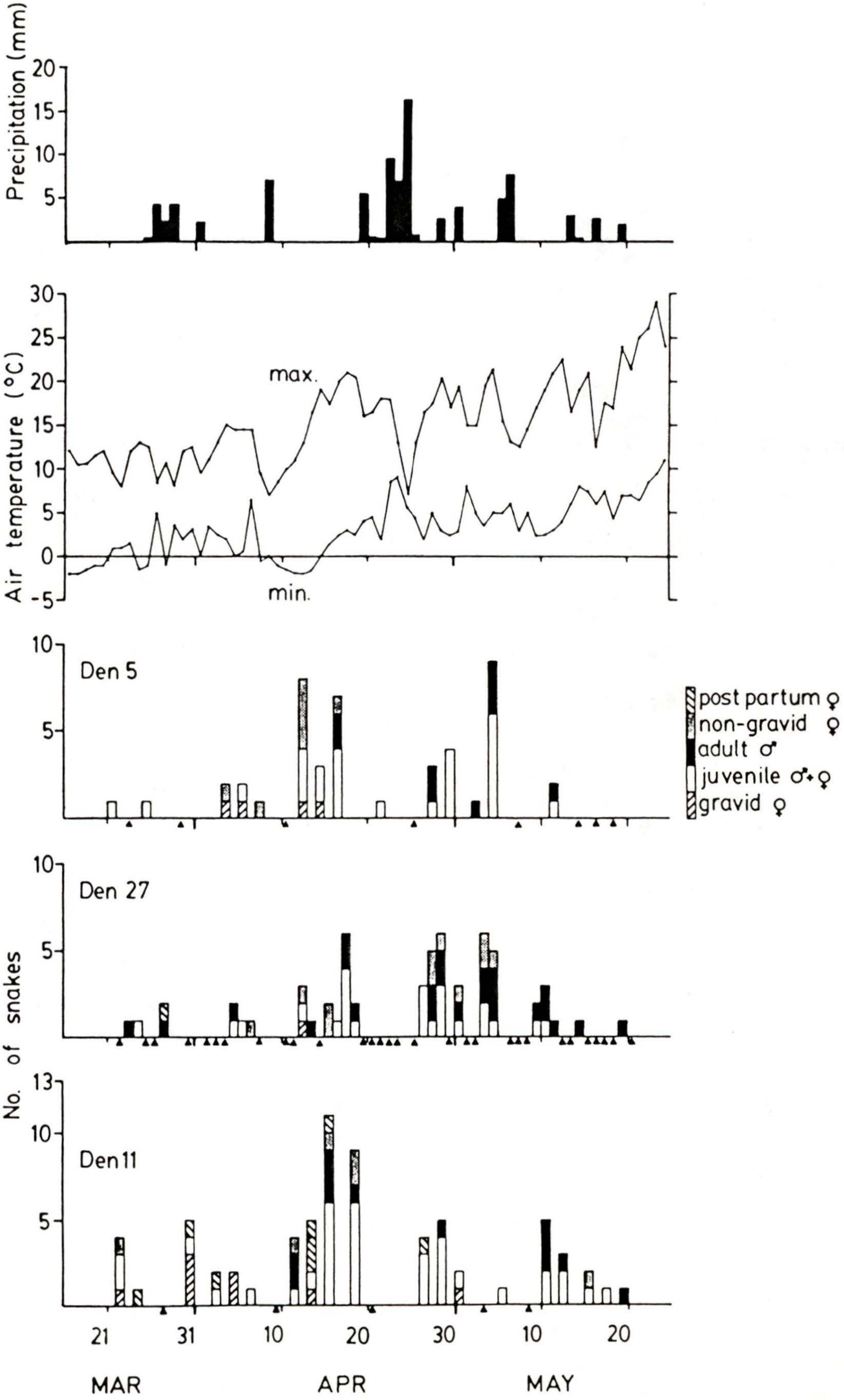

Precipitation (mm)
15
10
5
Air temperature (°C)
30
25
20
15
10
5
0
-5
max.
min.
No. of snakes
15
10
5
Den 5
Den 27
Den 11
postpartum ♀
non-gravid ♀
adult ♂
juvenile ♂+♀
gravid ♀
21
31
10
20
30
10
20
31
9
MAR
APR
MAY
JUN

Figure 3: Pattern of emergence of rattlesnakes from three dens in spring 1983 in relation to air temperature and precipitation. Triangles denote days on which dens were visited but no new snakes (marked or unmarked) were caught. Den 5, n=45; Den 27, n=59; Den 11, n=68.


Precipitation (mm)
20
15
10
5
Air temperature (°C)
30
25
20
15
10
5
0
-5
max.
min.
No. of snakes
10
5
Den 5
10
5
Den 27
13
10
5
Den 11
post partum ♀
non-gravid ♀
adult ♂
juvenile ♂+♀
gravid ♀
21
31
10
20
30
10
20
MAR
APR
MAY

the night under cover of rocks. A yearling rattlesnake was found dead near the entrance of den 11 on March 22, 1982 (minimum air temperature on that day was -3.5°C) and a second yearling was found dead 1 m from the den on April 11, 1983 (min. air temperature was 0°C). Neither snake bore evidence of injury; both presumably died of exposure.

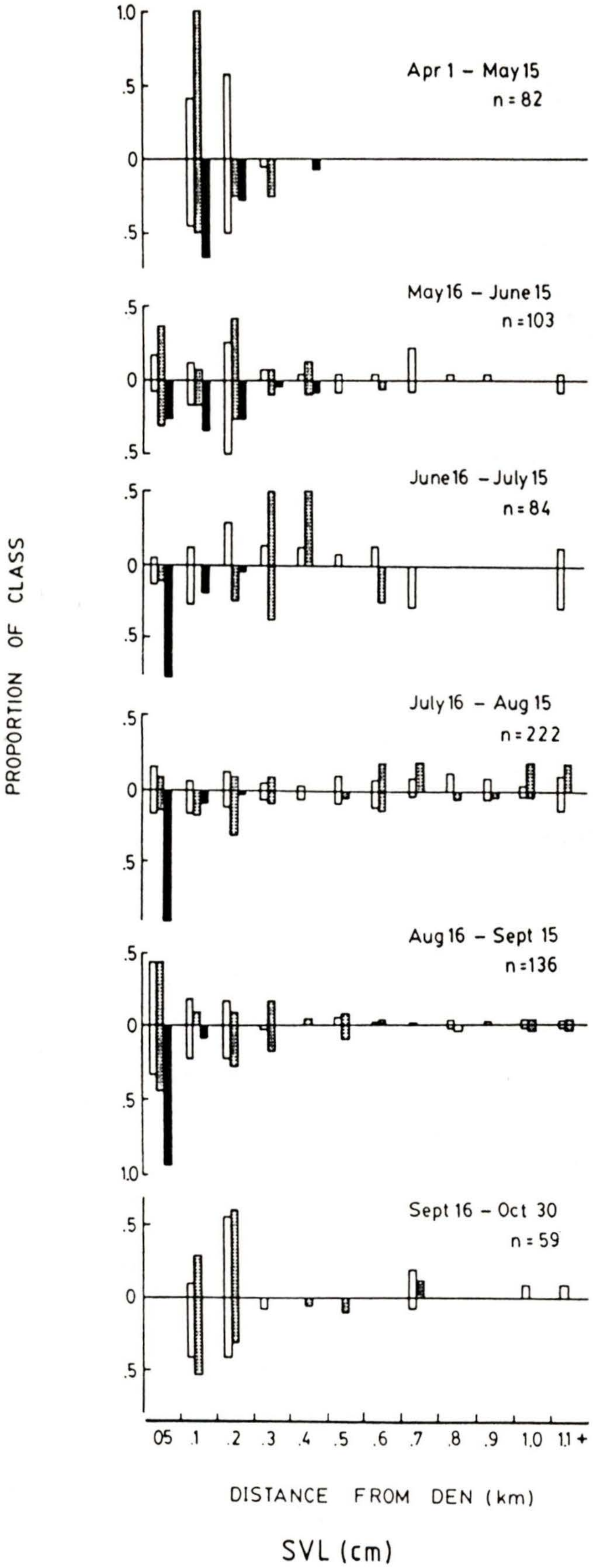
2.3.3 Dispersal patterns

A total of 701 location records was collected on rattlesnakes during this study. There was no apparent sex related bias in sampling (males 350, females 351 : overall sex ratio in the population was 1:1, see Population Dynamics); however, juveniles comprised only 23% of all records. The intensity with which each study site was searched varied in time and space; records totalled 258, 392 and 51 for Sites A, B and C respectively. There were no apparent topographical features which could physically restrict the distances travelled by individuals from different dens on any of the study sites. Therefore, for the analysis of seasonal movements, data were pooled over all sites and both years.

Snakes were divided into 5 classes: juvenile males, juvenile females, adult males, nongravid females and gravid females. The proportion of each class present in 100 m intervals in all directions from the dens were plotted for six periods during the active season (Fig. 4). Dispersal from hibernacula began shortly after emergence in April and May, during which time most of the snakes encountered were within 300 m of their den. In both years, emergence was completed in late May so that, in the early part of June, many late emerging individuals were still within 300 m of their dens while others had dispersed between 500 and 1100 m from dens. Juveniles of both sexes appeared either to leave dens later or disperse less rapidly than adults (Fig. 4).

Between mid-July and mid-August snakes in all classes except gravid females were relatively evenly distributed in distance from the dens, and most had probably travelled their maximum distance from dens during the summer. Juveniles were found as far afield as adults during the summer; the maximum distance travelled from a den was recorded for a juvenile that moved 1575 m from den 11. Distances of 1100 to 1300 m from dens were not unusual for snakes from either Site A or B. Outcrops within 200 m of dens appeared to be preferred shedding sites of nongravid females. During late July and early August, 87.5% of nongravid females within 200 m were shedding compared to a mean of 44% shedding females in other 100 m intervals. Males however, were less inclined to choose shedding sites near dens (<200 m from dens 27% of males were shedding; in other intervals the mean percentage of males shedding was 38%).

Figure 4: Seasonal distribution (distance from dens) of rattlesnakes during the active season (March-October). Males above, females below. Open rectangles = adult males and nongravid females, stipled rectangles = juveniles and filled rectangles = gravid females.


PROPORTION OF CLASS
1.0
.5
0
.5
Apr 1 – May 15
n = 82
.5
0
.5
May 16 – June 15
n = 103
.5
0
.5
June 16 – July 15
n = 84
.5
0
.5
July 16 – Aug 15
n = 222
.5
0
.5
1.0
Aug 16 – Sept 15
n = 136
.5
0
.5
Sept 16 – Oct 30
n = 59
05
.1
.2
.3
.4
.5
.6
.7
.8
.9
1.0
1.1 +
DISTANCE FROM DEN (km)
SVL (cm)

Late August and early September marked the beginning of movement of snakes back to hibernacula, and by mid-October most snakes had returned to the dens.

Gravid females generally remained in close proximity to their dens during the active season. A few individuals dispersed short distances (100-400 m) in early spring, presumably to forage, but returned within a few weeks to spend the remainder of the summer at or near the den (Fig. 4).

When dispersing from hibernacula most rattlesnakes initially moved northward (upslope) until reaching the ridge tops and then radiated out in NE to NW directions (Figs. 5 and 6). Associated with some dens, there appeared to be corridors along which snakes travelled to reach the ridge tops. For example, snakes from den 24 travelled upslope past den 2 and snakes from both dens 2 and 24 moved further upslope past den 23 to reach the crest of Rattlesnake Hill. Similarly, on Site B snakes from den 11 travelled uphill past den 9 to reach the ridge top. Individuals from some dens did disperse in southerly directions (downslope) and this was more frequently observed at dens located nearer the valley floor (e.g. dens 4, 8, 14 and 24). Downslope movements from some dens appeared to be prevented by precipitous cliffs lying directly below the dens (e.g. dens 10, 16, 17, 21). During

Figure 5: Circular histograms showing the direction of dispersed snakes from dens (underlined number) on Site A. The inner circle represents 25%, the outer circle 50% of records from each den (sample size in parentheses). The histogram for den 2 also includes records for snakes from two closely situated dens (23 and 24).

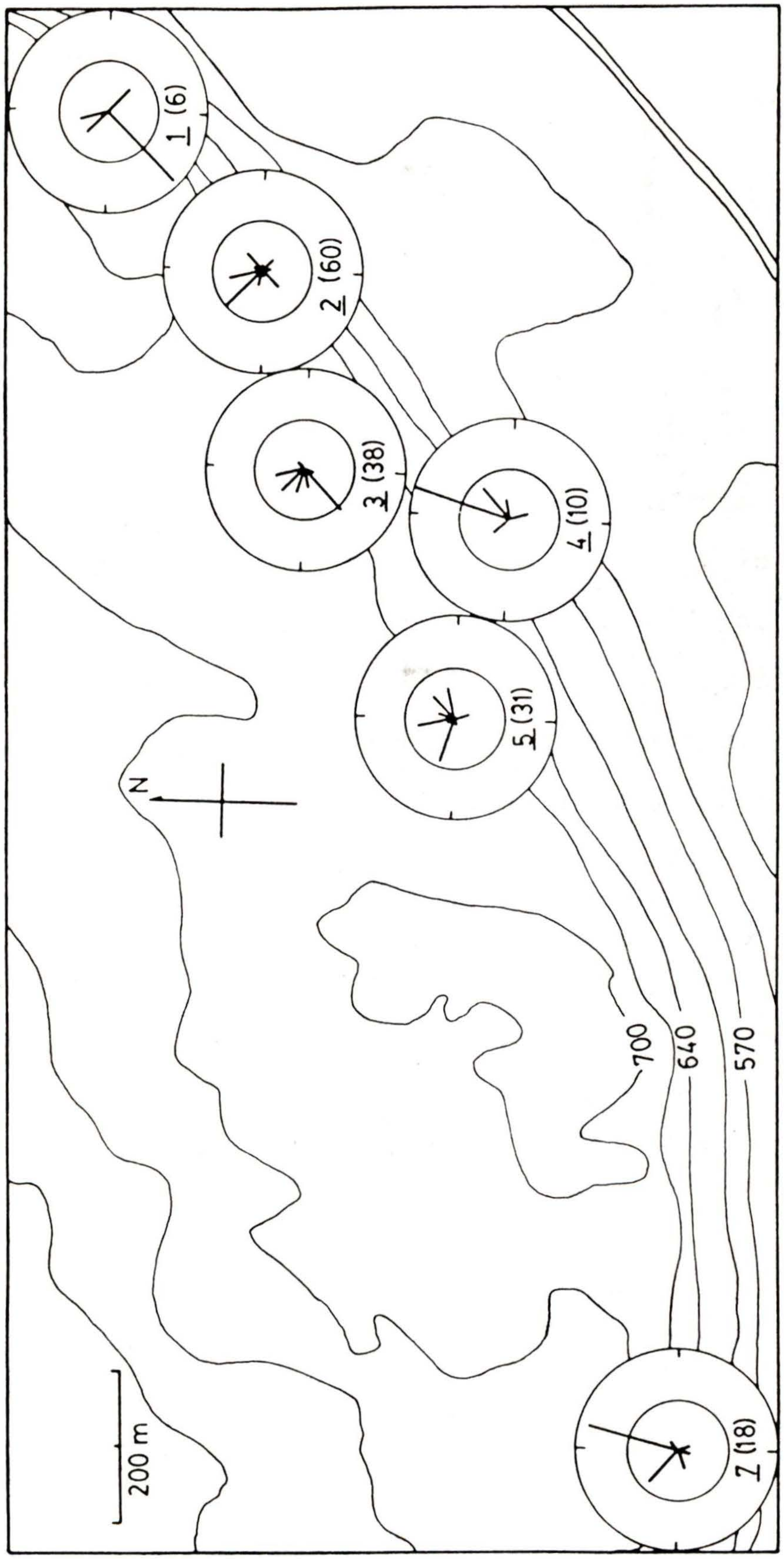
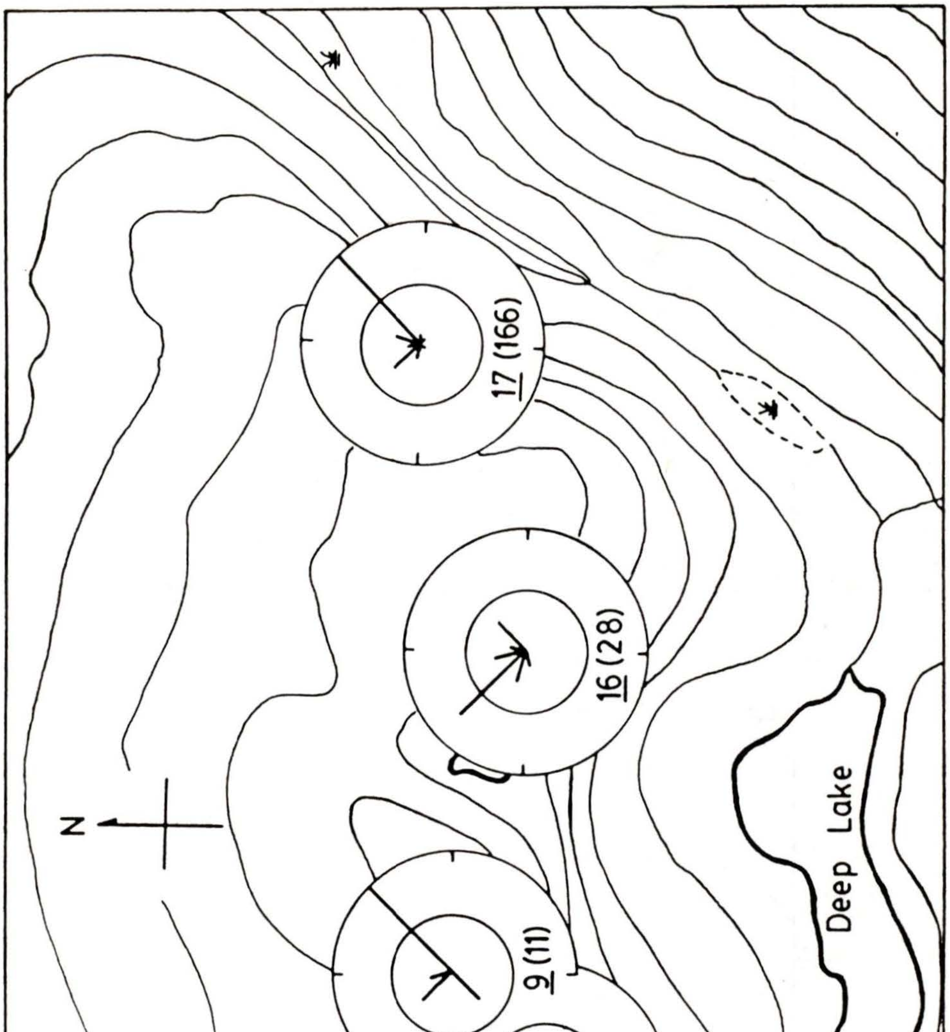

1 (6)
2 (60)
3 (38)
4 (10)
5 (31)
7 (18)
N
700
640
570
200 m

Figure 6: Circular histograms showing direction of dispersed snakes from dens on Site B. Notation as in Figure 5.


N
200 m
555
615
675
8 (65)
11 (41)
9 (11)
16 (28)
17 (166)
Deep Lake

the summer months most snakes were located in the two northern compass quadrants from their dens despite a lack of barriers to southern dispersal.

2.3.4 Movements of individuals

Data for determining activity ranges based on recaptures were insufficient because of the difficulty of consistently relocating individuals during the summer. Radiotelemetry enabled the movements and activity ranges to be determined for three adult rattlesnakes.

The two radiotracked gravid females remained within 75 m of their dens during the summer and made only periodic, short-distance movements between three or four basking sites (usually table rocks) (Fig. 7). Gravid females spent long periods (up to 40 days, Snake A, Fig. 7) at a basking site before changing locations. Both returned to their hibernaculum before parturition. As far as I could tell, neither female fed during the weeks that they were monitored by telemetry. The activity ranges of snakes A and B were 0.22 ha and 0.16 ha respectively.

The movements of an adult male from den 24 were also monitored by telemetry. As with the gravid females, this male rattlesnake had already dispersed from its den prior to its recapture (June 22) and implantation of the transmitter (July 16). The movements of this snake during

Figure 7: Movements of two gravid females during the summer of 1982. Double underlined numbers refer to den number. Date (month/day) of location for female A (780 m SVL) from den 4, underlined dates are for locations of female B (750 mm SVL) from den 3. T = date of release with transmitter. Broken lines are movements known from recapture, solid lines are between radiotracked locations and arrows indicate the direction of movement. Female A was radio-located 30 times over a 61 day period and female B was radio-located 28 times over a 64 day period.

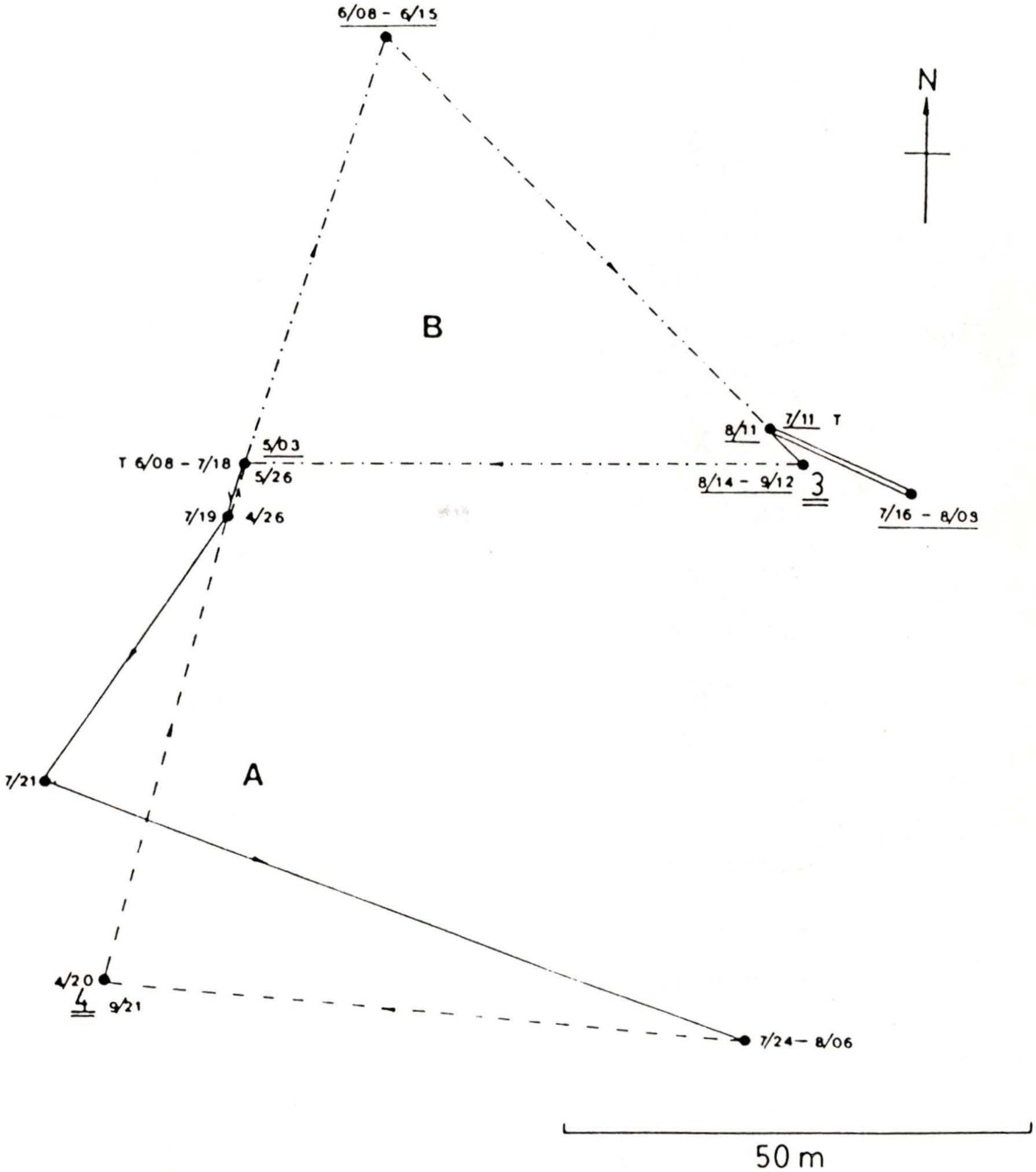
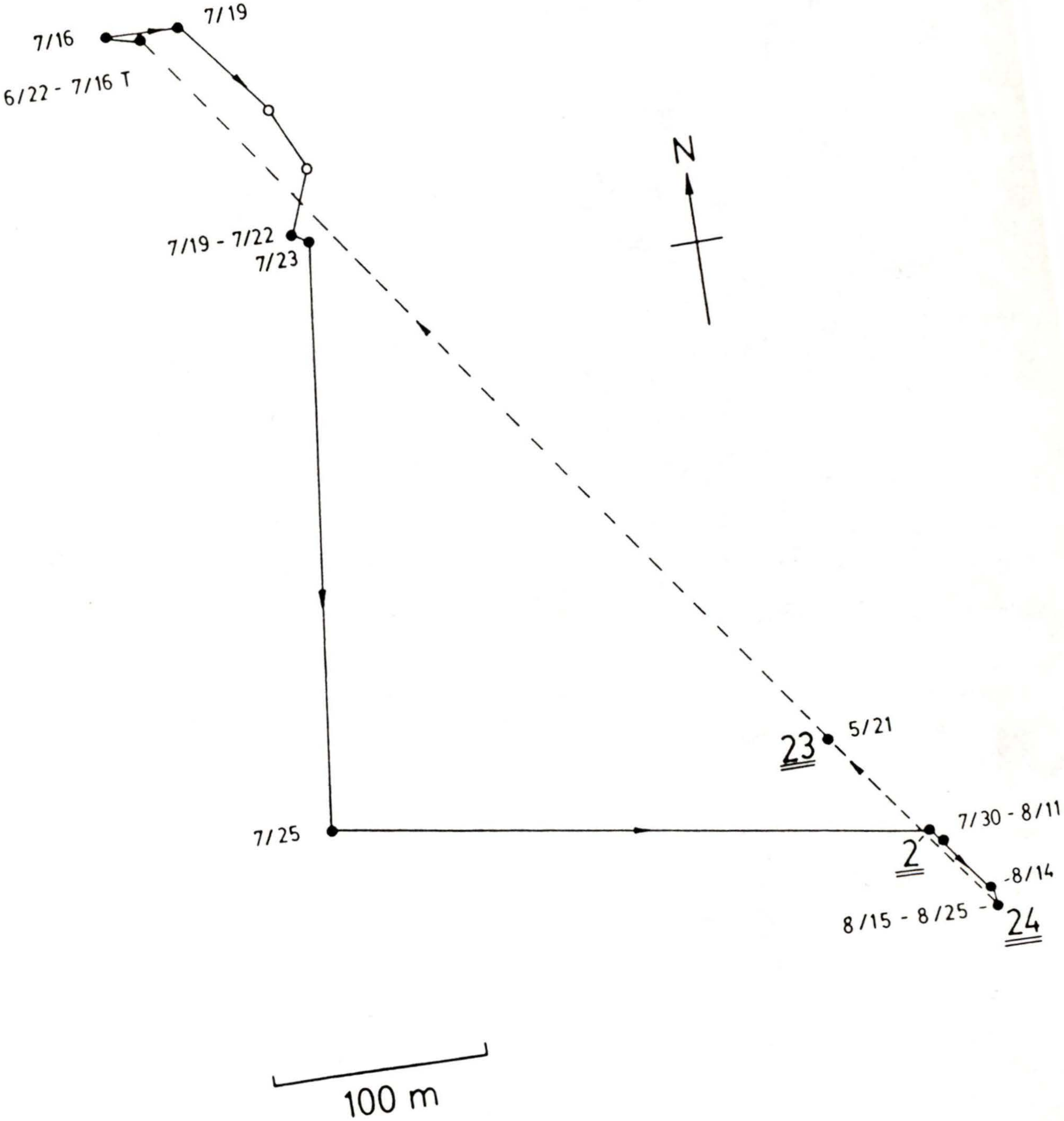

6/08 - 6/15
N
B
8/11
7/11
T
T 6/08 - 7/18
5/03
5/26
8/14 - 9/12
3
7/16 - 8/03
7/19
4/26
A
7/21
4/20
4
9/21
7/24 - 8/06
50 m

Figure 8: Movements of an adult male (880 mm SVL) during the summer of 1982. Solid circles represent overnight locations, open circles are locations at which the direction of travel changed during a day's movements. Other symbols as in Figure 7. This male was radio-located 23 times over a 41 day period.


7/16
7/19
6/22 - 7/16 T
N
7/19 - 7/22
7/23
23
5/21
7/25
7/30 - 8/11
2
-8/14
8/15 - 8/25 -
24
100 m

late July and August presumably represented the return migration to den 24. The return trip to the den was not direct but was fairly rapid. The rate of travel recorded on the afternoon of July 19 was about 1 m/min. Ten days were spent at den 2 before finally moving to den 24. This snake entered den 24 on August 25 and was not recaptured until April 1983. The activity range of this male was 8.0 ha.

2.3.5 Population home range

Population home ranges (PHR's) for dens on Site A, B and C are presented in Table 3. PHR's for most dens at Site A are grossly underestimated because recaptures were most often obtained during the spring or fall when dispersing from or returing to dens, and hence locations were often clustered along dispersal routes. PHR's for dens on Site B ranged from 83 to 171 ha, or approximately 30 to 70% of the total area of Site B. Pairwise PHR overlaps were calculated only for the 5 major dens on Site B. Overlap ranged in value from 0.07 to 0.73 (Table 4). Dens located midway along the hillside (9, 11, 16) shared between 60 and 70% of the PHR area with each other. Dens 8 and 17, located 1400 m apart on opposite ends of Deep Lake ridge, had PHR's which barely overlapped. For each den the correlation between O_{jk} and distance between dens D_{jk} was negative (Table 4).

Table 3: Population home range (PHR) estimates and number of individual location points for each den on study sites A, B and C.

Den	PHR area (ha)	n	Maximum distance (m) dipersed by an individual
Site A			
1	3.3	6	450
2	25.9	30	575
3	13.4	38	300
4	1.2	10	170
5	155.3	31	1400
7	32.3	18	715
14	2.0	11	315
22	1.7	9	170
23	10.9	15	450
24	13.9	15	565
Site B			
8	82.8	65	1350
9	101.9	12	1345
11	171.1	41	1575
16	137.5	28	1220
17	118.0	167	1190
Site C			
27	8.6	18	515

Table 4: Population home range overlaps (O_{jk}) for each den-wise comparison at Site B. D_{jk} (in parentheses) = the distance between dens i and j in meters, r_i = coefficient of correlation between O_{jk} and D_{jk} for den j and the four other dens.

Den j k	8	9	11	16	17
9	0.69				
	(465)				
11	0.69	0.71			
	(425)	(40)			
16	0.32	0.68	0.73		
	(820)	(650)	(690)		
17	0.07	0.43	0.64	0.71	
	(1400)	(955)	(990)	(600)	
r_i	-0.98	-0.80	-0.57	-0.90	-0.90
Mean O_j	0.44	0.63	0.69	0.61	0.46

In the field, mixing of individuals from different dens was most frequently observed at outcrops which provided sheltered basking and shedding sites. For example, a long discontinuous chain of rock piles on the valley floor on the north side of Deep Lake Ridge provided the only available shelter once snakes had moved off the ridge top and onto the open, grass covered north face. Sections of this chain of rock piles were used by rattlesnakes from every major den and the northern boundary lines of PHR's for these dens lay along this chain. Individuals from different dens also congregated at numerous isolated rock outcrops along the ridge top. One particular cluster of outcrops on the center of the ridge top (200 m from den 9) was utilized by snakes from all dens, often simultaneously, during the active season.

2.3.6 Fidelity to summer range

As an adjunct to the small body of data on individual activity ranges, I compared locations (distance and bearing from an individual's den) of rattlesnakes captured in two or more consecutive summers to determine whether individuals showed fidelity to sites used in previous summers and hence exhibited perennial use of what may be called a home range. A snake was considered to show site fidelity if it was recaptured at the same location (within a time frame of ± 30 days) in two or more summers. If a

Table 5: Proportion of adult snakes captured in two or more successive summers, that exhibited site, directional or no fidelity.

	N	Site Fidelity		Directional Fidelity		No Fidelity	
		n	p	n	p	n	p
Males	25	14	.56	21	.84	4	.16
Females: nongravid to nongravid	9	5	.56	8	.89	1	.11
Females: gravid to nongravid (vice versa)	13	3	.24	8	.85	5	.38

snake was located at any time during the summer within 250 m and ±45 degrees (bearing from the den) of its capture site in the previous year it was considered to show at least direction fidelity. Snakes showing site fidelity also showed direction fidelity, by definition. These classifications only provide a coarse measure of summer range fidelity because the timing of appearance at summer sites may fluctuate according to the time of spring emergence, weather, foraging success at other sites and the timing of shedding etc.. Forty-seven adult snakes were recaptured in at least two successive summers on Sites A and B. The results are presented in Table 5. Both sexes showed a high degree of direction fidelity and slightly more than half of the males and females (nongravid in two years) exhibited site fidelity. Gravid females were unlikely to return to sites used the previous year; however, nongravid females occassionally returned to within 250 m of the den or rookery used when gravid the previous summer. Of 8 such females, 7 were undergoing ecdysis at the time of capture; three females chose the same shedding site that they had used when gravid.

Outcrops to which adult males showed site fidelity averaged 647 m (SE = 95 m) from their den; for nongravid females, the average distance was 160 m (SE = 74). Three adult males were recaptured in three consecutive years at the same outcrop each had occupied the first year.

Distances to these sites were 1020 m, 875 m and 445 m from dens. A high proportion of snakes that showed site fidelity had used the site for ecdysis in at least one of the years (10/14 males and 4/5 nongravid females).

2.3.7 Food habits

The distribution of feeding records during the active season is presented in Table 6. Upon emergence from hibernacula, stomachs were empty and only fluid or hardened lumps of uric acid could be palpated from the cloaca. Snakes captured with food during April and May had already dispersed from the hibernacula. Since sampling efforts were directed mainly at dens rather than surrounding areas during these months, the proportion of snakes with food may be slightly underestimated from my data. June, July and August were the major feeding months of rattlesnakes. Foraging continued into September and October but, as in the spring, most of the activity occurred away from the dens. Snakes occasionally returned to dens in the fall with recently ingested prey in their stomachs; most, however, either lacked fecal material on their return or voided it at the den before beginning hibernation, as is suggested by accumulations of scats around den entrances in the fall.

Ten mammal and four bird species were identified from the stomach contents or fecal material of 79 juvenile and

Table 6: Proportion of rattlesnakes with stomach contents or fecal material in each month of the active season. Based on the total number of snakes from all dens and sites (recaptures included) from spring 1981 to spring 1983.

Month	Number of snakes examined	Number of snakes with food	Proportion with food
March	42	0	0.0
April	1059	2	0.002
May	956	20	0.02
June	112	19	0.17
July	202	36	0.18
August	342	56	0.16
September	945	75	0.08
October	569	13	0.02
Total	4227	221	0.05

Table 7: Composition of the diets of juvenile and adult *C. v. oreganus* (percent occurrence of prey types in stomach and fecal samples).

Prey species	Juveniles	Adults	Combined
Cinereus Shrew (*Sorex cinereus*)	11.5	0.8	4.9
Deer Mouse (*Peromyscus maniculatus*)	40.5	10.5	22.1
Great Basin Pocket Mouse (*Perognathus parvus*)	0.0	2.4	1.5
Montane and Meadow Vole (*Microtus montanus* and *Microtus pennsylvanicus*)	40.5	50.0	46.3
Northern Pocket Gopher (*Thomomys talpoides*)	5.1	13.7	10.3
Northwestern Chipmunk (*Eutamias amoenus*)	1.2	2.4	2.0
Bushy-tailed Wood Rat (*Neotoma cinerea*)	0.0	0.8	0.5
Red Squirrel (*Tamiasciurus hudsonicus*)	0.0	12.1	7.3
Yellow-bellied Marmot (*Marmota flaviventris*)	0.0	0.8	0.5
Total Mammalian Prey	98.8	93.5	95.6
Avian prey	1.2	6.5	4.4

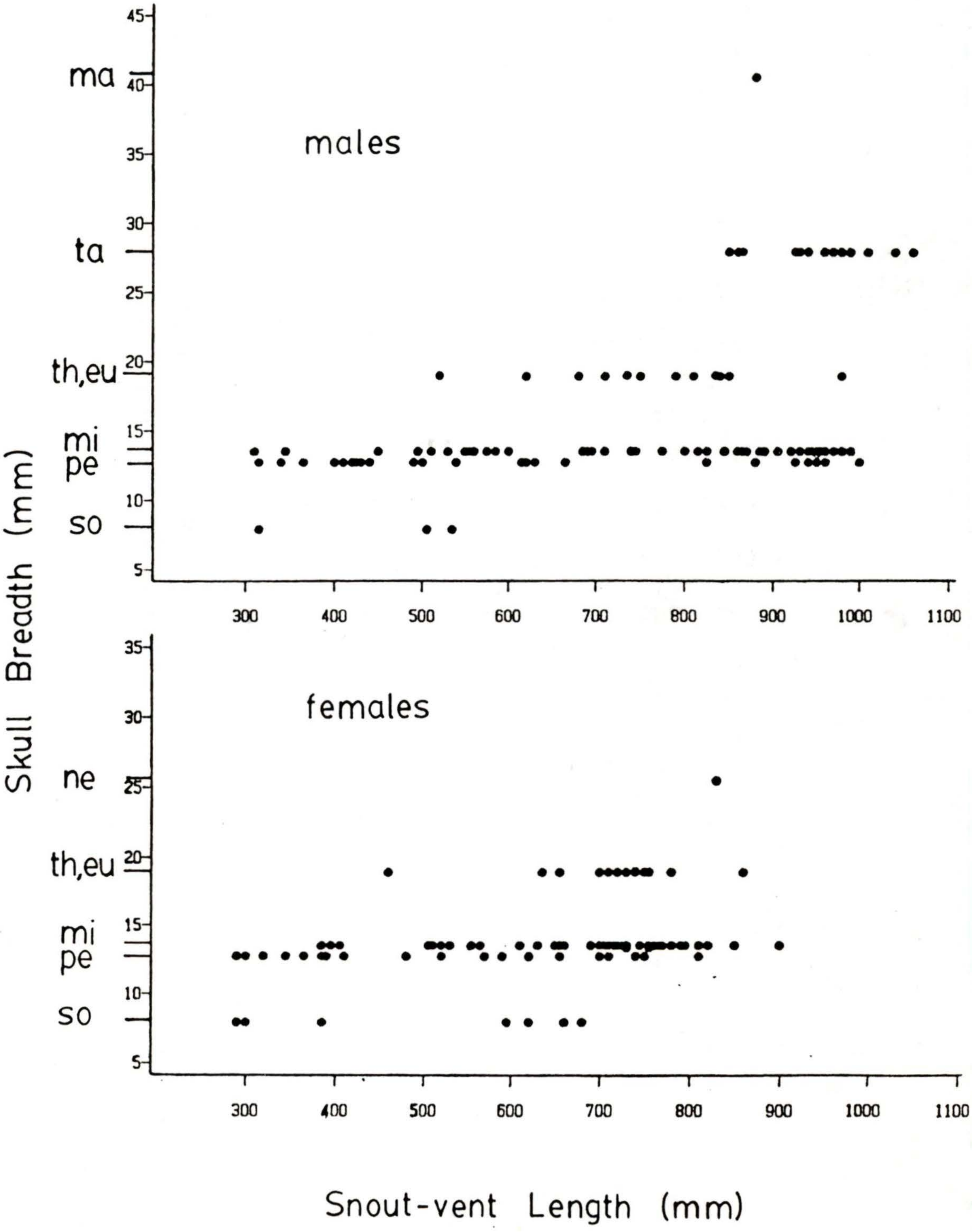
124 adult *C. v. oreganus* (Table 7). Feces from five rattlesnakes lacked guard hairs and prey items could not be identified. Two species of vole, *Microtus montanus* and *Microtus pennsylvanicus*, were distinguished from stomach samples in 1981; however, no attempt was made to separate these species using characteristics of the guard hairs, tail or hind feet and all records of *Microtus* species were pooled.

The stomachs of most snakes did not contain food and those with stomach contents had usually ingested a single prey item. One adult male, however, had three recently ingested *Microtus* and an adult female was found with a shrew (*Sorex cinereus*) and a vole in the stomach. Similarly, most fecal samples were composed of hairs from one prey species. The only exception was an adult male whose feces contained unidentified bird feathers and hairs of a deer mouse (*Peromyscus maniculatus*).

The diet of these snakes consisted mainly of small mammals (Table 7). Four species of ground dwelling rodents, *P. maniculatus*, *M. montanus*, *M.pennsylvanicus* and *Thomomys talpoides*, comprised 78.7% of the diet of the population as a whole. Among juveniles, 92.5% of the diet was made up of three mammalian genera, *Sorex*, *Peromyscus* and *Microtus*. Adults fed on a wider spectrum of prey, and larger rodents (*Microtus*, *Thomomys* and *Tamiasciurus*) figured prominently in the diet. Birds and larger mammals (e.g. *Eutamias, Neotoma, Tamiasciurus* and *Marmota*) were preyed upon almost exclusively by adults. Avian prey identified from stomach contents included a Starling (*Sturnus vulagris*), a Common Bushtit (*Psaltriparus minimus*), a Dark-eyed Junco (*Junco hymenalis*) and a Rufous-sided Towhee (*Pipilo erythrophthalmus*). No other prey types were collected from field captured rattlesnakes, but cannibalism by an adult on a juvenile occurred in captivity.

The diets of juveniles and adults differed mainly with respect to size of prey taken, but there was considerable overlap in species of prey in the diets of the two size/age groups of rattlesnakes. Juveniles tended to use the smallest mammal species available and stomach contents revealed that snakes less than 400 mm SVL (neonates to 2 years old) selected mainly *Sorex* and juvenile *Microtus* and *Peronmyscus*. There was a strong positive correlation between prey size (average skull breadth for each of the nine genera of mammalian prey) and average snake SVL ($r = 0.833$, $P = 0.005$, $n = 9$, Spearman rank correlation, sexes combined, Fig. 9). Sex related differences in prey preference for the major small mammal prey (*Sorex, Peromyscus, Microtus* and *Thomomys*) were not evident ($P(\chi^2_3 > 3.26) > 0.35$, contingency table).

Figure 9: Relationship between size of prey (average skull breadth) and SVL of male (n = 105) and female (n = 98) rattlesnakes. Abbreviations for prey species are: ma=*Marmota flaviventris*, ta=*Tamiasciurus hudsonicus*, th=*Thomomys talpoides*, eu=*Eutamias amoenus*, mi=*Microtus sp.*, pe=*Peromyscus maniculatus*, so=*Sorex cinereus*.


males
females
ma
ta
th,eu
mi
pe
so
ne
45
40
35
30
25
20
15
10
5
300
400
500
600
700
800
900
1000
1100
Skull Breadth (mm)
Snout-vent Length (mm)

From 362 captures and recaptures of gravid females only eight individuals captured (2.2%) had stomach contents. Recently ingested prey were found in the stomachs of six gravid females collected shortly following their emergence from hibernation (April 20 - May 30). All of these females were captured short distances from dens. Two gravid females captured at dens in mid-July also had fed recently.

It was also rare for females to forage after giving birth in the fall. Postpartum females began hibernation soon after giving birth or remained active on the surface but seldom left the den area. One postpartum female captured at den 15 in late September had a partially digested pocket gopher in her stomach. These fossorial mammals do not inhabit the steep rocky slopes around the den area and, since gravid females generally give birth at the den, it is probable that this female returned to the grassy hilltop (55 m from the den) to forage following parturition. A pocket gopher was palpated from another postparturient female found 50 m below den 27 in early October. In addition, none of the newborn rattlesnakes that were examined at dens in the fall, prior to their first hibernation period had stomach contents.

2.3.8 Predation

From approximately 100 coyote (*Canis latrans*) and striped skunk (*Mephitis mephitis*) scats examined, rattlesnake remains were found in only three skunk scats. The relative size of vertebrae, ribs and scutes indicated that one of the ingested rattlesnakes was an adult, another a juvenile and the third a neonate (confirmed by the presence of the prebutton scute). Vertebrae of a juvenile were also found in the droppings of a black bear (*Ursus americanus*). Rattlesnake remains were not found in any of the coyote scats (about 1/4 of the scats examined).

The rattlesnake remains in the skunk scats may have been scavenged but there was evidence that skunks dig up and kill rattlesnakes. Skunk tracks were often seen at excavations made at basking areas adjacent to several hibernacula. These digs were observed mainly in the spring and were found at dens 2, 5, 7, 11, 16 and 17. The success rate of predation of skunks could not be determined since at most digs neither live snakes nor remains were found. A chewed tail found at one dig near den 7, indicated that at least some attempts were successful. Five meters below den 7 the body of a juvenile male (510 mm SVL) was found on a large rock near a dig; its head was crushed laterally and bore small tooth marks. A gravid female (810 mm SVL) bearing similar injuries on its head and a chewed tail was discovered at a rookery near den 11. In neither instance were any major portions of the body eaten.

Large puncture wounds present on the corpses of two gravid females found in the spring of 1982 and 1983 at den 17, were probably caused by the talons of a large raptor. The body of one of these females was extracted from under a rock to where it appeared to have escaped and died. The carcass of the second gravid female was found in the open and was partially eaten.

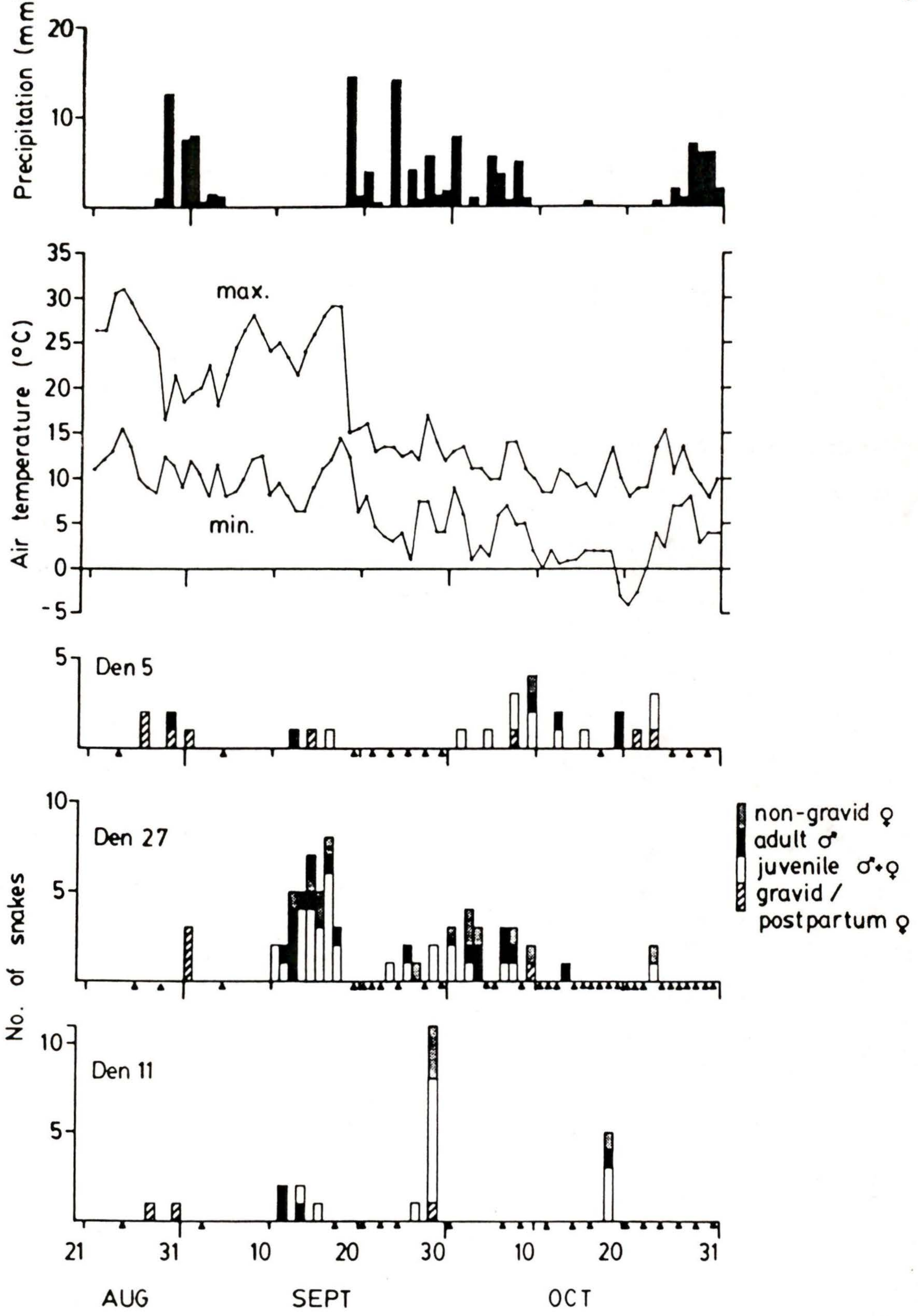
Scars or injuries were present on about 13% of all adult rattlesnakes and about 3% of all juvenile rattlesnakes (see Appendix I).

2.3.9 Patterns of arrival at hibernacula

Rattlesnakes arrived at dens in 1981 over an average period of 48 days (n = 6 dens, SE = 3.7, range 35-59). In 1982 the arrival period spanned an average of 46 days (n = 13 dens, SE = 3.1, range 20-59). Although the number of snakes returning on any given date varied among dens, the peaks in arrival dates were similar within years. By way of example, the pattern of fall arrival is shown for three of the larger dens in 1981 (Fig. 10). The most complete records are for den 27 since it was fenced and visited daily and the precise dates of arrival were therefore known.

In both years, snakes first arrived back at dens during the last week of August, when daily maximum air temperatures ranged between 24 and 34°C. The nonmigratory

Figure 10: The pattern of arrival at three dens in the fall of 1981 in relation to air temperature and precipitaion. Arrows denote the last day on which snakes were seen at the den. Triangles denote days on which the dens were visited but no new (marked or unmarked) snakes were seen. Den 5, n=26; Den 27, n=71; Den 11, n=24.


Precipitation (mm)
20
10
Air temperature (°C)
35
30
25
20
15
10
5
0
-5
max.
min.
Den 5
5
Den 27
10
5
No. of snakes
Den 11
10
5
non-gravid ♀
adult ♂
juvenile ♂+♀
gravid / postpartum ♀
21
31
10
20
30
10
20
31
AUG
SEPT
OCT

gravid females were usually present at dens before the arrival of other den members. Adult males and juveniles were among the first of the migratory snakes to return, arriving in late August or early September. In 1981, rattlesnakes returned *en masse* over an eight day period of warm, dry weather in mid-September (Fig. 10). The pattern was slightly different during the fall of 1982. Again there was a major peak in arrival during mid-September but it extended over a two week warm spell. By the end of September 1982, an average of 86% of the total overwintering population at dens had returned (n = 13 dens, range 70-100%). After the onset of cold fall weather, snakes returned in greatest numbers on days with little or no rain and with daily maximum air temperatures exceeding about 10°C (Fig. 10).

Aside from the general tendency for adult males and juveniles to be among the first to arrive at dens, there were no evident sex related differences in arrival times of juvenile or adults (Fig. 10). Individuals were seen at dens as late as 58 days after their return. In general, the last snakes seen at the dens in late October included gravid or postpartum females and newborn snakes undergoing ecdysis. Neonates appeared to be reluctant to enter hibernation until they had completed their initial moult and it was not uncommon to find neonates coiled up near den entrances on overcast days in late fall when air temperatures recorded at dens were as low as 5°C.

2.3.10 Fidelity to hibernacula

Den fidelity refers to an individual's use of the same hibernaculum in successive years. Inter-den movements were recorded for 26 of 380 (7%) snakes recaptured at dens on Sites A and B between the winters of 1980-81 and 1981-82, and of 1981-82 and 1982-83. Juveniles changed dens more frequently than adults (19 juveniles, 7 adults) and males switched dens more frequently that females (17 males, 9 females).

Of 42 snakes recaptured from three dens on Site A in 1981, only 2 (6.7%) yearling rattlesnakes from den 5 hibernated in different dens (Table 8). The discovery in the fall of 1982 of dens 23 and 24, approximately 50 m above and below den 2 respectively, and two other dens (21 and 22) between den 2 and den 1 in the spring of 1983, added considerable new information on inter-den movements. Fidelity to dens 1 and 2 was relatively low in 1982 (Table 8) and eight of the 12 recorded changes were made to these four "new" dens (Table 9).

In 1981, 86.2% of all snakes captured from three dens on Site B returned to the same den, while in 1982, 99.3% of snakes from 6 dens showed den fidelity (Table 10). Six of the nine snakes (67%) that were observed to change dens on

Table 8: Fidelity to dens on Site A in 1981 and 1982.

	1980-81 to 1981-82				1981-82 to 1982-83			
	Returned to the same den		Returned to a different den		Returned to the same den		Returned to a different den	
Den	n	%	n	%	n	%	n	%
1	-	-	-	-	18	81.8	4	18.2
2	-	-	-	-	22	73.3	8	26.7
3	-	-	-	-	9	100.0	0	0
4	2	100.0	0	0	5	100.0	0	0
5	28	93.3	2	6.7	41	95.4	2	4.6
7	10	100.0	0	0	23	95.8	1	4.2
Total	40	95.2	2	4.8	118	88.7	15	11.3

Table 9: Inter-den movements of individuals at Site A in 1981 and 1982.

Original Den	Den returned to	Sex	SVL	Distance between dens (m)
<u>1981</u>				
5	1	M	330	1035
5	*	F	330	530
<u>1982</u>				
2	3	F	750	210
"	3	M	575	210
"	5	M	320	575
"	23	M	790	65
"	22	F	555	310
"	22	M	485	310
"	24	M	410	50
"	24	F	380	50
1	22	F	685	190
"	23	F	550	370
"	24	M	620	450
"	8 (Site B)	M	720	≅1500
5	25	M	365	240
"	4	M	530	300
7	14	M	935	480

* hibernated in an abandoned marmot burrow.

Site B in 1981 and 1982 were juveniles (between one and three years of age, Table 11).

A 1-2 km wide valley separates the east end of Rattlesnake Hill from the western end of Deep Lake Ridge. One adult male from den 1 (the easternmost den on Site A) crossed the valley and was recaptured 50 m below den 8 (the westernmost den on Site B); however, whether the individual overwintered in den 8 was not determined.

Ten individuals that had changed dens in 1981 or 1982 were recaptured during the spring or fall periods bracketting the subsequent overwintering period. Five of these returned to the den to which they had switched, four returned to their original den and one juvenile female overwintered in yet a different den.

Four outcrops other than known hibernacula were used for overwintering on Sites A and B during the winters of 1981-82 and 1982-83. Unlike traditional communal hibernacula, whose populations characteristically included snakes of all ages (see Population Dynamics), these alternative sites were used only by juveniles (<550 mm SVL, but mostly yearlings). These outcrops were located between 80 and 180 m from the nearest communal den and each was a known stop-over spot for snakes during the spring and fall migrations. Frequent searches at these sites virtually ruled out the possibilty that snakes had left or returned

Table 10: Fidelity to dens on Site B in 1981 and 1982.

	1980-81 to 1981-82				1981-82 to 1982-83			
	Returned to the same den		Returned to a different den		Returned to the same den		Returned to a different den	
Den	n	%	n	%	n	%	n	%
8	21	91.3	2	8.7	36	100.0	0	0
9	3	100.0	0	0	5	100.0	0	0
11	26	81.2	6	18.8	27	96.4	1	3.6
16	-	-	-	-	18	100.0	0	0
17	-	-	-	-	60	100.0	0	0
Total	50	86.2	8	13.8	146	99.3	1	0.7

Table 11: Inter-den movements of individuals at Site B in 1981 and 1982.

Original Den	Den returned to	Sex	SVL	Distance between dens (m)
<u>1981</u>				
11	8	F	325	425
"	8	F	385	425
"	9	F	295	40
"	13	M	350	400
"	16	M	480	695
"	17	M	380	990
8	11	M	870	425
8	16	M	980	820
<u>1982</u>				
11	9	M	940	40

there between their last fall sighting and recapture the following spring. Two yearlings (one had been born at den 5) hibernated during 1982 in an abandoned marmot burrow on an outcrop 140 m N of den 23. Two *Coluber constrictor* and two *Thamnophis sirtalis* also overwintered there. The only newborn snake known to have overwintered outside a traditional den hibernated within an outcrop 180 m from den 7. Three juveniles also emerged from this outcrop in 1983 and in 1984, another juvenile emerged. None of these snakes had been marked previously; therefore their den of birth was unknown.

2.3.11 Hibernation

Entrances to most rattlesnake hibernacula were protected by overhanging rock ledges and therefore remained dry and free of snow during the winter. The exception was den 27; its entrance, on the apex of a small earth covered hill, was only partially sheltered by rocks. On a visit to this den in December 1981 the external air temperature was -14°C while .5 m inside the entrance the temperature was 1.6°C. Warm air (relative to the outside) rising from within the den kept the entrance free of snow. Water droplets were present on the underside of rocks lying directly over the entrance and moss growing on adjacent rocks was green and wet. Snakes at this den always bore a thin coat of dried mud upon emergence in the spring which indicated a damp internal environment possibly due to water draining into the den during snow melt. This coating was not observed on snakes at any other den; therefore conditions were probably dry inside most hibernacula.

The body temperatures of hibernating rattlesnakes were monitored by telemetry during the winter of 1982-83 (see Appendix III). Body temperatures of hibernating rattlesnakes dropped gradually in the late fall, stabilized during the winter between 4 and 7°C, and increased slightly during the early spring.

Summary statistics for the time spent in hibernacula during the winters of 1981-82 and 1982-83 are presented in Table 12 for rattlesnakes grouped according to sex/age classes (and reproductive condition in adult females). *C. v. oreganus* hibernated for about 7 months of the year from fall ingress in late August to late October until emergence in late March through late May.

Two-way ANOVA's were performed to examine differences in the number of days spent in hibernation between years and among age/sex groups. Difference due to year were non-significant in all but 1 order ($F_{C(1,370)} = 1.9$, $P = 0.17$; $F_{O(1,370)} = 4.25$, $P = 0.04$). There were significant differences in the period of hibernation among the age/sex groups ($F_{C(6,370)} = 10.46$, $P<0.0001$). The interaction was significant in 4 of the 6 possible orders ($F_{C(6,370)}$ =

Table 12: Length of the overwintering period for different age/sex classes in the population. Data from all dens combined. Mean ± 1 SE, (range).

Age / Sex Class	Days spent in hibernation n	1981	n	1982
Neonates (Both sexes)	11	207 ± 6 (169 - 243)	25	196 ± 4 (161 - 239)
Juvenile Males	38	211 ± 3 (176 - 253)	25	208 ± 4 (178 - 236)
Juvenile Females	35	214 ± 4 (150 - 252)	32	215 ± 3 (191 - 247)
Adult Males	31	223 ± 4 (189 - 248)	75	216 ± 2 (172 - 246)
Gravid Females (enlarged follicles)	12	210 ± 5 (186 - 243)	27	200 ± 2 (177 - 225)
Nongravid Females (anestrous follicles)	11	201 ± 4 (176 - 222)	26	214 ± 2 (194 - 233)
Postpartum Females	16	198 ± 5 (164 - 233)	20	195 ± 4 (163 - 226)

2.01, P = 0.063; $F_{0(6,370)}$ = 3.31, P = 0.003). One-way ANOVA's, followed by Duncan's multiple range test were then performed for each year. In both years there were significant difference among the mean hibernating periods of age/sex groups (1981-82, $F_{(6,147)}$ = 3.7, P = 0.002; 1982-83, $F_{(6,223)}$ = 11.9, $P<0.0001$). The results of the multiple range tests did not yield identical groupings for both years but they showed a fairly consistent trend. Adult males and juvenile females were grouped together (longest hibernation periods) while postpartum females and neonates generally spent the shortest periods in hibernation.

2.4.0 Discussion

Few studies of eastern or western species of *Crotalus* have documented in detail the patterns of fall ingress and spring emergence at communal hibernacula. In the Okanagan valley, rattlesnakes begin emerging from dens in late March but the major peaks occur in April and early May. (For a more detailed consideration of the pattern of emergence of rattlesnakes in relation to ambient and internal den temperatures see Appendix III). The earlier emergence of adult females compared with adult males is the reverse of the general pattern of emergence shown by most other species of communally denning snakes studied to date

(Gregory, 1982). For some temperate zone snakes earlier emergence of males is related to spring mating which occurs at the dens. For example, in the european viper, *Vipera berus*, a few weeks are required following emergence to complete spermatogenesis prior to mating (Nilson, 1980); in all spring-mating species, early emergence may also confer an advantage in competition between males for mates (e.g. *Thamnophis sirtalis*, Gregory, 1974). Only late summer and early fall matings were observed in the Okanagan populations of *C. v. oreganus* and thus early emergence does not provide reproductive benefits to males. Reproductive frequency depends largely on the rapidity with which females can recuperate fat reserves after parturition (see Reproduction) and there are usually neither the time nor the appropriate conditions for foraging immmediately after parturition. By emerging early in the spring, females can make maximum use of the time available for feeding and completing the reproductive cycle.

Juveniles and neonates emerged over the same period spanned by adults. Juvenile *Vipera berus* emerge later than adults (Viitanen, 1967; Prestt, 1971), but in *Vipera aspis* the emergence period largely overlaps that of adults (Duguy, 1963). Gannon (1980) reported that juvenile *C. v. viridis* emerge and disperse later than adults. Juvenile rattlesnakes may benefit from delaying spring dispersal until a time when the possibility of death by exposure is reduced. As suggested in this study, juveniles may be vulnerable to freezing; presumably this is because they are smaller and/or may have higher critical minimum temperatures than adults as in *Agkistrodon contortrix* (Sanders and Jacob, 1981).

The patterns of dispersal and summer movements exhibited by *C. v. oreganus* in this study are similar to the general pattern emerging from studies of movements in other communally denning viperids. Common to most species are highly directional spring migrations in which den members disperse within the bounds of one to two adjacent compass quadrants (e.g. *C. v. oreganus*, Preston, 1961; *C. v. lutosus*, Hirth *et al.*, 1969; *V. berus*, Viitanen, 1967; *C. horridus*, Galligan and Dunson, 1979, *C .v .viridis*, Gannon, 1980; Brown *et al.*, 1982; Duvall *et al.*, 1985). Reasons for dispersal along highly directional routes are puzzling, particularly when apparently suitable summer habitat exists in other directions from the den. Snakes on Sites A and B travelled up steep slopes following natural corridors (gullies, draws, etc.) onto the ridge tops and then dispersed in northeasterly to northwesterly directions over the ridge and down the north faces. This trend was consistent among dens and may be related to differences in prey availablility, habitat and thermal regimes offered on the northern versus southern slopes. In general, prey may be more patchily distributed and less abundant (especially burrowing mammalian prey such as pocket gophers and voles) on the rocky, sparsely vegetated south-facing slope than on the more heavily and homogeneously vegetated ridge tops and north-facing slopes. Insolated surfaces on the southern slopes commonly reach 60°C or more during summer days. Brush, tall grass and forested areas on the ridge top and northern slopes offer protective microhabitats that may enable rattlesnakes to forage above ground for longer periods during the hot summer days (see Appendix II). Dense vegetation also retards radiational cooling at night and this may enable snakes to be active for longer periods after dusk. These ideas require further study before conclusive statements about the directionality of dispersal can be made.

In addition to the directional component, spring migrations of communally denning rattlesnakes are typically long, direct and rapid (Hirth *et al.*, 1969; Landreth, 1973; Sehman, 1977; Galligan and Dunson, 1979; Dumas, 1982; Duvall *et al.*, 1985). In this study, some adults had travelled 500-1200 m from dens before others had left the dens in the spring. In *Crotalus horridus* the movements to summer habitats may be interrupted for periods of 2-3 weeks while ecdysis is completed (Galligan and Dunson, 1979; Brown *et al.*, 1982). Duvall *et al.* (1985) determined that the lengthy (5 km), unidirectional spring movements of *C. v. viridis* terminated when snakes first encountered areas of prey abundance; movements thereafter were short and more or less random in direction. They suggested that the rapid linear movements away from dens are an optimal search strategy in habitats where prey are patchily distributed. In this study, the directionality of the spring dispersal movements of individuals was not determined because radiotransmitters were not available for implantation until after most of the snakes had dispersed.

Despite the increased use of telemetry to study movement patterns of rattlesnakes, individual snakes have seldom been monitored for the entire active season (cf. Reinert and Kodrich, 1982) or over 2 or more active seasons. Consequently the kinds of small, discrete and perennial summer home ranges established away from hibernacula as shown by *Coluber constrictor* (Brown and Parker, 1976) have not been demonstrated in rattlesnakes. Fitch (1949) concluded that *C. v. oreganus* in California had home ranges because he recaptured many individuals within a few hundred meters of their original capture site over intervals between 6 months to 7 years.

Hirth *et al.* (1969) advocated the use of "total range" to describe the area over which annual movements occur in snakes. Total range is considered to be the area travelled through and utilized for all activities by an individual, including the hibernaculum. They concluded that snake movements during the summer were unpredictable and that snakes behave like ecological opportunists, remaining in an area so long at it provides adequate cover, basking sites and prey, and then moving to new areas. Fitch and Shirer (1971) reported similar erratic movements in C. *horridus* and concluded that minimum home ranges (polygon method) of snakes can vary in size and shape depending on the seasonal accumulations of recapture locations and that much of the area within the overall home range may go unused. Others yet have avoided the used of the term home range and referred to the area used by snakes during the active season as the activity range or simply the range (Reinert and Kodrich, 1982). I used the term activity range (definition = Hirth *et al.*'s total range) because home ranges as described by Brown and Parker (1976) for C. *constrictor* were not readily apparent.

Implicit in the concept of home range is a temporal component; i.e. there may be daily, seasonal or lifetime home ranges. Most studies on snakes have characterized only portions of annual activity ranges. The high level of summer range fidelity shown by adult rattlesnakes in this study is evidence that rattlesnakes are familiar with the topography of the summer habitat, can relocate areas used in previous years and may establish perennial home ranges. Instances of fidelity to areas on the summer range have also been recorded for rattlesnakes by Preston (1961) and

Landreth (1973).

The adult male rattlesnake radiotracked in this study ranged over an area of 8 ha and attained a maximum recorded distance from the den of 570 m. Many of the adults and juveniles on Sites A and B dispersed distances > 1 km from dens and therefore may have activity ranges far greater than 8 ha. Large, vagile viperid and colubrid snakes have been reported to utilize areas of 3-34 ha (reviewed in Parker and Brown, 1980). The "home ranges" that Fitch (1949) estimated for *C. v. oreganus* in California were about 12 ha for males and 6.5 ha for females (reproductive condition not stated). However, because of poor recapture success he was unable to determine if rattlesnakes prowled regularly over the area or whether individuals returned to exactly the same hibernating site. The home ranges he described for individual snakes overlapped considerably. For smaller, less vagile viperid snakes that have hibernacula in close proximity to summer habitats, dispersal distances are short, individuals occupy small (< 1 ha), overlapping activity ranges and sex related differences in these variables are not prominent (e.g *Sistrurus catenatus*, Reinert and Kodrich, 1982; *Vipera berus*, Viitanen, 1971).

Male rattlesnakes have been reported to disperse greater mean distances than females (Fitch, 1949; Preston, 1961;

Brown *et al.*, 1982), but sex related differences were not subjected to close scrutiny in this study. The sedentary habits of gravid females have been well documented in rattlesnakes (Preston, 1961; Keenlyne, 1972; Klauber, 1972; Sehman, 1977; Gannon, 1980; Brown *et al.*, 1982; Duvall *et al.*, 1985). Activity ranges of gravid females are smaller than nongravid female or males, are localized near dens and contain specific sites (rookeries) which may be used by one or more females (see also Reproduction). The periodic, short distance movements exhibited by gravid females between basking sites in this study have been reported elsewhere (Sehman, 1977; Reinert and Kodrich, 1982; Brown *et al.*, 1982). Sehman (1977) reasoned that since gravid females do not feed, these movements were probably in response to frequent disturbance while being radiotracked. While this may also have been true to some extent in this study, periodic movements to new cover objects may serve to reduce the risk to predation by making the location of gravid females less predictable to predators.

Movements of juveniles are poorly known for most snake species. Various authors have suggested that juvenile rattlesnakes may wander haphazardly (Preston, 1961; Dumas, 1982) and are more prone to immigrate to new areas than are adults (Fitch, 1949). Juveniles in this population appeared to disperse later than adults but they did disperse similar distances and directions to adults.

Den fidelity in communally denning colubrids is generally 95% or greater (Lang, 1971; Gregory, 1982; Parker and Brown, 1980). Although den fidelity in communally denning rattlesnakes is also thought to be very high (Woodbury, 1951; Klauber, 1972; Duvall *et al.*, 1985), this phenomenon has been poorly quantified for most rattlesnake species. Den fidelity in this study varied between 74% and 100% and for most dens it was 100%. Of particular interest was the observation that inter-den movements were most frequent to neighbouring dens and for juveniles. Lang (1971) recorded similar observations for colubrid snakes that overwintered in ant mounds. Young snakes have been shown to follow pheromone trails of conspecifics (Parker and Brown, 1980; Heller and Halpern, 1981; Brown and MacLean, 1983) and this has been suggested as a mechanism by which neonate rattlesnakes initially locate a hibernaculum after leaving birth sites. It has also been suggested that each den may have a unique odour associated with it upon which snakes may become imprinted during their first hibernation (Galligan and Dunson, 1979). High fidelity to dens used in previous years suggests that most snakes are able to recognize their native den, possibly by using landmarks or olfactory cues. The higher incidence of inter-den movements and use of nontraditional hibernacula by juveniles, compared to adults, reinforces the idea that juveniles are less familiar with their surroundings and/or have less developed homing ability to dens than adults. It also suggests that colonization of new hibernacula may be accomplished largely through juvenile immigration.

Despite high fidelity to overwintering sites, den populations are not reproductively isolated demes. Changes in den affiliation may increase panmixis, but since changes were more common among juveniles and fidelity to a new den may not be permanent, their effects are probably relatively minor. The large overlap in PHR's for dens on Site B means that individuals from different denning populations may intermix during the summer months. A high degree of PHR overlap is not surprising considering that the directions travelled by snakes from each den were similar (NE-NW) and that maximum distances travelled by many snakes exceeded inter-den distances. On Site A fewer observations of inter-den aggregations were recorded. Eleven hibernacula were located within a linear distance of 1350 m on the east end of Rattlesnake Hill and the mean distance between neighbouring dens was 166 m (SE = 38, range 50-300). Since distances dispersed from dens generally exceeded inter-den distances and direction of dispersal from each den was similar, considerable overlap of PHR's on Site A is also expected. The eleven dens on the eastern end of Rattlesnake Hill were separated from the three major dens on the western end by a distance of 1-1.5 km. Rattlesnakes were rarely encountered in the gap and mixing of populations at opposite ends of this hill is probably infrequent.

Mating occurs in late summer, often at shedding sites used by snakes from many dens, and all three of the courting pairs or groups seen on site B were composed of snakes from different dens (see Reproduction). These are grounds to believe that there is probably considerable gene flow between neighbouring den populations on Sites A and B.

Most reports on the food habits of *C. v. oreganus* throughout its range stress a strong preference for mammalian prey (Klauber, 1972). Mackie (1944) included in his list of prey eaten by *C. v. oreganus* in the Okanagan valley all but two of the small mammal species (*S. cinereus* and *P. parvus*) that were recorded in this study. Additional prey species reported by Mackie (1944) were a juvenile muskrat (*Ondrata zibethica*), White-crowned Sparrow (*Zonotrichia leucophrys*), Vesper Sparrow (*Pooecetes gramineus*), Savannah Sparrow (*Passerculus sandwichensis*) and Blue Grouse (*Dendragapus obscurus*). *S. cinereus*, which made up 11.5% of the juvenile diet in this study, was probably overlooked by Mackie since his dissections included mainly adult snakes. *P. parvus* prefer areas where sagebrush and grasses in association are the dominant vegetation (Cowan and Guiguet, 1965). This habitat type did not exist on any portion of my study sites and it is probable that the low incidence of predation on *P. parvus* reflects the rareness of this species at the study sites. In the south Okanagan valley, where sagebrush-grassland habitat is common, *P. parvus* was recorded in three of four stomach samples from *C. v. oreganus* (Preston, 1961).

The most complete published account of the diet of this subspecies of rattlesnake is for a population from Madera Co., California (Fitch and Twining, 1946). In that area 86.2% of the known diet was mammalian. Seven species of mammals, including five genera taken by *C. v. oreganus* in B.C. (*Microtus*, *Peromyscus*, *Neotoma* and *Perognathus*), were recorded by Fitch and Twining (1946). The major mammalian prey species were ground squirrels (*Citellus beechi*, 34.3%) and kangaroo rats (*Dipodomys herrmani*, 16.6%). Other prey items included birds (2.3%), small lizards (10.3%) and amphibians (1.2%). Although *Peromyscus*, *Perognathus* and amphibian and reptile prey represented only a small portion of the diet, they were the major species preyed on by yearling rattlesnakes in California.

Fitch and Twining (1946) found emaciated yearlings in late summer and suspected that many yearlings starve to death because they are unable to locate prey of sufficiently small size to swallow. Similar conclusions were reached in this study. Young of the year are probably unable to swallow prey much larger than half grown

Microtus. One lizard (*Gerrhonotus coeruleus*) and three amphibian species (*Ambystoma macrodactylum*, *Hyla regilla* and *Spea intermontana*) occur on the study sites. All are uncommon and patchily distributed, and thus are generally unavailable to small rattlesnakes. A lack of small ectothermic prey, which form the bulk of the juvenile diets of many rattlesnake species from more southern areas (Klauber, 1972) may be a contributing factor to high levels of neonate mortality through starvation. Mackie (1944) postulated that newborn *C. v. oreganus* feed on insects and spiders, but I found no evidence that juveniles ate anything but small mammals. Since newborn rattlesnakes begin feeding only after their first hibernation period, natal yolk bodies are relied on heavily until the first meal is obtained. Under circumstances of low prey availability, newborn snakes with proportionately greater yolk reserves would stand a better chance of surviving than neonates with moderate or small quantities of internal yolk.

A reduction or cessation of feeding by gravid females has been reported in several species of viperids and other snakes (Volsøe, 1944; Fitch, 1960; Prestt, 1971; Keenlyne, 1972; Keenlyne and Beer, 1972; Saint Girons, 1979). The two gravid females with food in early July would have had only early stage embryos (based on a gravid female dissected in July, see Reproduction). Most females do not feed during the reproductive year and must rely entirely upon fat reserves sequestered the previous year(s) for their sustenance and the nourishment of developing embryos. Keenlyne and Beer (1972) found that gravid *Sistrurus catenatus* in captivity refused all food offered, which suggests their prolonged aphagia is not due simply to a reduced ability to forage efficiently during pregnacy (Volsøe, 1944). Following parturition, female *S. catenatus* (Keenlyne and Beer, 1972) and *Vipera berus* (Prestt, 1971) feed readily. In British Columbia, parturition occurs late in the year and post partum females generally do not have time to feed prior to hibernating. Fat stores, already depleted at parturition, must be sufficient to sustain snakes through an additional overwintering period. Combined weight loss during this 18 month period of aphagia ranges between 40 to 45% of the fall pre-gravid weight (see Reproduction). Consequently, by the spring, post partum females appear extremely emaciated.

Declining temperature and photoperiod during the fall are generally believed to stimulate snakes to return to dens and begin hibernation (Gregory, 1982). Peak arrival following the first period of cool autumn weather suggests that a sharp decline from normal summer temperatures may trigger fall migration to dens. The early arrival of some adult males at dens in late August may be related to reproduction since mating was observed at a den in early

September (see Reproduction). Some juveniles also arrived at dens in late August; therefore reproduction may be only one advantage to returning early. Young rattlesnakes (particularly neonates) have been reported to arrive at dens and enter hibernation later than adults (Hirth, 1966b; Klauber, 1972; Galligan and Dunson, 1979; Duvall *et al.*, 1985). Juveniles in Okanagan populations arrived over a similar time span as adults and there were no obvious differences in timing of arrival related to age or sex.

Many rattlesnakes remain active on the surface for a few days to several weeks after returning to dens in the fall. Gregory (1982) has suggested that a period of fasting may be required to clear the digestive tract in order to prevent poisoning through putrefaction of gut contents during hibernation. Accumulations of scats at den entrances and the observation that most snakes are devoid of stomach contents or fecal material by late fall, adds credence to this idea. Temperatures below 15°C have been shown to inhibit feeding, increase the incidence of regurgitation and lower digestive rates in *Vipera aspis* (Naulleau, 1983). For snakes that had been feeding, basking on warm days following their return to the den would enhance the passage of any recently ingested food.

The overwintering period ranges from five to eight months and averages about seven months. The trend for post partum females and neonates to spend the shortest time in hibernation is due to early emergence of females and late entry of neonates. For *C. v. lutosus* in Utah, Hirth (1966a) recorded average overwintering periods of 193 days for neonates and 219 days for adults (both sexes); neonates both arrived later and emerged earlier. The period of hibernation for *C. v. oreganus* differs little from those reported by Hirth (1966a). Unfortunately few studies have quantified intrapopulation differences in the length of hibernation with sufficient detail to enable comparisons to be made with this study. Most, however, list the months in which arrival/entrance and emergence occur, and these are summarized for 11 populations of four subspecies of *C. viridis* in Table 13. An expected trend of a decrease in the overwintering period with a decrease in latitude, as in the genus *Vipera* (Viitanen, 1967) is not evident. This appears to be because, with the exception of the two California populations, the decrease in latitude is also accompanied by an increase in altitude. The active season is in some areas shorter at lower latitude, high elevation sites than it is in British Columbia (Table 13).

Within the subspecies *oreganus* the winter dormancy period lasts about 2 months longer in British Columbia and Idaho than in central California. Hibernation is also continuous in northern areas, whereas in California rattlesnakes may come to the surface to bask during warm

Table 13: Geographic variation in the duration of the overwintering and active periods of eleven populations of four subspecies of *Crotalus viridis*. E = early, M = mid and L = late. Data on the number of frost-free days taken from Anonymous, 1974.

Subspecies	Location	Lat., Long.	Elev. (m)	Frost free Days	Arrival/entrance Period	Emergence Period	Hibernation Period (months)	Authority
oreganus	British Columbia	50 N, 119 W	600	153	L Aug. - L Oct.	L Mar. - L May	6 - 8	present study
	Idaho	46 N, 117 W	600	150	L Sept. - E Nov.	L Mar. - M Apr.	6 - 8	Diller and Wallace, 1984
	California	37 N, 120 W	350	260	L Oct. - E Nov.	M Mar	4 - 5	Fitch and Glading, 1947; Fitch, 1949
viridis	Saskatchewan	51 N, 109 W	675	115	E Sept. - E Oct.	L Apr. - E May	6 - 8	Gannon, 1980
	Wyoming	42 N, 107 W	2100	100	L Sept. - E Oct.	May	6 - 8	Duvall *et al.*, 1985
	Colorado	40 N, 105 W	1500	145	M Sept. - M Oct.	E Apr.	6 - 8	Klauber, 1937
	Colorado	40 N, 105 W	1800	160	M Sept. - E Nov.	L Mar. - L May	6 - 8	Ludlow, 1981
	New Mexico	35 N, 106 W	1900	200	E Nov.	E Apr.	5 - 6	Jacob and Painter, 1980
lutosus	Idaho	43 N, 112 W	1580	125	E Sept. - L Oct.	May	6 - 8	Sehman, 1977
	Utah	41 N, 113 W	1500	170	Sept. - Oct.	Apr. - May	6 - 8	Vetas, 1951; Hirth, 1966b; Parker and Brown, 1974
helleri	California	33 N, 121 W	-	270-365	L Nov.	E Mar.	3 - 4	Klauber, 1937

winter days (Fitch and Glading, 1947; Fitch, 1949). In addition, rattlesnakes in central California hibernate singly or in small groups (2-7) rather than communally, although Klauber (1972) reported communal denning for high altitude sites in northeastern California. Scarcity of suitable hibernacula has been suggested as one of several possible explanations for the common occurrence of communal denning in north temperate zone snakes (Gregory, 1984). The milder winters in California allow snakes to hibernate in a variety of sites (mammal holes, shallow rock crevices and piles of vegetation, Klauber, 1937) since the requirements of a suitable hibernaculum (depth, insulative capacity, etc.) are far less stringent than in northern regions or at high elevations.

Finally, the similarity in the timing of emergence from hibernacula in northern and southern populations (late March and April, Table 13) appears to be related to lower threshold temperatures for activity in northern populations. Rattlesnakes in British Columbia began emerging when air temperatures were about 10°C. Vetas (1951) concluded that 15.5°C was the threshold temperature for surface activity for rattlesnakes in Utah and, in California, rattlesnakes first emerge when air temperatures reach 21°C (Fitch and Glading, 1947).

3.0 GROWTH

3.1.0 Methods

To test the consistency of measurements of snout-vent lengths (SVL) two captive rattlesnakes were measured (to the nearest 5 mm) daily over a seven day period. Measured lengths varied between 1.4% and 1.9% of the mean SVL; therefore an increase of greater than 2% of initial SVL was considered to be measurable growth in an individual.

During winter dormancy the mean relative growth of rattlesnakes was 0.21% (n = 433, SE = 0.08, range -7.0 - 4.9%) of the fall SVL and therefore in analyses of annual growth, I considered growth during hibernation to be zero. Absolute annual growth was calculated as the SVL increment of marked snakes measured at dens in two consecutive overwintering periods. Individuals measured either in the fall or spring of one overwintering period and again in the fall or spring of the next overwintering period were included in the sample. 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 gain in rattle segments) was determined. Since the four study sites were in close proximity (< 15 km apart), snakes were expected to experience growing seasons that were equal in terms of duration and climate; therefore growth records were pooled for rattlesnakes from all sites and both years.

In instances where a recaptured snake's SVL was less than the original SVl, both absolute and relative growth were set to zero. A dividing size of 650 mm SVL between juveniles and adults was chosen on the basis that this was the smallest size at which females attain sexual maturity (see Reproduction). Although males mature at smaller lengths relative to females, for comparative purposes all males >650 mm SVL were also considered as adults.

Analysis of variance was used to test for sex related and year to year differences in absolute and relative growth rates of adults and juveniles. To compensate for lack of orthogonality due to unequal sample size, two-way ANOVA's were performed with all possible orders of effects and a most conservative - most optimistic F table constructed for each effect (see Methods - Annual cycle). When main effects were significant in all possible orders, a multiple comparison of means (GT-2 method, Sokal and Rohlf, 1981) was used to identify specific differences.

Walford (1946) plots of SVL_{t+1} against SVL_t were constructed for each sex and the slopes and intercepts of these lines were derived by linear regression. Differences in regression coefficients were tested using a modified t-test (Zar, 1974). Growth curves (SVL versus age) were then derived for each sex as follows. Length at a given age n is determined by $SVL_n = a[(1-b^n)/(1-b)]$ where a = the intercept and b = the slope of the line. The asymptotic length thus equals $a/(1-b)$. Rearranging the first equation enables age at a given length to be calculated by:

$$\text{Age} = [\ln (1-(\text{SVL} \times (1-b)/a))/(\ln b)] - c$$

where c is a constant which sets age at birth equal to zero. Substituting the mean SVL at birth for SVL in this equation enables the constant to be calculated.

Measurement of body weight did not begin until fall of 1981, therefore data on weight change during the active season were available for only 127 rattlesnakes weighed in both the spring and fall of 1982. The amount of weight lost during hibernation was calculated for the interval between the last autumn capture and the first spring capture. Individuals frequently remained at dens for short periods following arrival or emergence; however, because of the number of snakes which had to be processed each day, only a small number of these snakes were reweighed during these periods.

Weight-length equations derived for rattlesnakes were based on all captures and recaptures of individuals for which both SVL and weight were measured ($n = 1055$ for males and $n = 1136$ for females). Sexual dimorphism in body form was examined by visual inspection for overlap of 95% confidence intervals placed around the linear regressions of log weight on log SVL .

The seasonal timing of ecdysis was determined from observations compiled during the summers of 1981 and 1982. Snakes in a premoult condition were identified by cloudy ocular scales and the presence of a new basal rattle (usually a whitish colour prior to shedding). The duration of shedding was determined as the time between when a snake was first observed in the cloudy eye stage and when its freshly shed skin (moist and sticky) was located at the shedding site.

3.2.0 Results

Annual growth was measured for 519 rattlesnakes and approximately equal proportions of males and females were present in yearly samples (1981, 80 males:67 females; 1982, 183 males:189 females).

3.2.1 Neonate growth

The average SVL and weight at birth was 269.9 mm (n = 68, SE = 1.7) and 17.9 g (n = 67, SE = 0.34) for males and 267.2 mm (n = 75, SE = 1.5) and 17.2 g (n = 75, SE = 0.34) for females. At birth, the rattle is composed of a single apical scute referred to as the prebutton (PB). The prebutton is shed along with the rest of the proto-integument at the first moult and the first permanent rattle segment, the button (B) is exposed. This moult precedes hibernation. The mean duration between birth and shedding to the B stage was 24.1 days (n = 37, SE = 1.1, range 11-40 days). Growth during this interval was negligible; neonates averaged 1.3% (SE = 0.42) increase over their SVL at birth (Table 14). Mean weight loss from birth to completion of the initial moult was 2.8 g (SE = 0.14, range 1.1 - 5.2 g), equivalent to 15.3% of the mean weight at birth (SE = 0.7, range 6.4 - 27.1). During the shedding period neonates bask singly or aggregate with litter mates and other members of the den. Young rattlesnakes begin their first overwintering period a few days to a week following the initial moult.

3.2.2 Juvenile growth

Annual growth during the first two years of life is summarized for males and females in Table 14. A majority of yearlings shed once during the first active season (B to 1+B). Males that shed once averaged approximately 20 mm longer than females of the same rattle class (1+B) at the end of the first year. Biannual shedding was more frequent in yearling females and growth was generally faster in these females. The average SVL of known one year olds (1+B and 2+B snakes) was 355 mm (n = 11, SE = 11.6) and 344 mm (n = 20, SE = 9.4) for males and females respectively.

It was not uncommon to recapture one year old rattlesnakes at dens in the autumn that weighed less than they had weighed at birth. Most of these individuals had undergone some growth and shed once since emergence, but their emaciated appearance and weight loss suggested that natal abdominal fat stores had been their only source of nourishment since birth. One starved yearling survived its second hibernation but was found dead at the den in the spring; others entering hibernation in this condition presumably died during hibernation.

At the start of the second growing season juveniles have one, or at most two, rattles in addition to the button. All rattlesnakes with 1+B in the fall or spring were definitely one year olds. Males that shed once during their second year averaged higher growth rates than females of the same rattle increment class. There was an increase in the proportion of males that shed biannually compared to the first year, but in females this proportion declined. In addition, growth of biannual shedding males was greater than for females with a few exceptions. Three females that proceeded fron B to 2+B in their first year, also showed rapid growth during their second year (Table 14). Pooling SVL's attained by all known two year olds, the average size was approximately 430 mm for males and 405 mm for females.

It is difficult to place juveniles into a third year class based on SVL or rattle size. Two year old snakes may have 2, 3 or 4 rattles in addition to the button; most females would have 2+B while males would have 3+B. About half of the males and one-third of the females in the 2+B class shed biannually but few snakes of either sex in the 3+B class have shed more than once per annum (Tables 14 and 15). Accordingly, a majority of three year old males were expected to have 4+B, having shed twice in one of the first three growing seasons. Females grow less rapidly and are not as likely to shed more than once per annum in previous years. Thus a rattle mode of 3+B was expected for three year old females while males of the same age were expected to have 4+B.

From individual snakes initially marked at B or 1+B and recaptured two or three years later, estimates of body and rattle size for known three year olds were available. In 10 of 12 three year old males the rattle size class was 4+B and the mean SVL was 548.5 mm (SE = 14.9). Two males that shed once per annum from birth had attained SVL's of 495 and 570 mm. Fewer known three year old females were recaptured. Three females had 4+B and a mean SVL of 570 mm (SE = 2.9), while another female with 3+B was 385 mm SVL. A female beginning her third year at 2+B would attain an average SVL of approximately 520 mm at the end of the third year and have 3 or 4 rattles if growth rates of 2+B females

Table 14: Growth of neonates prior to hibernation and growth during the first and second year of life (based on snakes of known age). 1981 and 1982 data combined. Mean ± 1SE are presented.

Rattle Increment	Sex	n	SVLt (mm)	SVLt+1 (mm)	Absolute Growth (mm)	Relative Growth
Neonate growth						
PB to B	M + F	37	276.8 ± 1.6	280.3 ± 1.8	3.5 ± 1.2	0.013 ± 0.004
First year growth						
B to 1+B	M	9	281.7 ± 6.4	348.9 ± 7.6	67.2 ± 6.7	0.24 ± 0.02
B to 1+B	F	15	283.7 ± 4.2	328.7 ± 7.7	45.0 ± 6.6	0.16 ± 0.02
B to 2+B	M	2	302.5 ± 12.5	385.0 ± 65.0	82.5 ± 52.5	0.27 ± 0.16
B to 2+B	F	5	272.0 ± 11.9	390.0 ± 18.4	118.0 ± 13.1	0.44 ± 0.05
Second year growth						
1+B to 2+B	M	13	353.1 ± 6.8	405.4 ± 8.5	52.3 ± 5.7	0.15 ± 0.02
1+B to 2+B	F	11	336.8 ± 6.3	377.3 ± 7.6	40.5 ± 7.0	0.12 ± 0.02
1+B to 3+B	M	12	360.0 ± 11.3	453.7 ± 14.4	93.8 ± 9.9	0.26 ± 0.03
1+B to 3+B	F	2	342.5 ± 27.5	410.0 ± 65.0	67.5 ± 37.5	0.19 ± 0.09
2+B to 3+B	M	1	425	535	110	0.26
2+B to 4+B	F	3	383.3 ± 14.7	505.0 ± 22.6	121.7 ± 16.3	0.32 ± 0.04

Table 15: Growth of juveniles in rattle classes 2+B and 3+B. Mean ± 1SE are presented.

Rattle Increment	Sex	n	SVLt (mm)	SVLt+1 (mm)	Absolute Growth (mm)	Relative Growth
2+B to 3+B	M	9	416.1 ± 10.2	491.1 ± 9.4	75.0 ± 4.7	0.18 ± 0.02
2+B to 3+B	F	13	440.0 ± 7.3	511.2 ± 8.4	71.2 ± 9.2	0.16 ± 0.02
2+B to 4+B	M	9	413.3 ± 12.5	544.4 ± 23.9	131.1 ± 14.0	0.31 ± 0.01
2+B to 4+B	F	7	425.7 ± 17.4	535.0 ± 19.8	109.3 ± 13.5	0.26 ± 0.04
3+B to 4+B	M	16	484.4 ± 8.6	554.4 ± 11.8	70.0 ± 7.6	0.15 ± 0.02
3+B to 4+B	F	17	497.0 ± 7.2	562.3 ± 7.4	65.3 ± 6.8	0.13 ± 0.02
3+B to 5+B	M	2	515.0 ± 15.0	605.0 ± 5.0	90.0 ± 10.0	0.18 ± 0.03
3+B to 5+B	F	1	470	580	110	0.23

Table 16: Growth of juveniles in rattle classes 4+B, 5+B and 6+B. Mean ± 1 SE are presented.

Rattle Increment	Sex	n	SVLt (mm)	SVLt+1 (mm)	Absolute Growth (mm)	Relative Growth
4+B to 5+B	M	21	556.0 ± 8.6	621.4 ± 9.4	65.4 ± 4.6	0.119 ± 0.009
4+B to 5+B	F	17	568.5 ± 7.5	612.6 ± 10.0	44.1 ± 4.9	0.080 ± 0.008
4+B to 6+B	M	4	578.7 ± 24.2	665.0 ± 11.9	86.3 ± 13.5	0.153 ± 0.029
4+B to 6+B	F	2	570.0 ± 21.8	650.0 ± 55.0	80.0 ± 5.0	0.141 ± 0.004
5+B to 6+B	M	15	631.3 ± 10.2	686.0 ± 10.8	54.7 ± 6.6	0.087 ± 0.01
5+B to 6+B	F	22	605.7 ± 9.5	650.0 ± 9.5	44.3 ± 3.8	0.074 ± 0.007
5+B to 7+B	M	2	685.0 ± 21.2	767.5 ± 32.5	82.5 ± 2.5	0.121 ± 0.001
6+B to 7+B	M	18	696.4 ± 11.6	741.7 ± 11.6	45.3 ± 11.6	0.066 ± 0.016
6+B to 7+B	F	10	676.5 ± 16.5	709.0 ± 14.7	32.5 ± 20.8	0.049 ± 0.011
6+B to 8+B	M	1	660	720	60	0.091

Table 17: Growth rates of adult rattlesnakes. Snakes placed in size classes according to initial SVL. Means ± 1SE are presented.

	Males			Nongravid Females		
Size Class (mm)	n	Absolute Growth (mm)	Relative Growth	n	Absolute Growth (mm)	Relative Growth
650 - 749	39	45.1 ± 3.6	0.065 ± 0.005	43	28.1 ± 3.3	0.040 ± 0.005
750 - 849	33	33.2 ± 3.4	0.042 ± 0.004	31	16.8 ± 2.3	0.022 ± 0.003
850 - 949	24	22.2 ± 4.5	0.025 ± 0.005	4	13.8 ± 5.2	0.016 ± 0.006
950 - 1049	24	17.1 ± 3.5	0.017 ± 0.003	-	-	-
> 1050	4	5.0 ± 2.9	0.005 ± 0.003	-	-	-

in Table 15 are pooled. The size of the average three year old male based on growth rates in Table 13 for males starting the year at 2+B or 3+B would be approximately 535 mm with 4+B.

Few rattlesnakes shed biannually after attaining 500 mm SVL (Fig. 11) or after attaining 4 rattles (Table 16). Both relative and absolute annual growth reach their maximum values in snakes between 400 and 500 mm SVL, corresponding to the third growing year; thereafter both absolute and relative growth decline with increasing SVL (Fig. 12).

Assuming a mimimum of one shed per annum the maximum age of a rattlesnake with an intact rattle is equivalent to the total number of rattles (excluding the button). For larger juvenile males, age can be estimated as the number of rattles less one. Assuming a rattle mode of 4+B at the start of the fourth year, males would grow to about 630 mm and have 5+B at four years of age (Table 16). At five years old males would be about 695 mm SVL and have 6+B; in their sixth year they would be about 740 mm and have 7+B according to average SVL's attained by snakes starting a growing season with 5+B and 6+B respectively (Table 16).

The age of larger juvenile females would be more closely approximated by the total number of rattles but as with males, the age of some females would be at least one year

Figure 11: Percent occurrence of annual shedding (open rectangles), biannual shedding (stipled rectangles) and no shedding (darkened rectangles) in rattlesnakes. Size class intervals encompass ± 50 mm of SVL printed on the X axis. Top figure = females and the bottom figure = males.

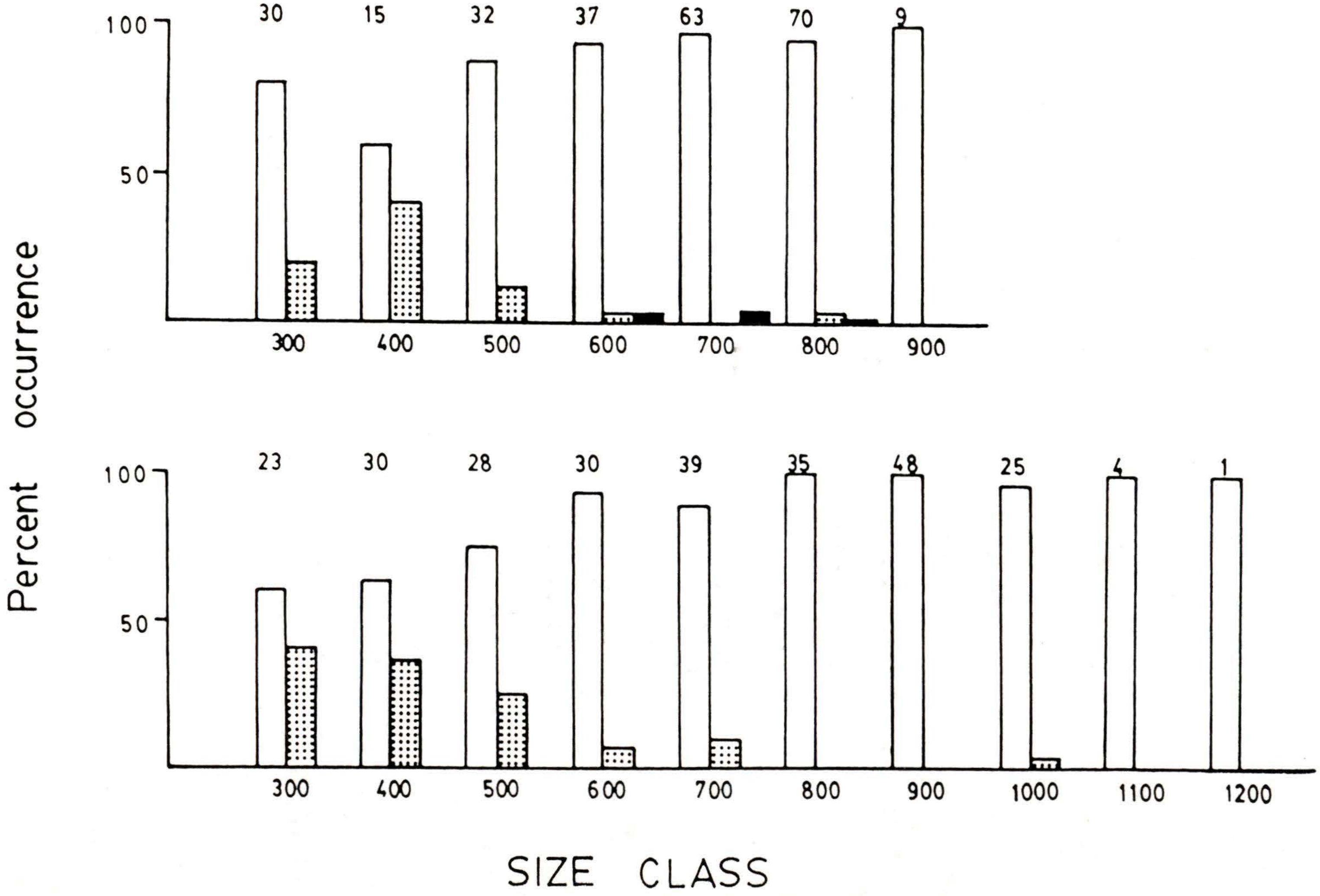
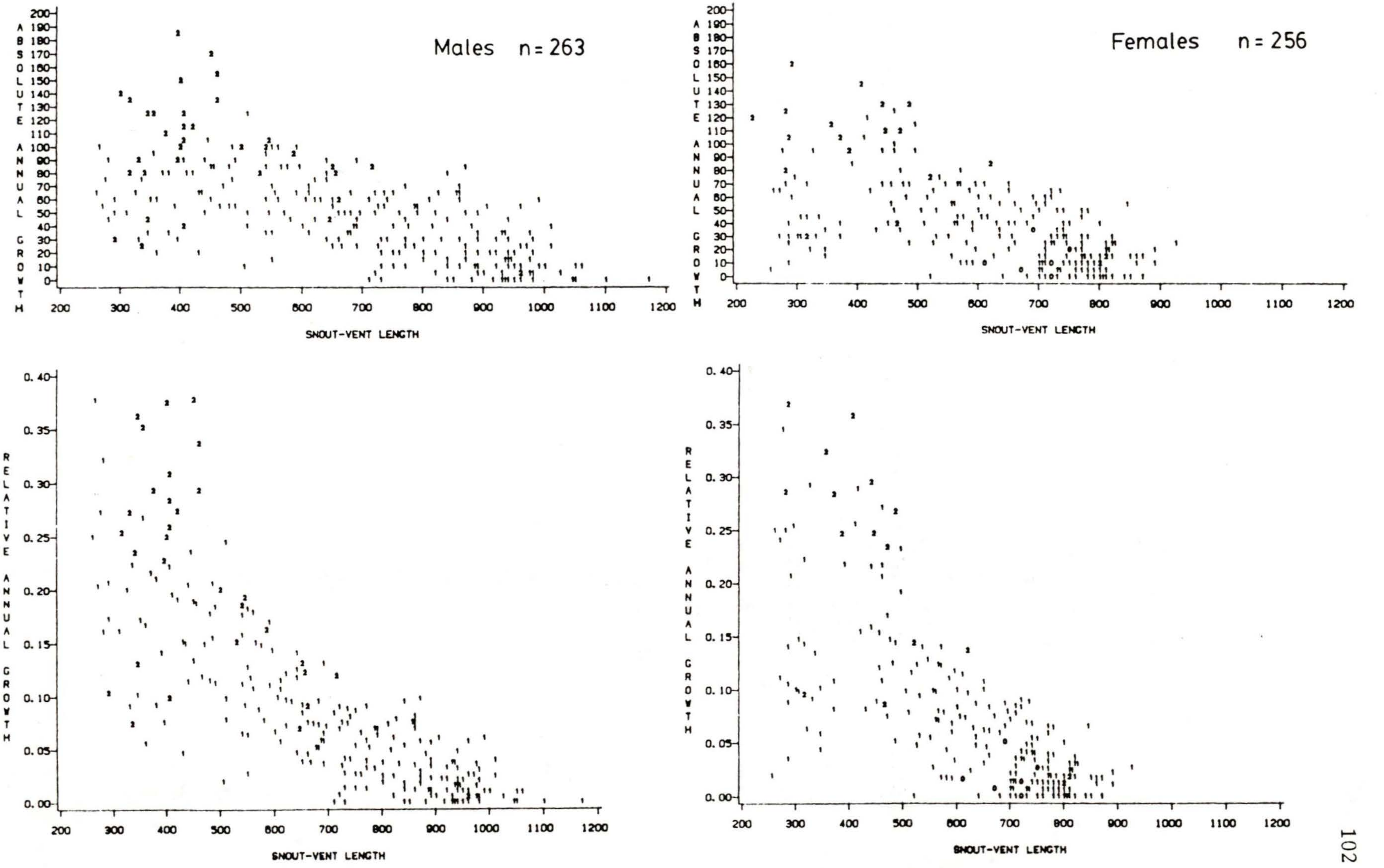

Percent occurrence
100
50
30
15
32
37
63
70
9
300
400
500
600
700
800
900
100
50
23
30
28
30
39
35
48
25
4
1
300
400
500
600
700
800
900
1000
1100
1200
SIZE CLASS

Figure 12: The relationship between absolute and relative annual growth and SVL for male and female *C. v. oreganus*. The SVL on the X axis is the length at the initial capture (SVL_t). Numbers on the figures are the number of times an individual shed per annum.


Males n = 263
Females n = 256
ABSOLUTE ANNUAL GROWTH
0 10 20 30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200
RELATIVE ANNUAL GROWTH
0.00 0.05 0.10 0.15 0.20 0.25 0.30 0.35 0.40
SNOUT-VENT LENGTH
200 300 400 500 600 700 800 900 1000 1100 1200

less than this number. Annual growth of females in the rattle classes 4+B, 5+B and 6+B were consistently lower than males in the same rattle class (Table 16). Female size at four years of age was estimated from data pooled for SVL's attained by females starting the fourth growing season in the 3+B class (Table 15) and the 4+B class (Table 16). A four year old female would average about 590 mm SVL with 4 or 5+B. Using the SVL's attained by females in these rattle classes, a four year old female would grow to about 635 mm SVL by five years of age. In the sixth year an SVL of about 670 mm and 6 or 7+B would be attained.

There was a consistent trend for juvenile males to grow more rapidly than females at least when growth rates of annual shedding snakes in the same starting rattle class are compared. ANOVA's were performed to examine difference in absolute growth between juvenile males and females which had shed once versus twice per annum. In all orders of effects there was a significant difference in growth rates between snakes that shed biannually versus annually ($F_{c(1,183)} = 78.3$, $P<0.0001$). The effects due to sex and the interaction term (sex x shedding frequency) were in most, but not all orders, non-significant. The unplanned comparison of means (Fig. 13) shows that among annual shedding snakes males grow somewhat more rapidly than females, but the difference in the mean growth rate was not quite significant. Biannually shedding males and females showed similar and higher average annual growth rates than their annual shedding counterparts (Fig. 13).

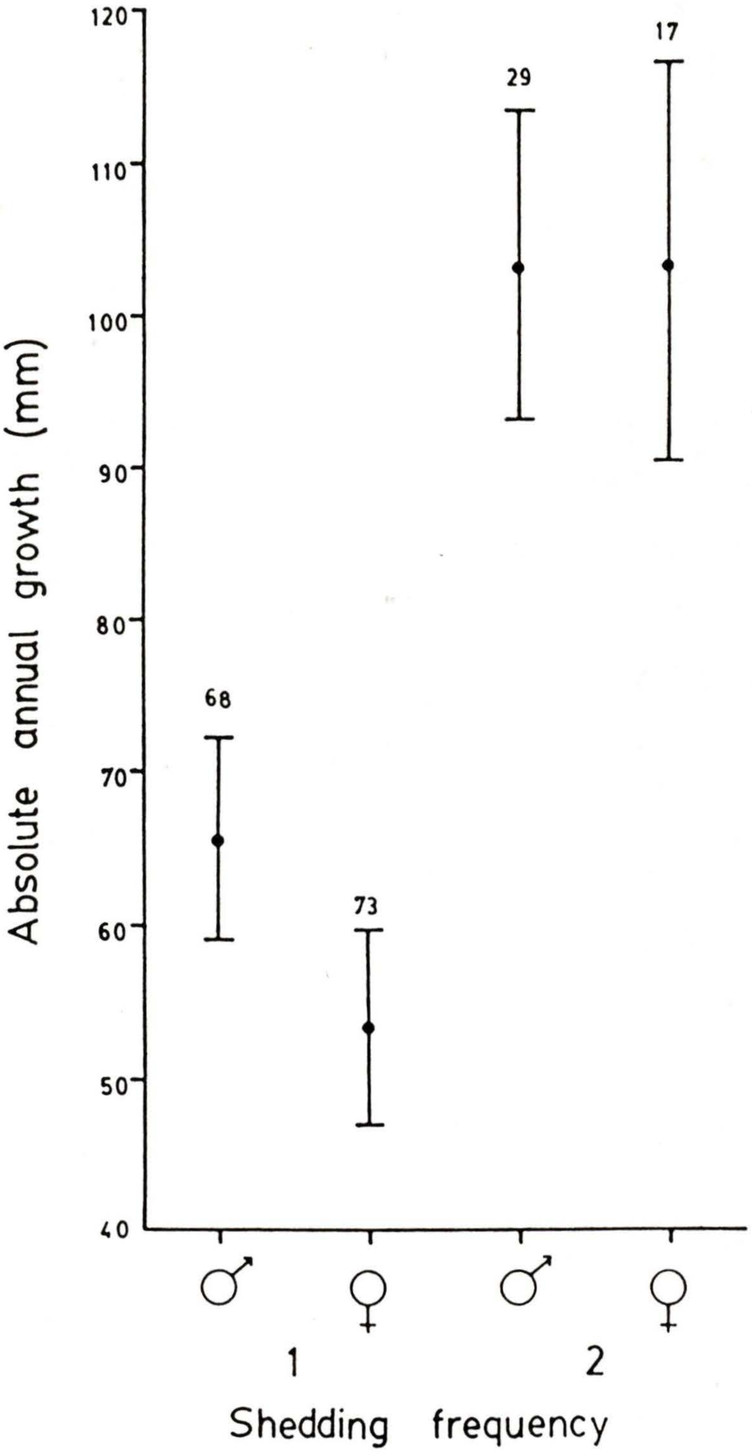
3.2.3 Adult growth

As a rule adults generally shed only once per annum (Fig. 11). Growth rates of males and females continued to decline after an adult size of 650-700 mm SVL is reached. The rate of decline of growth with increasing SVL was about the same in both sexes, but males exhibited greater absolute and relative annual growth than females (Table 17). The average size of adults (>650 mm SVL, at first capture) was 822.6 mm (n = 395, SE = 5.4, maximum SVL = 1170 mm) for males and 751.2 mm SVL (n = 330, SE = 3.1, maximum SVL = 950 mm) for females. Growth rates of females during gravid and nongravid years are discussed below.

3.2.4 Annual variation in growth

Year to year variability in growth rate of juveniles was examined by ANOVA. Two factor (sex, year), two level (male:female; 1981:1982) ANOVA's were performed on all possible orders of effects using absolute or relative growth as the dependent variable. With either measure of annual growth as the dependent variable, there were in all orders significant effects due to sex (absolute $F_{c(1,221)} = 11.6$, $P = 0.001$; relative $F_{c(1,183)} = 8.0$, $P = 0.005$) and year (absolute $F_{c(1,221)} = 7.6$, $P = 0.006$; relative

Figure 13: A comparison of mean absolute annual growth of juveniles that shed annually and biannually. Vertical bars are 95% comparison intervals by the GT-2 method. Means whose intervals do not overlap are significantly different. Number above bar = sample size.


Absolute annual growth (mm)
120
110
100
90
80
70
60
50
40
68
73
29
17
♂
♀
♂
♀
1
2
Shedding frequency

$F_{c(1,221)} = 14.9$, $P<0.0001$). The interaction term was in most orders non-significant with relative growth ($F_{o(1,221)} = 6.4$, $P = 0.015$, $F_{c(1,221)} = 2.45$, $P = 0.119$) and was non-significant in all orders with absolute growth ($F_{o(1,221)} = 3.2$, $P = 0.073$). Unplanned comparisons of mean growth revealed two trends : 1) overall, 1982 was a poorer year for growth than 1981 and 2) growth rates were not significantly different between sexes in 1981, but in 1982 juvenile females grew less rapidly than juvenile males (Fig. 14).

Annual differences in adult growth rates was also analyzed by ANOVA. The factor sex, however, was divided into three levels; males, nongravid and gravid females. There were significant effects in all orders due to sex (absolute $F_{c(2,279)} = 29.9$, $P<0.0001$; relative $F_{c(2,279)} = 18.8$, $P<0.0001$) and year (absolute $F_{c(1,279)} = 48.6$, $P<0.0001$; relative $F_{c(1,279)} = 46.8$, $P<0.0001$). The interaction was non-significant in all but one order with either absolute or relative growth as the dependent variable. Multiple comparisons of mean growth of adults in 1981 and 1982 are presented in Figure 15. Mean annual growth of adult males was not significantly different from nongravid females but both groups of adults showed higher growth than gravid females, when compared within years. Compared across years annual growth rates were significantly lower in 1982 for males and nongravid females

Figure 14: Year to year variability in absolute and relative annual growth of juvenile rattlesnakes. Vertical bars are 95% comparison intervals by the GT-2 method. Means whose intervals do not overlap are significantly different. Number above bar = sample size.

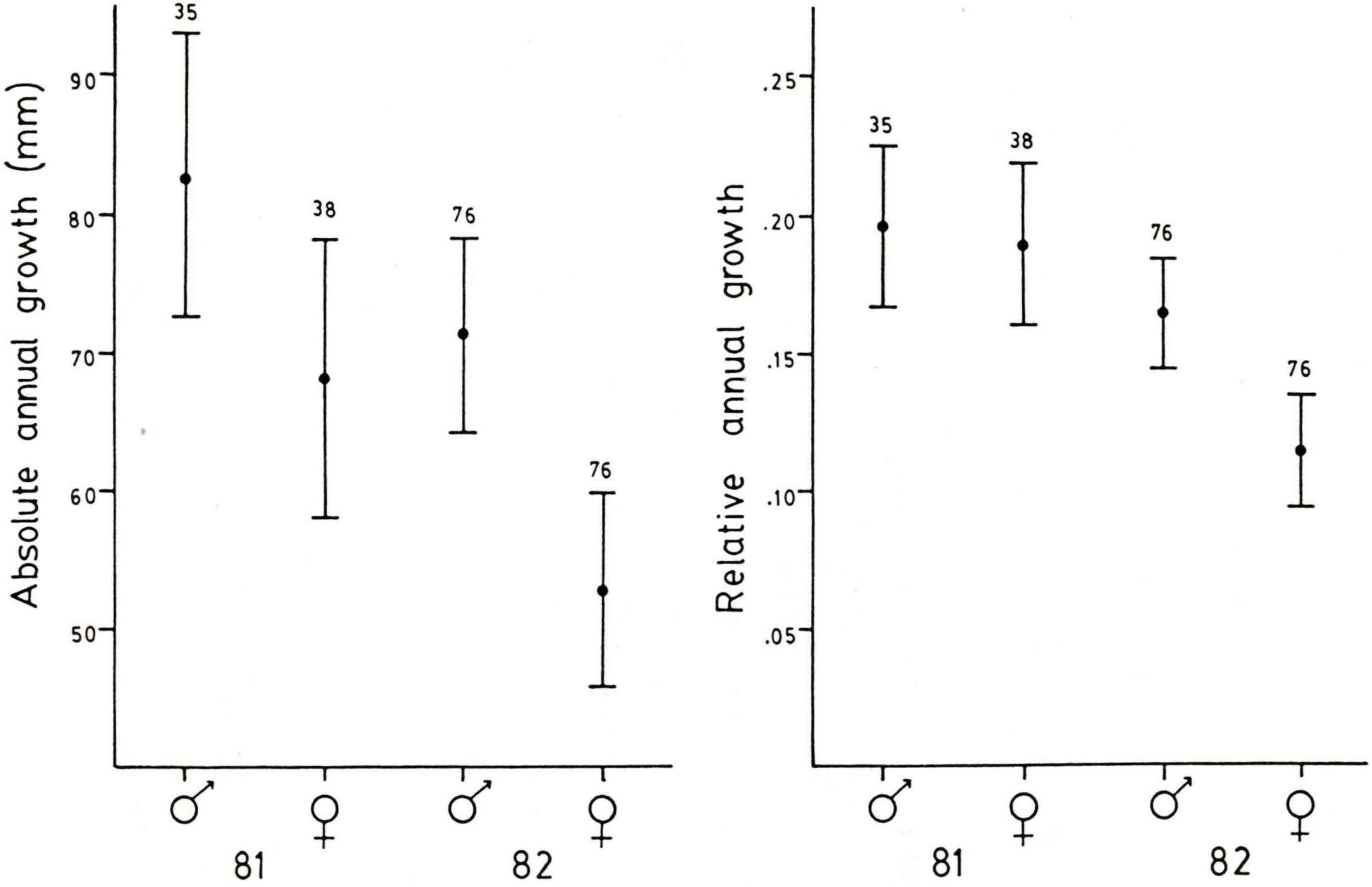
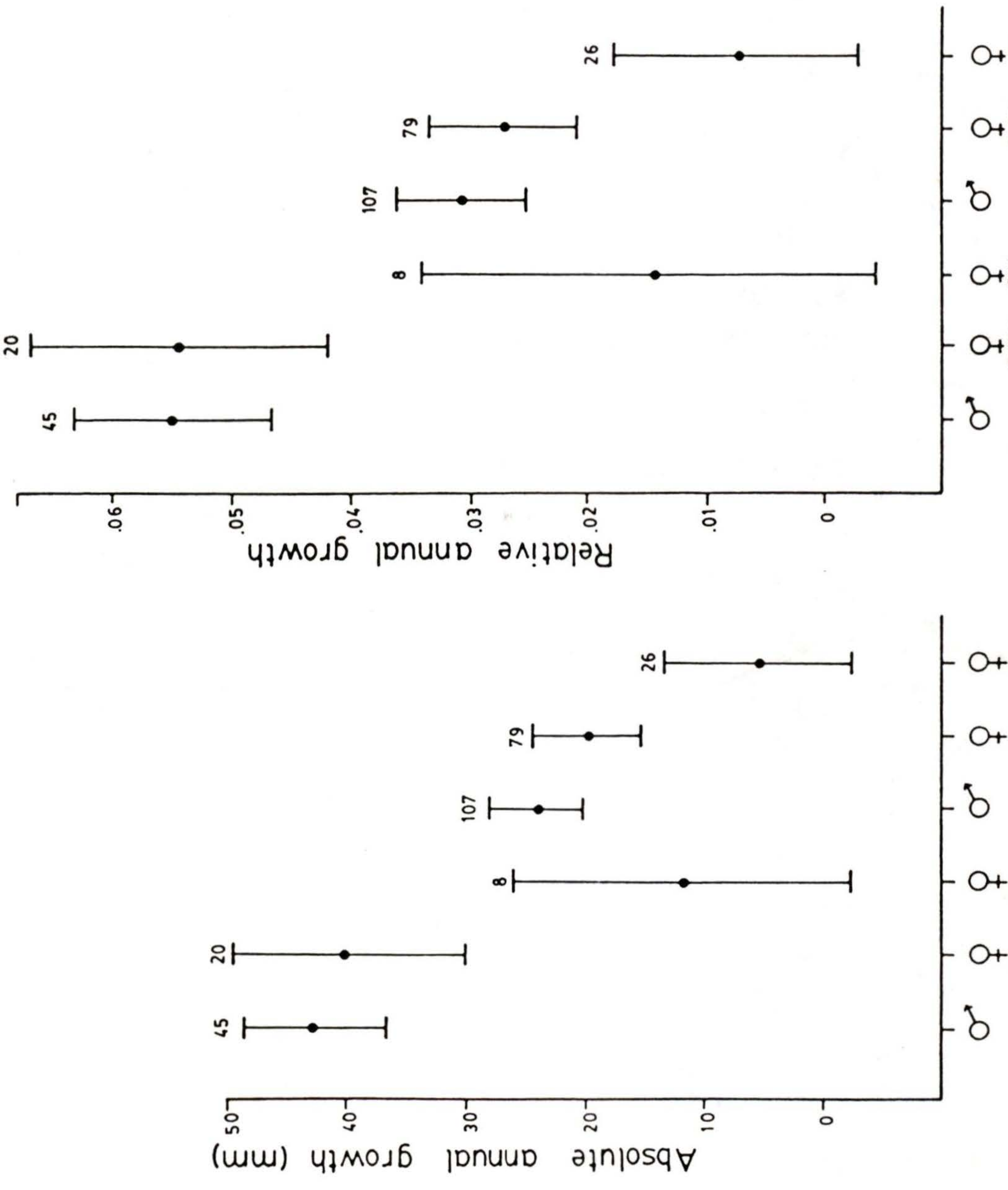

Absolute annual growth (mm)
90
80
70
60
50
35
38
76
76
♂
♀
♂
♀
81
82
Relative annual growth
.25
.20
.15
.10
.05
35
38
76
76
♂
♀
♂
♀
81
82

Figure 15: Year to year variability in absolute and relative growth of adult rattlesnakes. Symbols ngv = nongravid females, gv = gravid females. Vertical bars are 95% comparison intervals by the GT-2 method. Means whose intervals do not overlap are significantly different. Number above bar = sample size.


Relative annual growth
0
.01
.02
.03
.04
.05
.06
45
20
8
107
79
26
♂
♀ ngv
♀ gv
81
♂
♀ ngv
♀ gv
82
Absolute annual growth (mm)
0
10
20
30
40
50
45
20
8
107
79
26
♂
♀ ngv
♀ gv
81
♂
♀ ngv
♀ gv
82

but not significantly so for gravid females. Mean growth of gravid females did not exceed what was previously defined as measurable growth.

3.2.5 Growth curves

Linear regression of Walford plots for males and females are presented in Figure 16a. The regression lines were based on data from all sizes of rattlesnakes pooled across years. Pooling was justified on the basis that individuals are subjected to growing seasons which may be variable in terms of duration and climate throughout their lifetime. The resultant growth curves are therefore composites of growth in a relatively good year (1981) and a poor year (1982).

The linear equations that describe the relationship between SVL_{t+1} and SVL_t were:

$$SVL_{t+1} = 122.46 + 0.891\ SVL_t \qquad \text{for males and}$$

$$SVL_{t+1} = 110.29 + 0.882\ SVL_t \qquad \text{for females.}$$

The intercepts but not the slopes of the two equations were significantly different (Ho: $a_1=a_2$, $t=15.6$, $t_{0\cdot05(2)514} = 1.97$; Ho: $b_1=b_2$, $t=0.68$, $t_{0\cdot05(2)513} = 1.96$). Asymptotic lengths for males and females were 1110 mm SVL and 935 mm SVL respectively. The growth curve for males was produced by the following equation:

$$\text{Age} = [\ln(1-(\text{SVL} \times 0.109/122.46))/\ln 0.891] - C_m \ .$$

For females the growth curve equation was:

$$\text{Age} = [\ln(1-(\text{SVL} \times 0.118/110.29))/\ln 0.882] - C_f \ .$$

The constants C_m and C_f were 2.38 and 2.68 respectively. The growth curve based on these equations are presented in Figure 16b. There was close agreement between predicted and known sizes of one and two year olds, but the Walford equations suggest a slower rate of growth in both sexes than was extrapolated from average growth within rattle classes of snakes greater than two years old (Fig. 17).

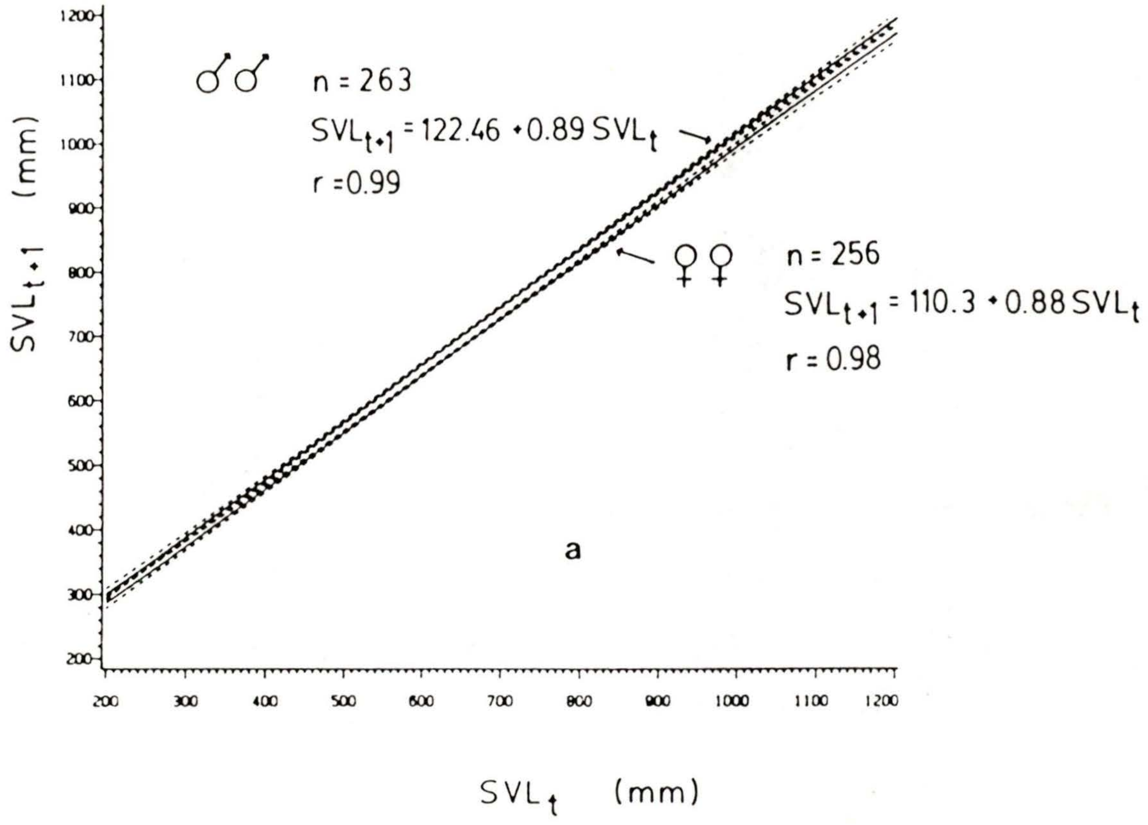
3.2.6 Ecdysis

The seasonal distributions of capture records for shedding snakes are presented in Figure 18. Gravid females shed once per annum and usually earlier than any segment of the adult population, in late June or early July. The major shedding period of adult males was from late June through early August but most males shed during the first three weeks of July. Adult males that shed in late August or early September were doing so for the second time that year.

Nongravid females generally shed 1-2 weeks later than adult males, peaking in the first week of August. It is possible that a second shed may occur in late summer or

Figure 16: a) Linear regession of Walford plots for male and female *C. v. oreganus*. Dashed lines are 95% confidence intervals around the regression lines.

b) The growth curves derived from the regressions of SVL_{t+1} on SVL_t for male and female rattlesnakes.


♂♂
n = 263
$SVL_{t+1} = 122.46 + 0.89\,SVL_t$
r = 0.99
♀♀
n = 256
$SVL_{t+1} = 110.3 + 0.88\,SVL_t$
r = 0.98
a
SVL_{t+1} (mm)
SVL_t (mm)
200
300
400
500
600
700
800
900
1000
1100
1200

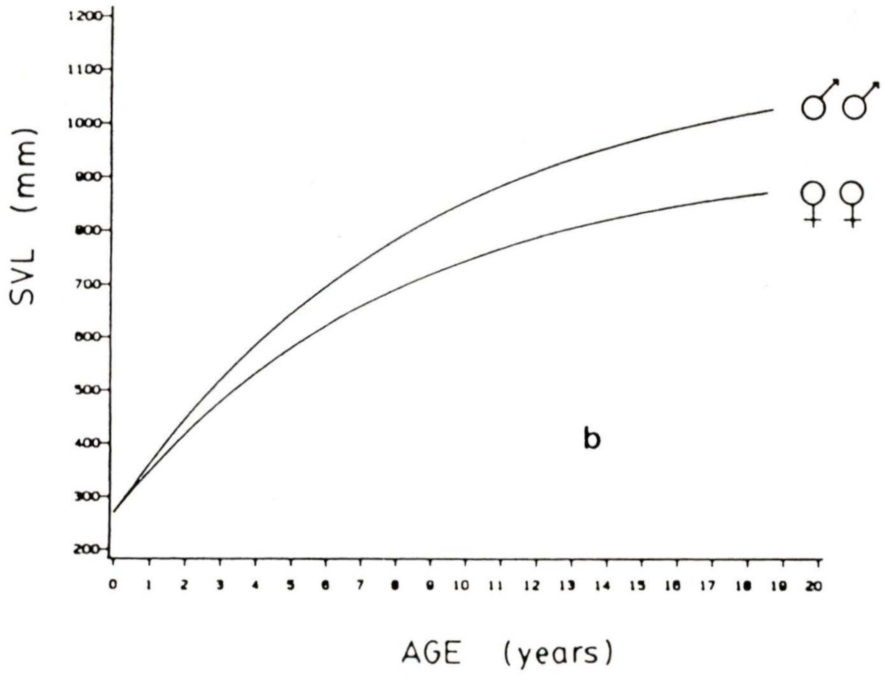
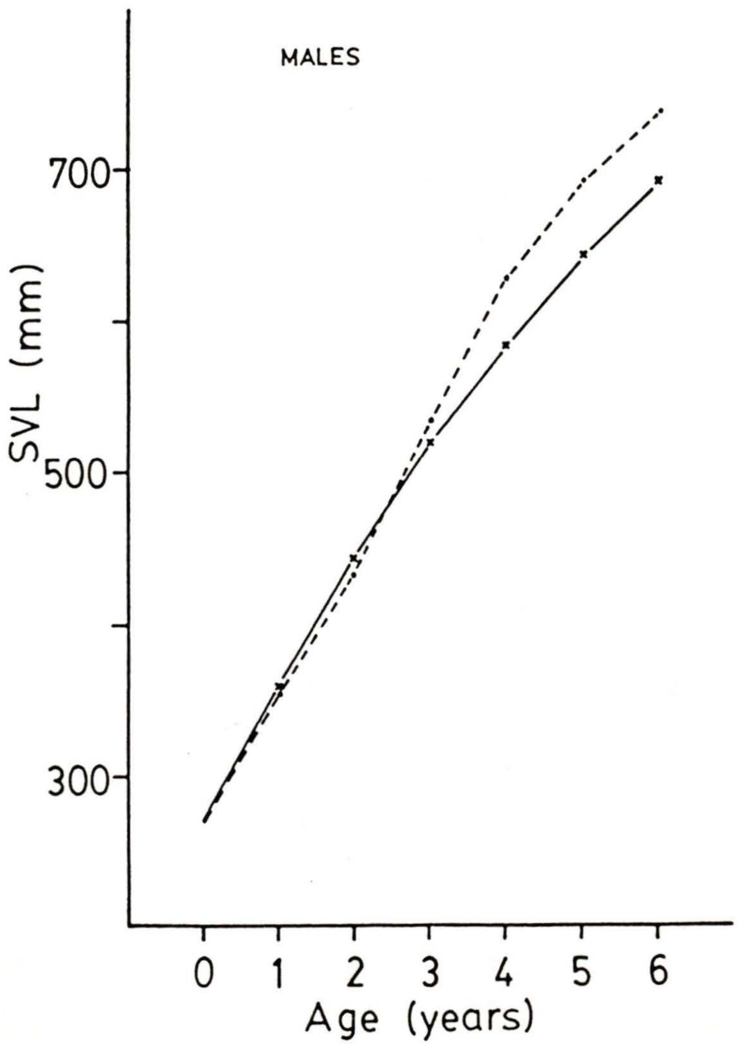

♂♂
♀♀
b
SVL (mm)
AGE (years)
200
300
400
500
600
700
800
900
1000
1100
1200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Figure 17: A comparison between growth curves generated from the Walford method (solid line) and estimated from growth of known age snakes (dashed line).


MALES
SVL (mm)
700
500
300
0
1
2
3
4
5
6
Age (years)

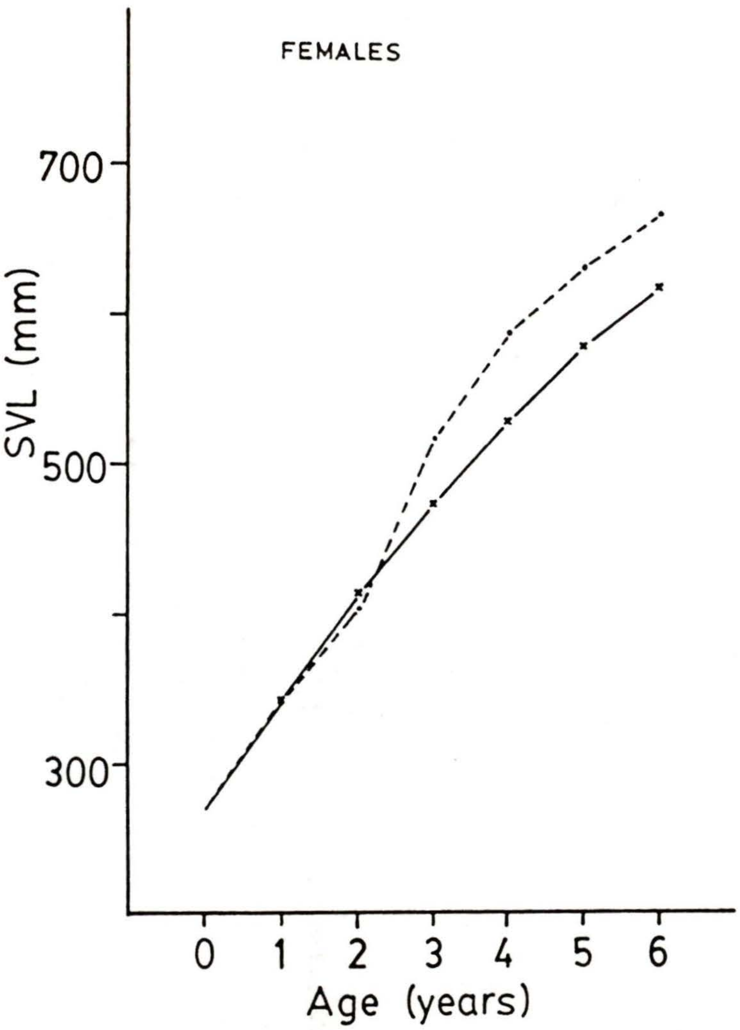
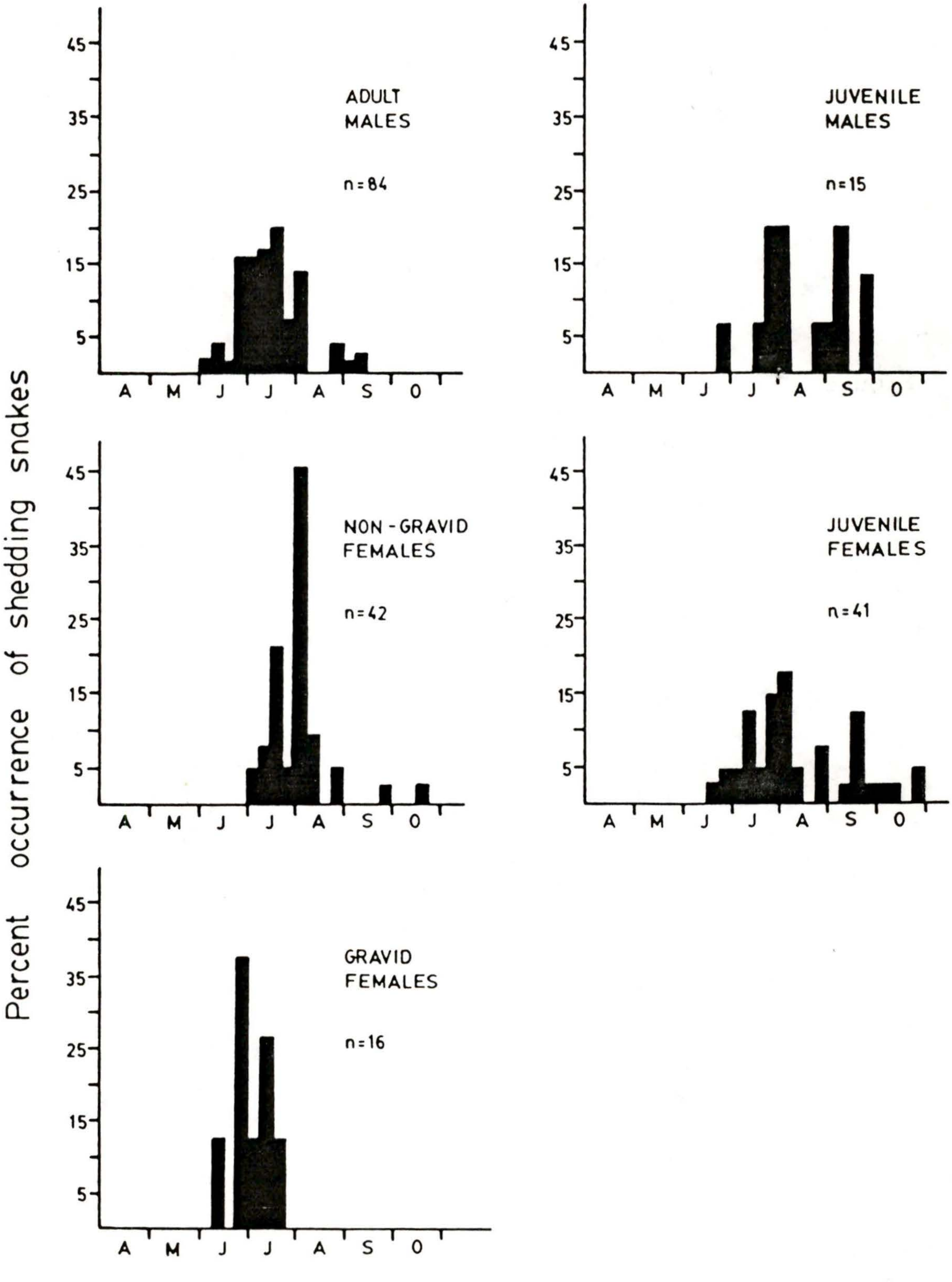

FEMALES
SVL (mm)
700
500
300
0
1
2
3
4
5
6
Age (years)

Figure 18: Percent occurrence of shedding snakes observed during the summers of 1981 and 1982.


Percent occurrence of shedding snakes
ADULT MALES
n=84
JUVENILE MALES
n=15
NON-GRAVID FEMALES
n=42
JUVENILE FEMALES
n=41
GRAVID FEMALES
n=16
45
35
25
15
5
A
M
J
J
A
S
O

fall but since the occurrence of biannual shedding in adult females was rare fall sheddings may actually be a delayed first shed (see Fig. 11), The bimodal distribution of shedding in juvenile male and females correspond with the higher incidence of biannual shedding in juveniles (Tables 14, 15 and 16).

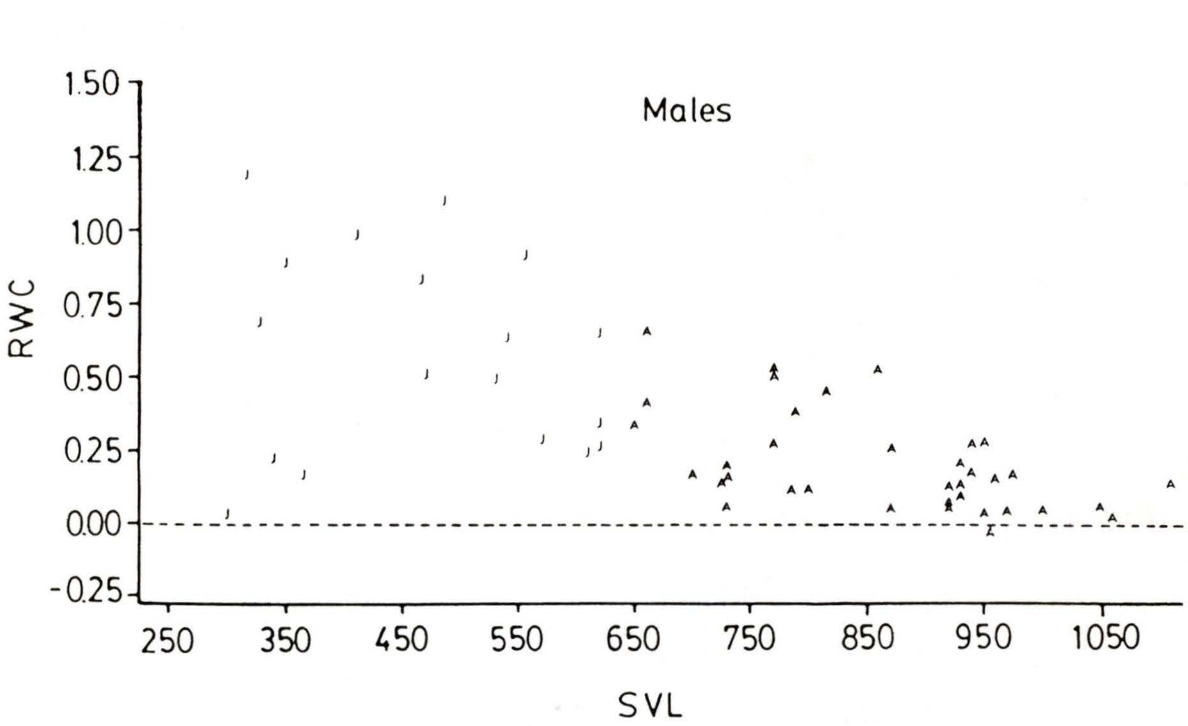
An estimate of the average duration of ecdysis was obtained from seven individuals (including three radiotracked snakes) for which repeated progess checks were conducted. The mean duration was 18 days (range 13-21).

3.2.7 Annual weight change

For juveniles of both sexes annual relative weight increments approached their maximum values during the second or third growing season at SVL's between 350 and 450 mm and thereafter declined with increasing SVL (Fig. 19). Annual relative weight gain continued to decrease as length increases in adult males. The extreme variability in relative weight change in adult females reflects the fact that two groups of nongravid females depicted in Figure 19 are composites of females in different years of a biennial or triennial reproductive cycle. The largest relative weight increases occurred in females which were destined to reproduce the next year.

Relative weight changes closely paralleled relative

Figure 19: Relative weight change (RWC) plotted against initial SVL for male and female rattlesnakes in 1982. Symbols are: j = juveniles, A = adult males, S = adult females with small follicles in the fall; E = adult females with enlarged follicles in the fall, G = gravid females.


Males
RWC
SVL
1.50
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
250
350
450
550
650
750
850
950
1050
J
A

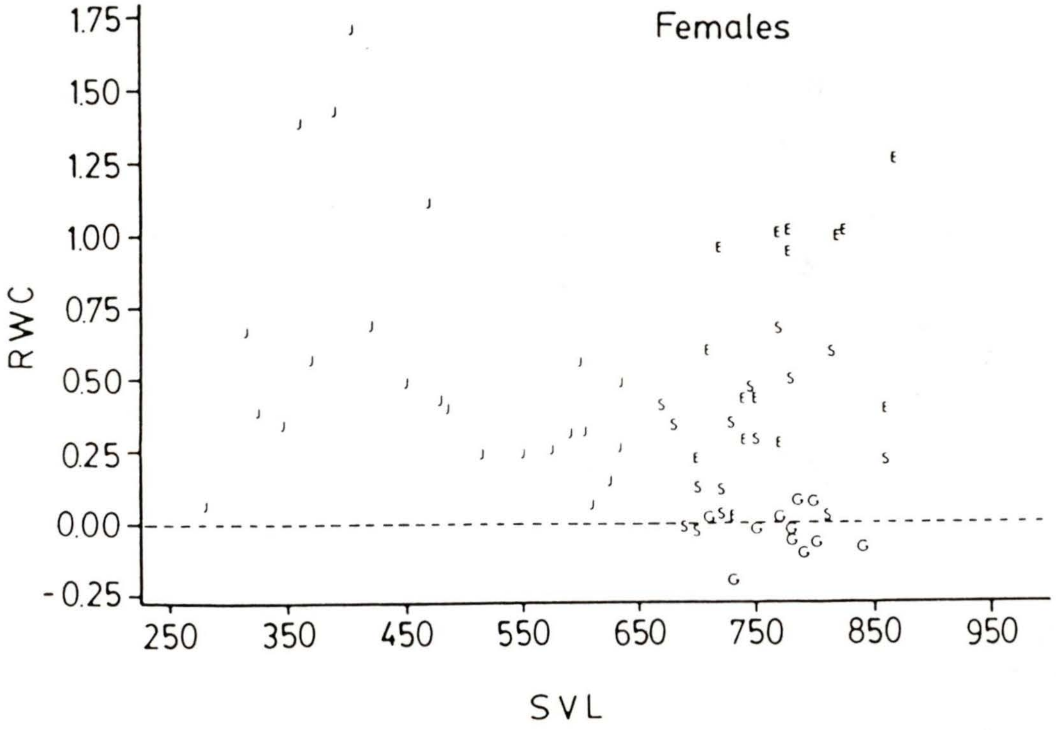
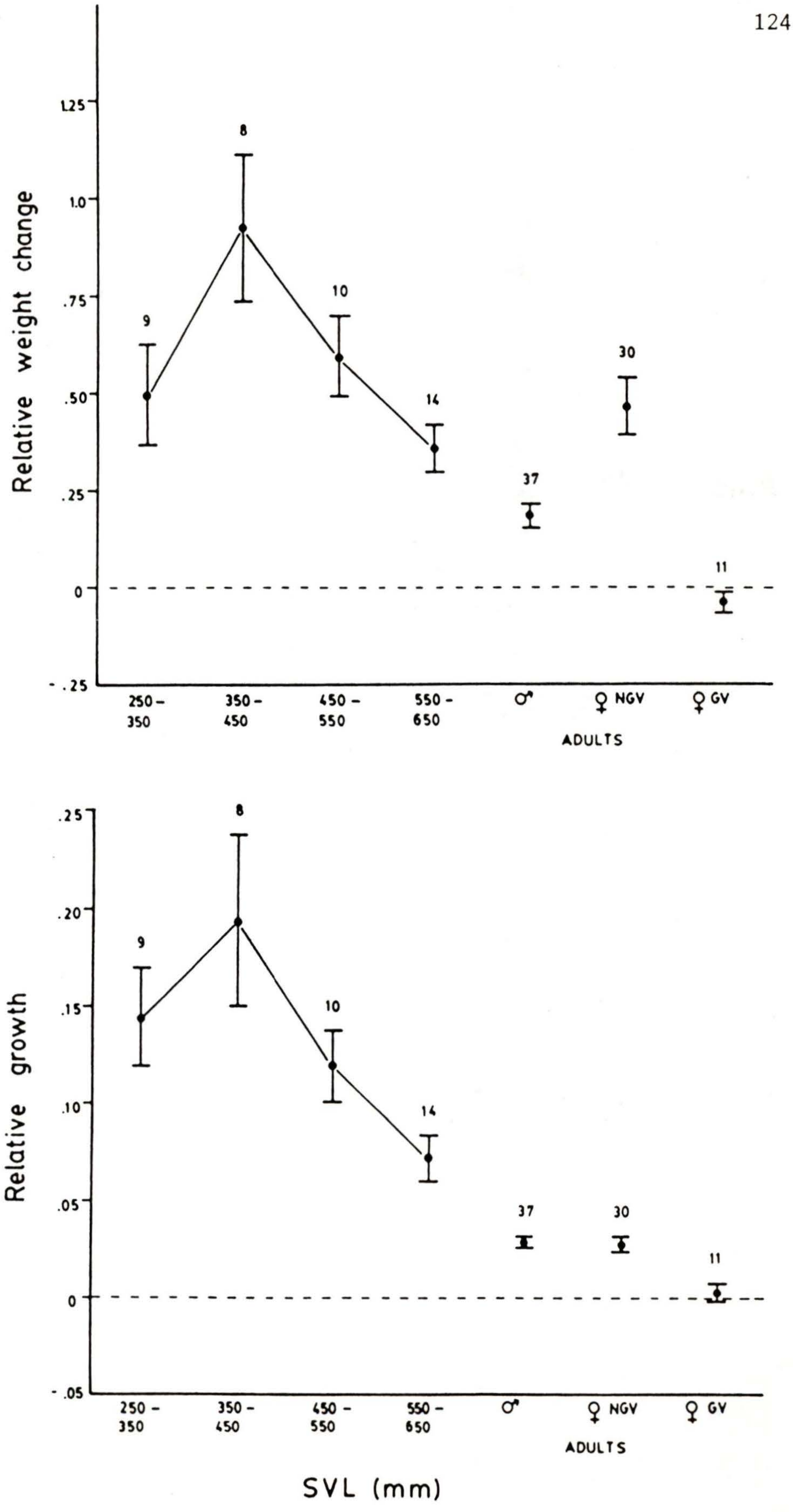

Females
RWC
SVL
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
250
350
450
550
650
750
850
950
J
E
S
G

Figure 20: Mean relative weight change ± SE and mean relative growth ± 1 SE for juvenile and adult rattlesnakes. Numbers above bars are sample sizes.


Relative weight change
1.25
1.0
.75
.50
.25
0
- .25
9
8
10
14
37
30
11
250 - 350
350 - 450
450 - 550
550 - 650
♂
♀ NGV
♀ GV
ADULTS
Relative growth
.25
.20
.15
.10
.05
0
- .05
9
8
10
14
37
30
11
250 - 350
350 - 450
450 - 550
550 - 650
♂
♀ NGV
♀ GV
ADULTS
SVL (mm)

length changes in juvenile rattlesnakes (Fig. 20). There were strong postive correlations between these measures of annual growth rate in juvenile males ($r = 0.87$, $P < 0.001$, $n = 18$) and juvenile females ($r = 0.81$, $P < 0.001$, $n = 23$). For adult males this relationship was not as strong ($r = 0.74$, $P < 0.001$, $n = 37$) and relative growth (SVL) explained only about 25% of the variation seen in relative weight change for nongravid females ($r = 0.52$, $P = 0.003$, $n = 30$). Relative growth rates (SVL) of nongravid females were similar to those of adult males, while relative annual weight gains by nongravid females were nearly double those of adult males (Fig. 20).

Among nongravid females, the largest growth in terms of SVL and weight were shown by females in the nongravid year of a biennial cycle (Table 18).

3.2.8 Weight losses incurred while at hibernacula

Females lost weight slightly more rapidly than males during the period between arrival at dens and ingress into hibernacula (Table 19). Relative weight loss of newborn snakes averaged about 16% during the 3-4 week period between birth and entering hibernation; the rate loss was slightly higher in 1982.

Summary statistics for relative weight loss and the rate of winter weight loss during hibernation are presented in

Table 18: Relative annual growth and relative annual weight gains by different reproductive classes of nongravid females. Data for adult males are provided for comparison.

			Relative Growth	
Reproductive Class	n	mean SVL (mm)	SVL	Weight
NGV year of a biennial cycle	8	834.3 ± 12.9	0.035 ± 0.005	0.96 ± 0.06
First year of a triennial cycle	12	775.8 ± 8.9	0.019 ± 0.004	0.39 ± 0.05
Second year of a triennial cycle	14	810.0 ± 8.8	0.024 ± 0.004	0.32 ± 0.03
Adult males	37	863.4 ± 19.7	0.028 ± 0.004	0.19 ± 0.03

Table 19: Relative weight loss and loss rate during the period between arrival at dens and ingress into hibernacula in the autumn. Mean ± 1 SE, (range) are presented.

Year	n	Relative weight loss	Days between captures	Loss rate % / day
1981				
Neonates	21	16.3 ± 1.7 (1.8 - 35.6)	29 ± 2 (14 - 43)	0.58 ± 0.05 (0.11 - 0.96)
Males	9	9.7 ± 2.4 (3.1 - 23.9)	26 ± 3 (11 - 39)	0.39 ± 0.09 (0.07 - 1.1)
Females	6	10.2 ± 2.4 (2.0 - 19.3)	21 ± 4 (7 - 33)	0.75 ± 0.40 (0.1 - 2.8)
1982				
Neonates	25	15.9 ± 0.8 (9.1 - 27.0)	23 ± 1 (15 - 40)	0.71 ± 0.03 (0.5 - 1.1)
Males	2	5.7 ± 0.4 (5.3 - 6.1)	16 ± 8.0 (8 - 24)	0.46 ± 0.20 (0.25 - 0.66)
Females	6	7.1 ± 2.0 (0.33 - 12.7)	12 ± 4 (1 - 29)	0.74 ± 0.30 (0.23 - 1.8)

Table 20: Percent weight lost and daily loss rate during hibernation in the winters of 1981-82 and 1982-83. Mean ± 1 SE, (range) are presented.

	1981-82			1982-83		
Age/Sex Class	n	Percent weight loss	Loss rate % / day	n	Percent weight loss	Loss rate % / day
Neonates (Both sexes)	11	7.4 ± 1.6 (1.7 - 18.5)	0.035 ± 0.007 (0.001 - 0.087)	25	12.4 ± 1.4 (-1.4 - 24.7)	0.064 ± 0.008 (-0.007 - 0.15)
Juvenile Males	38	8.1 ± 0.9 (-3.3 - 21.9)	0.039 ± 0.004 (-0.01 - 0.11)	25	5.5 ± 0.7 (0.33 - 14.2)	0.027 ± 0.003 (0.001 - 0.08)
Juvenile Females	35	6.6 ± 0.9 (-3.4 - 16.6)	0.030 ± 0.003 (-0.016 - 0.083)	32	4.6 ± 0.7 (-2.3 - 14.5)	0.021 ± 0.003 (-0.01 - 0.08)
Adult Males	31	7.4 ± 0.6 (2.8 - 19.8)	0.032 ± 0.004 (0.014 - 0.083)	75	5.0 ± 0.4 (-3.8 - 16.3)	0.023 ± 0.002 (-0.01 - 0.08)
Gravid Females	12	6.6 ± 1.1 (1.3 - 11.0)	0.031 ± 0.005 (0.006 - 0.048)	27	5.8 ± 0.6 (2.1 - 12.6)	0.029 ± 0.003 (0.01 - 0.064)
Nongravid Females	11	7.3 ± 1.6 (2.3 - 20.0)	0.037 ± 0.008 (0.01 - 0.1)	26	4.7 ± 0.7 (-2.4 - 15.9)	0.022 ± 0.004 (-0.01 - 0.082)
Postpartum Females	16	7.5 ± 0.9 (2.9 - 15.0)	0.038 ± 0.004 (0.013 - 0.07)	20	5.4 ± 1.0 (-5.7 - 16.0)	0.028 ± 0.005 (-0.03 - 0.08)

Table 21: Relative weight loss and loss rate while present at hibernacula in the spring. Juveniles and adults pooled. Mean ± 1 SE, (range) are presented.

Year	n	Relative weight loss	Days between captures	Loss rate % / day
<u>1981</u>				
Males	11	1.8 ± 1.3 (-3.8 - 8.4)	20 ± 3 (6 - 38)	0.20 ± 0.13 (-0.19 - 1.4)
Females	8	3.6 ± 1.6 (-1.5 - 11.0)	22 ± 5 (5 - 46)	0.17 ± 0.06 (-0.09 - 0.39)
<u>1982</u>				
Males	4	1.5 ± 3.0 (-7.3 - 5.1)	23 ± 7 (2 - 34)	0.60 ± 0.50 (-0.21 - 2.2)
Females	4	1.3 ± 1.2 (-0.07 - 4.8)	25 ± 7 (11 - 43)	0.06 ± 0.05 (-0.003 - 0.21)

Table 20 for rattlesnakes grouped according to age and sex (and reproductive condition in adult females). Two-way ANOVA's were performed for all orders of effects to test for differences in relative weight loss between years and among the designated qroups. Differences due to year were significant in all but one order ($F_{c(1,370)} = 2.76$, $P = 0.097$; $F_{o(1,370)} = 10.3$, $P<0.0001$). Differences among groups were significant in all orders ($F_{c(6,370)} = 7.5$, $P < 0.0001$), as was the interaction ($F_{c(6,370)} = 8.2$, $P < 0.0001$). In the winter of 1981-82 there was no significant difference in relative weight loss among the groups ($F_{(6,147)} = 0.37$, $P = 0.89$, one-way ANOVA) but relative weight loss was found to differ significantly among groups in 1982-83 ($F_{(6,223)} = 11.3$, $P < 0.0001$). Duncan's multiple range test grouped neonates as distinct from the other six groups in 1982-83. The much greater weight loss in 1982 neonates (60% > 1981) explains the significant interaction in the two-way ANOVA's. For juveniles and adults the relative weight loss in 1982-83 was about 30% higher than in the previous winter.

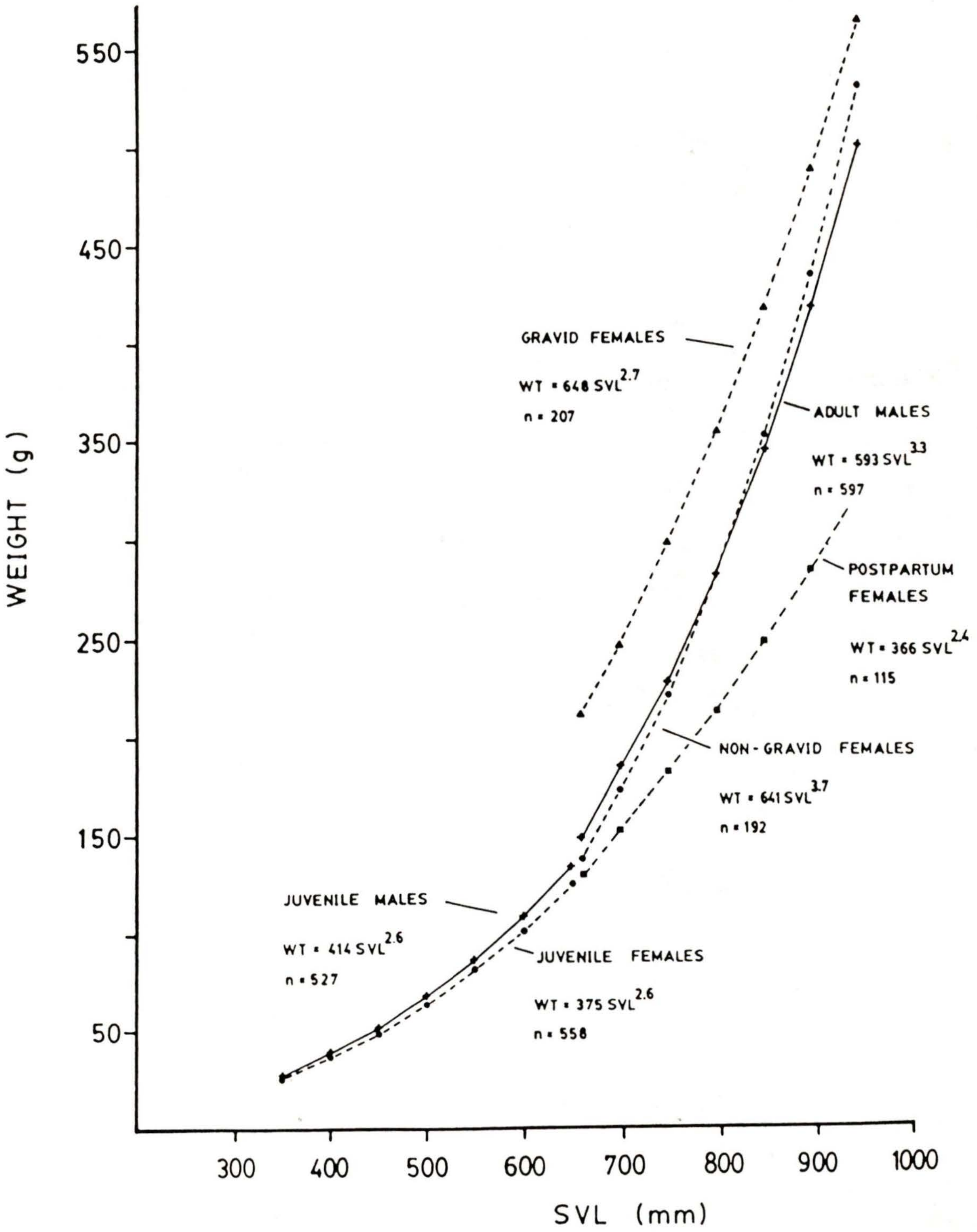
Twenty-nine snakes showed slight increases in weight during the winter. Handling frequently caused water to be expelled from the stomachs of snakes collected on rainy spring days. Weight gains were probably due to the drinking of water by snakes when they first emerged from the hibernacula.

The period spent at dens before dispersing ranged from a few days to 5 weeks. Relative weight loss during this period was more variable and generally lower than during the period spent at dens in the fall (Table 21). Small sample size and weight gains contributed to the variability. Rate of weight loss during hibernation was about 10-20 times lower than during the period spent at dens prior to or following hibernation.

3.2.9 Weight-length relationships

The equations describing the relationship between weight and length were $WT = 510\ SVL^{2.85}$ for females and for males $WT = 535\ SVL^{2.88}$ where WT = weight expressed in grams and SVL is expressed in meters. These equations are based on all capture and recapture records of individuals from all sites and in all seasons. Ninety-five percent confidence intervals placed around the linear regression of log weight on log SVL showed complete overlap, indicating no sexual dimorphism in this relationship. Klauber (1937) pointed out that the large size of adult males relative to females and the inclusion of greater or lesser numbers of snakes from different size classes in the sample will confound the examination of sex related difference in body form. As a result weight-length relationships were determined for juveniles and adults of both sexes. Among juveniles there was little overlap of 95% confidence intervals around the

Figure 21: Weight-length curves and equations for juvenile and adult *C. v. oreganus*. The gravid female category includes fall caught females with enlarged follicles as well as gravid females, while the nongravid category includes only adult females with small follicles. Units used in equations are grams (WT) and meters (SVL).


550
450
350
250
150
50
WEIGHT (g)
300
400
500
600
700
800
900
1000
SVL (mm)
GRAVID FEMALES
WT = 648 SVL^2.7
n = 207
ADULT MALES
WT = 593 SVL^3.3
n = 597
POSTPARTUM FEMALES
WT = 366 SVL^2.4
n = 115
NON-GRAVID FEMALES
WT = 641 SVL^3.7
n = 192
JUVENILE MALES
WT = 414 SVL^2.6
n = 527
JUVENILE FEMALES
WT = 375 SVL^2.6
n = 558

log-log plots, females being slightly lighter in weight for any given SVL than males (Fig. 21). Among the adult segment of the population there was complete overlap between males and nongravid females with anestrous follicles; however, at any given SVL, gravid females were heavier and postpartum females lighter than the former groups (Fig. 18). Higher values for the coefficients c and p in the equation $WT = c\ SVL^p$ indicate that gravid females have a stouter body form than other members of the population (Klauber, 1937).

Large gravid females typically weighed between 350 and 550 g. An exceptionally large female (950 mm SVL) weighed 691 g. Large adult males often weighed between 500 and 900 g; the largest male in this population was 1170 mm SVL and weighed 961 g.

3.3.0 Discussion

Ecological studies of natural populations of *Crotalus viridis* have generally included data pertaining to growth rates and/or a formal analysis of growth (Klauber, 1937; Fitch and Glading, 1947; Fitch, 1949; Heyrend and Call, 1951; Preston, 1961; Parker and Brown, 1974; Diller and Wallace; 1984; Gannon and Secoy, 1984). Analyses of rattlesnake growth have historically involved a mixture of direct and indirect methods, the former based on seasonal distributions of size classes (SVL and/or rattle size) and the latter through measurements of individual growth by mark-recapture. Klauber (1937) recognized the difficulties involved and the possibility for error when estimating age from size class groupings, especially if data are not available for different seasons, if only small samples are obtained or when little is known about the shedding frequency of different sized individuals in the population.

Most studies of growth in *C. viridis* have based their results on some mark-recapture data and provide reasonably reliable information, at least for growth rates of juveniles. These are summarized for four subspecies of *C. viridis* in Table 22. Despite individual variability in growth for juvenile rattlesnakes within each population, a trend towards slower first year growth in populations from higher latitudes is evident. Gannon and Secoy (1984), however, report yearling growth in *C. v. viridis* in Saskatchewan to be 33.7 cm, a value higher than was reported for the most southern populations of *C. viridis* (Klauber, 1937). Their estimates of juvenile growth were derived from a single size frequency histogram in which juveniles were poorly represented; consequently their interpretation is questionable (see Population Dynamics).

Rapid growth of neonates in southern California relative to those found in this study results from extended spring

Table 22: Summary of juvenile growth of four subspecies of *Crotalus viridis* from seven geographic locations. Approximate SVL and number of rattles are presented for males where specified, otherwise sexes combined.

				Age (years)			
Subspecies	Locality	Sex	Birth	1	2	3	Authority
oreganus	Vernon, British Columbia	M	270 (B)	355 (1-2+B)	430 (2-3+B)	535 (4+B)	present study
oreganus	Oliver, British Columbia	M	290 (B)	375 (2+B)	560 (5+B)	750 (8+B)	Preston, 1961
viridis	Leader, Saskatchewan	-	250 (B)	590 (?)	800 (?)	-	Gannon and Secoy, 1984
oreganus	Nez Perce and Latah Co., Idaho	M*	280 (B)	395 (1-2+B)	480 (3-4+B)	-	Diller and Wallace, 1984
lutosus	Tooele Co., Utah	M	290 (B)	450 (1+B)	550 (2-3+B)	645 (4-5+B)	Heyrend and Call, 1951 Parker and Brown, 1974
oreganus	Madera Co., California	-	280 (B)	500 (3-4+B)	630 (5+B)	720 (7+B)	Fitch, 1949 Fitch and Glading, 1947
helleri	San Diego Co., California	M	275 (B)	540 (3+B)	800 (7-8+B)	-	Klauber, 1937, 1972

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

and fall activity periods in California. Newborn *C. v. helleri* in San Diego Co. complete their initial moult 7 to 14 days after birth (Klauber, 1940) and growth during the 1-2 month period prior to the start of hibernation at the end of November was reported to be 45 mm (Klauber, 1937). Klauber believed that young may feed and shed for a second time prior to overwintering and that some growth also occurs during the 3-4 month overwintering period since B stage rattlesnakes average 350 mm upon emergence in early March. In British Columbia the early onset of hibernation and cold winters effectively inhibit growth of neonates for the first 7-8 months of life. At 6 months of age *C. v. helleri* are nearly the length of 12 month old *C. v. oreganus* in British Columbia. The disparity in size at a given age between these populations increases with age. A yearling from San Diego Co. is equivalent in size to a three year old from British Columbia and at 2 years of age attains a size that is reached at 7 or 8 years in British Columbia.

The differences are less pronounced when annual growth of juvenile *C. v. oreganus* in British Columbia are compared to conspecific populations from increasingly higher latitudes. The SVL and rattle size of snakes at 1, 2 and 3 years of age in central California (Fitch, 1949) approximate those of 3, 4 and 5 year olds in British Columbia (Table 22). The size of *C. v. lutosus* in Utah at

1, 2 and 3 years of age, are about the same size as 2, 3, and 4 years old in British Columbia. First year growth in the three northern populations of *C. v. oreganus* is not appreciably different. Preston's (1961) estimate of size at 2 years suggests more rapid growth during the second year than was found in this study or was estimated from Diller and Wallace's (1984) data. There is, however, an apparent gap in Preston's data in that his one year olds enter hibernation with either 1+B or 2+B, while the snakes he placed at the beginning of their second growing season all had 3+B. My interpretation of his data is that his snakes with 3+B were probably beginning their third growing season and that the size of 560 mm SVL attained at two years should actually correspond to the size at 3 years of age. If this interpretation is correct then there do not appear to be gross differences in juvenile growth between these closely situated populations (about 130 km apart) in British Columbia. The average size I estimated for 1 and 2 year olds from Diller and Wallace's (1984) data suggest, tentatively, faster growth for juveniles in Idaho; these values, however, are within the range of sizes attained by rapidly growing juveniles in British Columbia.

Rattlesnakes are active in southern California for about 9 1/2 months (early March to late November, Klauber, 1937) and for 7-8 months in central California (Fitch and Glading, 1947; Fitch, 1949). In both localities rattlesnakes were occasionally active above ground during the winter months. For populations in Idaho and British Columbia there is an abbreviated active season of 5-7 months (usually April to October) and hibernation is continuous. Geographic differences in growth rates therefore appear to be related in part to the length of the growing season. Yearling rattlesnakes in British Columbia have an average growth rate of 13 mm/month during the active season. In California, monthly growth was estimated to be 24 mm for yearlings (Fitch, 1949). Greater annual growth in California is the result of a higher rate of growth and a longer period for growth.

The interaction of biotic factors (e.g. the productivity of the environment, prey abundance, etc.) and abiotic factors (temperature, precipitation, etc.) will also contribute to annual and geographic variability in growth rates. Genetic differences may also account for some of the variablity in growth among populations of rattlesnakes from different localities as has been shown for *Sceloporus* lizards (Ferguson and Brockman, 1980).

In this study, growth rates were lower in 1982 than 1981. Between years there was a pronounced difference in seasonal climate but not in the actual length of the active season. In 1981 a wet spring was followed by a hot, dry summer and fall, whereas in 1982 a dry spring preceded an exceptionally wet, cool summer and fall. Winters in the Okanangan valley are typically cold and dry and considerable spring precipitation is required for the vegetation to flush early in the year. A wet spring in 1981 may have enhanced the primary productivity of the ecosystem and the favourable summer weather may have allowed snakes to forage more frequently compared to the summer of 1982. Platt (1984) found that annual differences in growth rates of *P. melanoleucus* were directly related to prey availability. Prey abundance was not monitored during this study so it is unknown if decreased growth rates were a result of lower prey abundance in 1982. It is also unclear why the growth of juvenile females was affected more than growth of juvenile males in 1982.

Heyrend and Call (1951) have shown an exponential decrease in relative growth with increasing size starting from birth in *C. v. lutosus*. Their results differ from *C. v. oreganus* in British Columbia because both relative and absolute annual growth were as high or higher during the second or third growing seasons than in the first year. Yearling rattlesnakes are faced with particular problems when it comes to securing prey. They are inexperienced foragers and probably have difficulty locating mammalian prey that are small enough to swallow. For these reasons, their annual food intake and growth rates may be very low. As juveniles grow in size and gain experience at foraging, a greater diversity of prey sizes (and species) are available for consumption. Increased foraging efficiency and relaxation of dietary size restrictions presumably enable two or three year olds to maximize food intake relative to body size and achieve higher growth rates than yearling rattlesnakes.

The growth curves derived from the Walford analyses predict a slower rate of growth than was determined by growth rates of known aged snakes. Despite the high correlation coefficient for the Walford plots, the lines are not linear for their entire length. At the lower range of SVL values the points actually take on a slightly sigmoid form, corresponding to the low absolute growth in yearlings and higher absolute growth in snakes between 400 and 500 mm SVL. Consequently the Walford equations tend to overestimate size for very young snakes and underestimate size in older snakes.

Asymptotic lengths derived from the Walford equations are very close to the maximum recorded SVL's of males and females from this population. Longevity in the natural situation may therefore approach 20 years. Maximum lengths and weights of adult *C. v. oreganus* in British Columbia are only slightly less than those of adults in California (Fitch, 1949). By comparison, adults of both sexes in Idaho are diminutive, reaching maximum SVL's of 930 and 780 mm for males and females respectively (Diller and Wallace, 1984).

Slower female growth and sexual size dimorphism is present in most species in the genus *Crotalus* (Klauber, 1972). The growth curves in this study show that the difference in SVL of males and females increases with age from about 3% at one year of age to about 16% (of the male's SVL) at asymptotic lengths. Growth is reduced or curtailed in females during reproductive years. Nongravid females appear to place more energy into growth through increased mass (for future reproduction) than increased length, when compared with males. Since litter size was found to be correlated with gravid weight and not SVL (see Reproduction), growth in terms of length after attaining sexual maturity is presumably less important to reproductive output than is growth in mass. Diller and Wallace (1984), however, found fecundity to increase with SVL of females. The weight-length curve for adult females in British Columbia predicts a relatively large increase in body mass accompanies a relatively small increase in SVL. Therefore even small increments in SVL during nongravid years may enhance fecundity in subsequent breeding years.

Rapid growth in males relative to females may be a major component of sexual size dimorphism in rattlesnakes. Where size dimorphism is strongly biased towards larger females (e.g. many species of colubrid snake), it is the females that show the most rapid juvenile growth, and where sexual size dimorphism is less apparent, so too are sex related differences in juvenile growth rates (see summary in Platt, 1984). Rapid growth of males relative to females in rattlesnakes conforms to Shine's (1978) hypothesis that larger male size (relative to female size) in snakes evolved because of the advantage large size confers on males in intrasexual competition for mates. Ritualized combat dances, apparently performed by rival males to gain access to receptive females, are common in viperids and elapids (Shine, 1978). In experimental trials larger *Vipera berus* invariably won out over smaller males in combat dances (Andrén and Nilson, 1981). Intrasexual combat was not observed in this study; however it has been been observed in most species of *Crotalus*, including *C. viridis* (Klauber, 1972). Competition among adult males for mates is likely to be intense because although adult sex ratios are about 1:1 (see Population Dynamics), adult males may outnumber sexually receptive females by a factor of three or more in any given year. Male rattlesnakes in British Columbia attain sexual maturity at a small size relative to the size at which they appear to participate in courtship and mating (see Reproduction). Selection for rapid growth in males will be favoured if by attaining a large size early in life, a male can achieve a stonger competitive advantage in intrasexual combat and thereby increase its lifetime opportunities for reproduction.

The greater rate of weight loss during fall and spring periods at the den than during hibernation are in agreement with Parker and Browns' (1980) data on *M. taeniatus*. Overwintering weight loss in adult *C. v. lutosus* showed annual variation between 4-9% and females lost slightly more than males (Hirth, 1966a, Parker and Brown, 1974). Klauber (1937) estimated winter weight loss for *C. v. viridis* in Colorado to be 4% and in Saskatchewan adult males lose between 9-14% (Gannon, 1980). These values fall within the range of relative weight loss by *C. v. oreganus* in the Okanagan; however, I found no significant differences among sex/age groups (except neonates) within years. These are in contrast to the 20% losses estimated by (Klauber, 1937) for juvenile *C. v. viridis*. Hirth (1966a) found that newborn *C. v. lutosus* average a 25.5% loss during hibernation, but some of this may have been due to inclusion of fall weight loss.

The consistent lower relative weight loss shown by juveniles and adults in the 1982-83 winter can be related to differences in winter temperatures and snowfall. Snow fell four weeks earlier, disappeared two weeks earlier and total snowfall was 30% lower in the winter of 1982-83 than 1981-82. On this basis rattlesnakes would have experienced cooler body temperatures for a greater proportion of the total overwintering period which would result in lower expenditure of energy or water reserves. The higher weight loss in neonates in 1982-83 does not negate this proposed explanation. In the fall of 1982, I focussed efforts on determining the percent weight lost between birth and the initial moult. The last fall weight was usually obtained at the completion of ecdysis which was up to 10 days prior to entry into hibernation and as such some winter loss may have included fall weight loss. In addition, because neonates weigh so little, small changes in absolute weight represent large changes in relative weight. In any case the difference in mean winter weight loss between years may have little biological significance because for adults and juveniles, at least, it represents only a small fraction of the total body weight.

Sources of energy during hibernation in reptiles are lipids, glycogen and proteins; however, their depletion during hibernation generally accounts for a smaller fraction of total weight loss than does water loss (Gregory, 1982). Fat bodies comprise similar percentages of total body mass (4-5%) in the spring and fall in male *C. v. oreganus* (Diller and Wallace, 1984) and in *Masticophis taeniatus* (Parker and Brown, 1980). Slight decreases in the fat body over the winter have been reported in *Vipera berus* (Saint Girons, 1957; Duguy, 1963). Lipids therefore appear to be used sparingly during hibernation in these species. Desiccation may be the major cause of weight loss in hibernating snakes. Water drinking on emergence suggests that dehydration occurs to some extent; however, water loss in snakes in relation to temperature and humidity levels has not been measured in artificial or natural hibernacula.

Newborn rattlesnakes delayed entry into hibernation until the completion of the first moult, during which time they incurred a 15% weight loss. A significant reduction in cutaneous water loss has been reported for newborn *C. v. viridis* after the shedding of the proto-integument (Duvall, *et al.*, 1985). Shedding prior to hibernation may be an important and perhaps necessary mechanism to prevent excessive dehydration during hibernation. Desiccation may be an important contributing factor to the high levels of overwintering mortality in neonate rattlesnakes (see Population Dynamics).

4.0 REPRODUCTION

4.1.0 Methods

Females were considered to be adults if they exeeded 650 mm SVL since this was the SVL of the smallest female found to have enlarged (vitellogenic) follicles. In each year females were assigned a reproductive status on the basis of abdominal palpation and physical appearance. Females were considered to be gravid if they possesed enlarged follicles (approximately 2 cm or greater in length) in the spring (March-June) or contained embryos in the the summer (June-September). Nongravid females possessed enlarged follicles in autumn (September-October) or lacked enlarged follicles at any time of the year. Postpartum females were readily distinguished by longitudinal skin folds, the collapsed appearance of the lower abdomen and absence of externally discernible ova. Females recaptured in at least three consecutive years enabled the reproductive schedules of adult females to be determined.

Data on the ovarian cycle, fat body weights and embryonic development were obtained through the dissections of 13 females (mostly snakes found dead or accidentally killed in transport from the field). The number, position and length of follicles or embryos in the reproductive tract were recorded. Smears of fluid extracted from the lower regions of the uteri were examined by microscopy for motile spermatozoa.

Data on litter size and weights, length and sex of neonates were collected in 1981 and 1982 by removing near-term females from the field and maintaining them in the lab at 25°C and 8:16 h (L:D) photoperiod until all young in a litter were born. In 1983, gravid females were collected in early August and housed individually in a greenhouse (25 - 33°C and natural photoperiod) until parturition.

The spermatogenic cycle of *C. v. oreganus* was determined by histological examination of the testes obtained from freshly killed specimens, or more frequently, from gonadectomized males. Males were killed with a lethal dose of chloroform and gonadectomies (Camazine *et al.*, 1981) were performed under halothane anaesthesia (Bonath, 1979). Over the three year study period testes from 18 specimens were collected; two samples were obtained for each month of the active season (April-September) and one sample from each month during the overwintering period. Winter samples were obtained from males which were collected in late October and kept in artificial hibernation (4°C; 0:24 h L:D) in a refrigerator until needed. Whole testes or portions thereof were preserved in Bouins' fixative, embedded in Tissue Prep, sectioned at 7 µm intervals and stained with eriochrome cyanin (Chapman, 1977).

The spermatogenic stages were determined using a modification of Licht's (1967) scheme. The relative abundance of spermatozoa in the lumen of seminiferous tubules and epididymes were recorded in "representative" sections. Spermatozoa were considered abundant if >20 were seen in a majority of tubules in the section(s). As an additional measure of testicular activity, crossectional diameters of 20 seminiferous tubules were measured. Larger diameters indicate a proliferation of gametogenic cells (Johnson *et al.*, 1982).

The vas deferens was usually not removed in surgery. Instead, snakes were palpated and cloacal smears were taken prior to the operation and checked by light microscopy for the presence of sperm in the distal portion of the vasa deferentia. To ascertain the size at which sexual maturity is reached in males cloacal smears were also taken on a sample of juvenile and adult size rattlesnakes during the late summer and fall. Sperm were considered to be absent if none were found after a maximum of five smears were examined.

4.2.0 Results

4.2.1 Female reproductive cycle

4.2.2 Size and age at sexual maturity

The smallest female that possessed vitellogenic follicles was 650 mm SVL and weighed 233 g. Eight females less than 700 mm SVL ($\bar{x}$SVL = 681.3 ± 5.7 mm SE, $\bar{x}$weight = 222.8 ± 7.8 g SE, mode rattle class = 7+B) contained enlarged follicles in the fall or spring samples. Ages of these females estimated from Walford equations ranged from 6.8 to 8.3 years ($\bar{x}$age = 7.6 ± 0.17 years SE). Assuming a minimum of one rattle segment added per annum, the number of intact rattles possessed by these females indicates that some females attain sexual maturity in seven years and will produce their first litter during their seventh or eighth year of life, thus confirming the estimates of age based on SVL. Some rapidly growing females (e.g. one female was 700mm SVL and had 6 rattles + B) may mature as early as six years. Recaptures of adult females which were initially captured as subadults (<650 mm SVL) provided evidence that certain females may not produce their first litter until they attain between 700 to 760 mm SVL and at probable ages of 8 or 9 years.

4.2.3 Reproductive frequency

Nongravid females consistently outnumbered gravid females in each year sampled (Table 23a). While some of the excess of nongravid probably results from some females not yet having attained sexual maturity (Table 23b), mark-recapture records of individual reproductive histories clearly indicate that females did not reproduce every year (Table 24). Nearly half of the adult females followed over the course of this study were nongravid when initially captured, became gravid the next year and were nongravid the third year. Although they followed a cycle which was at least biennial, the proportion of these females that were truly biennial or followed longer cycles could not be determined because data were lacking on their reproductive status two years after the gravid year. Elimination of these snakes left 81 snakes whose reproductive schedules were better known. Sixty females (74%) exhibited a triennial or longer cycle and 21 (26%) definitely reproduced in alternate years. Of the former category 53 were at least triennial (14 definitely so) and seven were nongravid for three consecutive years.

The occurrence of both biennial and triennial cycles in this population warranted closer inspection of the possible differences between females that followed these cycles. The mean SVL (measured when snakes were first gravid or

Table 23: a) Ratio of gravid (GV) to nongravid (NGV) females (>680 mmSVL) in each year.

Year	Number of females examined	Ratio GV:NGV (n)
1981	124	.39 : .61 (48) : (76)
1982	214	.26 : .74 (57) : (157)
1983	187	.38 : .62 (71) : (116)
Total	525	.33 : .67 (176) : (349)

b) Proportion of female gravid (all years combined) in three adult size classes.

SVL class (mm)	n	P
680-739	172	.19
740-799	220	.39
800-950	133	.43

Table 24: Reproductive schedules of 142 females followed by mark-recapture for periods of three or four years. GV = gravid, NGV = nongravid. All females except the last group were adults at the time of first capture.

		Reproductive Condition				
n		Year 1	Year 2	Year 3	Year 4	Reproductive Frequency
61		NGV	GV	NGV	-	at least biennial
21		GV	NGV	GV	NGV	biennial
39	either a)	GV	NGV	NGV	-	at least triennial
	or b)	NGV	NGV	GV	-	
14		GV	NGV	NGV	GV	triennial
7		NGV	NGV	NGV	-	at least quadrennial
34		NGV	NGV	GV	-	immature to first litter

postpartum) of females that reproduced biennially ($\bar{x}$SVL = 799 mm, SE = 10.5, n = 21) was greater than that of triennially reproducing females ($\bar{x}$SVL = 776, SE = 7.6, n = 14), but the difference was not significant ($t' = 1.77 > t'_{0.05(2)} = 2.11$, t-test for samples of unequal variance, Snedecor and Cochran, 1967)

A prominent distinction between biennial and triennial females was shown in their ability to regain body mass during the year following parturition. The mean percent increase in body weight of postpartum females that contained enlarged follicles one year after parturiton was 96.2% (n = 8, SE = 5.1%, range 63 - 125%). Postpartum females whose ovaries contained only small follicles (anestrous) the next autumn showed an average weight increase of only 39.2% (n = 12, SE = 4.6%, range 22 - 70%). The difference between weight gains by these two groups was significant ($P(t_{0.05,(2)} > 7.54) < 0.001$). Another group of females for which weight changes were measured in the second nongravid year (the year of follicular enlargement) of a triennial cycle averaged a 32.0% (n = 14, SE = 3.2%, range 16 - 43%) increase over spring weights. Triennial females appear to require two seasons to gain roughly the same proportion of body mass that biennial females can recuperate in one season (Fig. 22). Records of annual weight changes for females that were nongravid for three consecutive years were available only for five females in

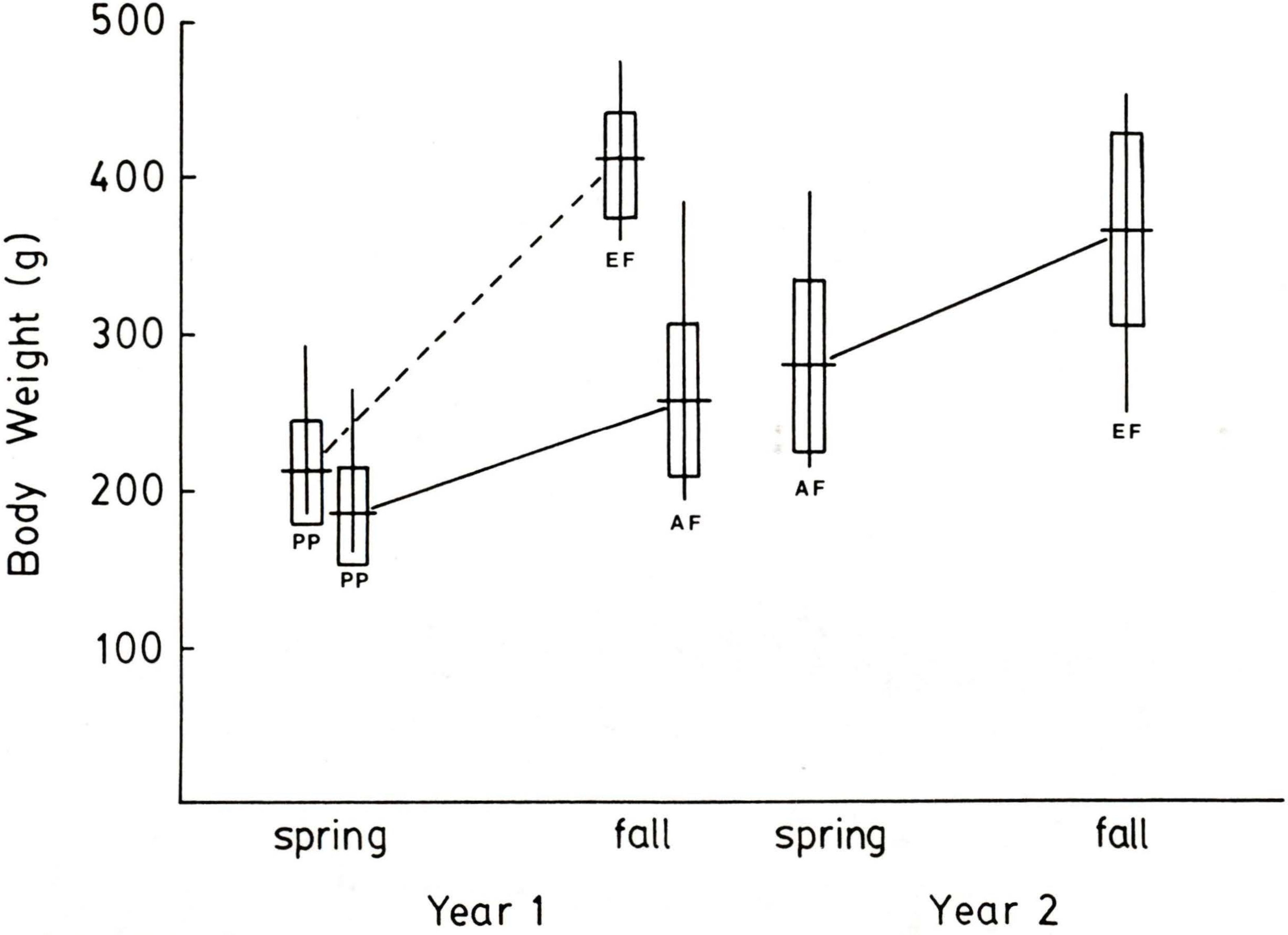
1982. The mean increase in body mass during that year was 8.7% (SE = 3.6, range -8.6 - 21.4%).

There was a positve correlation between female SVL and percent weight increase in the years following parturition when data for biennial and triennial females were pooled (r = 0.66, P = 0.004). Larger females appeared to be able to gain weight more rapidly during the summer following parturition than smaller females.

4.2.4 Ovarian cycle

Adult females examined at dens in the fall or spring belonged to one of three reproductive classes. They either lacked enlarged follicles, possessed enlarged follicles or were postpartum (=gravid in early fall samples). The ovaries of eight females necropsied either prior to or following hibernation contained two distinct follicle size classes: small white coloured follicles (< 1.6 cm in length) referred to as anestrous follicles and larger yolk-filled follicles (> 1.6 cm in length) known as estrous follicles (Dessauer and Fox, 1959; snakes 1 to 8, Table 25). The terms estrous, vitellogenic and enlarged are used interchangeably in this study. The term enlarged is used simply because follicle size was usually estimated indirectly by palpation of females in the field. Mark-recapture records revealed that females which contained enlarged follicles in the fall or spring were gravid the

Figure 22: Annual weight gains shown by female rattlesnakes during nongravid years in biennial (dashed line) and triennial (solid line) reproductive cycles. PP = postparturient females, AF = females with anestrous follicles, EF = females with enlarged (vitellogenic) follicles. Horizontal bar = mean, vertical line = range, rectangle = ± 1SD.



Body Weight (g)
500
400
300
200
100
EF
PP
PP
AF
AF
EF
spring
fall
spring
fall
Year 1
Year 2

subsequent summer.

There was considerable variation in length of vitellogenic follicles in both fall and spring females ($F_{s(6,49)}$ = 15.26, P<0.001; subgroup comparison of a two-way nested ANOVA for unequal sample size, Sokal and Rohlf, 1981); however, follicle lengths of fall females were not significantly different from spring females ($F'_{s(1,6)}$ = 2.61, P>0.25).

In five females with enlarged follicles that were examined in the fall or spring, abundant motile spermatozoa were present in the uteri (Table 25). Spermatozoa were confined to the constricted tubular region of the uterus which lies directly anterior to the vaginal pouch and were absent from all other areas of the reproductive tract.

A gravid female dissected in July contained numerous anestrous follicles within each ovary and a total of 7 embryos in early stages of development in the uteri (snake 11, Table 25). The embryos and their yolk sacs averaged 13.5 ± 1.1 g which represents a four to five fold increase in mass over enlarged follicles of females caught in the fall or spring.

Vitellogenic follicles were absent from the ovaries of two postpartum females and only incubation chambers (vascularized pouches in the uteri where embryonic development occurs, Rahn, 1942) were present (snakes 9-10, Table 25). Enlarged follicles were not detected in any postpartum female in the spring or fall. Furthermore, conspicuous follicular enlargement (at least to external palpation) was not observed in nongravid females until early fall. Another group of nongravid (and obviously not postparturient) females examined at dens in the fall or spring did not contain enlarged follicles. Females belonging to this group were not gravid the subsequent summer.

Fat bodies comprised a higher percentage of body mass in fall females with enlarged follicles than in gravid or postpartum females (Table 25). Two nongravid females dissected in June also had large fat bodies (snakes 12 and 13, Table 25). One of these females was immature (snake 12). The other nongravid female collected in June, contained only small anestrous follicles.

4.2.5 Gestation and parturition

Gestation occurs over a 4 to 5 month period between ovulation in June and birth in September or October. The average weight loss during gestation was 6.1% (n = 14, SE = 2.1, range -6.8 - 20.7). While pregnant, females were relatively sedentary and remained in close proximity to dens. Sites occupied for extended periods by gravid females are referred to as rookeries (Klauber, 1972). In

Table 25: Results of dissections of 13 female rattlesnakes. Abdominal fat body weight (FBW) is expressed as the percentage of total body weight (TBW). All weights are fresh weights.

				Enlarged Follicles		Anestrous Follicles		
Female	SVL (mm)	TBW (FBW)	Date	n mean length ± SD (cm) (mean weight ± SD (g)) Right ovary	n Left ovary	n Right ovary	n Left ovary	Sperm in uteri
1	650	233.5 (8.0%)	Apr. 5	4 3.0 ± 0.6	1 3.4	8	2	not examined
2	780*	336.2 (5.6%)	Apr. 22	5 2.6 ± 0.4	3 2.7 ± 0.0	11	2	present
3	850	379.0 (6.5%)	Apr. 22	6* 3.3 ± 0.3 (3.6 ± 0.3)	5 3.3 ± 0.1 (3.3 ± 0.7)	3	3	present
4	795	375.0 (8.8%)	Sept. 23	3 2.4 ± 0.1	4 2.3 ± 0.3	5	4	not examined
5	820	373.6 (8.3%)	Oct. 21	4 2.9 ± 0.2 (2.9 ± 1.4)	5 2.9 ± 0.4 (3.5 ± 1.3)	17	6	present
6	750	283.3 (6.5%)	Nov. 29	2 3.7 ± 0.4	3 3.3 ± 0.1	5	3	not examined
7	835	413.3 (7.5%)	Sept. 24	3 3.0 ± 0.1 (3.0 ± 0.1)	4 3.2 ± 0.1 (3.0 ± 0.4)	10	9	present
8	785	303.0 (6.4%)	Sept. 24	4 2.2 ± 0.4 (1.1 ± 0.5)	2 2.2 ± 0.4 (1.0 ± 0.6)	9	7	present
9	750**	184.0 (2.2%)	Sept.24	0	0	15	11	absent
10	880**	330.0 (4.2%)	Sept. 24	0	0	13	9	absent
11	800***	363.3 (2.3%)	July 18	3 5.1 ± 0.2 (13.4 ± 1.1)	4 5.0 ± 0.1 (13.5 ± .1.2)	14	8	absent
12	620	132.6 (7.7%)	June 20	0	0	12	8	not examined
13	780	372.0 (8.6%)	June 21	0	0	15	16	absent

* - one follicle burst prior to measurement
** - postparturient female
*** - gravid female

this study area, rookeries were usually regions on the den outcrop (<8 m from the den entrance) or medium to large size table rocks or rockpiles located <50 m from most dens. Gravid females from the same den typically aggregated at one or more of these sites during the late spring and usually remained there until parturition.

Most gravid females returned to their resident den to give birth in the fall; however, parturition was also recorded at some of the other rookeries. Birth dates of 34 litters born in captivity or in the field were recorded between September 12 and October 23 (all years combined). There was a slight peak in the birth of young during the last two weeks of September. In captivity most females had their young over a 4-24 h period and birth frequently occurred at night.

4.2.6 Litter characteristics

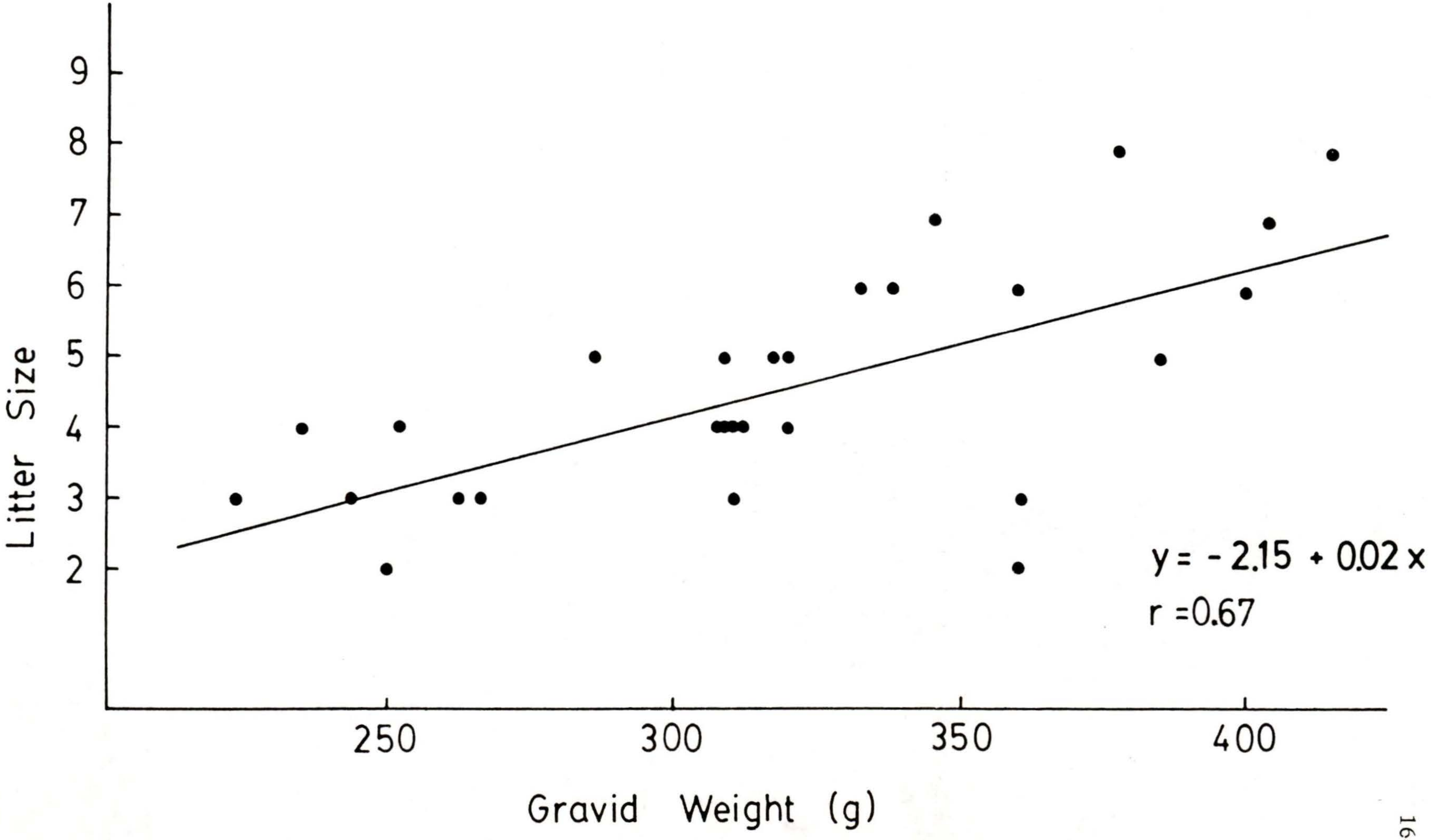
The mean litter size was 4.6 (n = 28, SE = 0.31, range 2-8). Stillborn young were included in the estimate of mean litter size when their death might have been attributable to handling of near-term females (e.g. repeated weighing, measuring and transporting from the field), however, aborted ova were not counted. Dysfunctions that resulted in embryo death and/or the occurrence of unfertilized ova were recorded in 9 litters (32%). Litter size was not correlated with female SVL (r =

0.25, P = 0.2), but it was positively correlated with female pre-birth weight (r = 0.67, P = 0.0001, Fig. 23).

The mean SVL of neonates was 267.2 mm (n = 75, SE = 1.5, range 210 - 290 mm) for females and was 269.9 mm (n = 68, SE = 1.7, range 210 - 290) for males. Mean SVL's at birth were not significantly different between sexes ($P(t>1.2) = 0.23$). The mean weight of newborn females was 17.2 g (n = 75, SE = .35, range 5.7 - 23.9 g) and was 17.9 g (n = 67, SE = .34, range 6.7 - 22.0 g) for males. The mean weights of newborn males and females also were not significantly different ($P(t>1.5) = 0.13$). The sex ratio of 28 captive born litters and 14 additional neonates collected at rookeries in the fall was 68 males:75 females. The sex ratio of 28 intact litters was determined by the method for estimation of proportions in cluster sampling (Cochran, 1963). The estimated proportion of males in the total sample was 0.496 (SE = 0.044). The secondary sex ratio in the population therefore does not deviate from 1:1.

Weight lost at parturition divided by gravid weight is used here as a measure of reproductive effort. The combined weight of viable neonates in a litter was always less than the total weight lost at birth. This was because fluids, extra-embryonic membranes, aborted ova and inviable neonates were also expelled at birth. I chose to use total weight loss through parturition in calculating reproductive

Figure 23: The relationship between litter size and female gravid weight.


Litter Size
2
3
4
5
6
7
8
9
250
300
350
400
Gravid Weight (g)
y = - 2.15 + 0.02 x
r =0.67

effort because it provides a better measure of a female's investment in reproduction than does the combined weight of viable young. The mean reproductive effort of 28 females was 0.37 (SE = 0.06, range 0.23 - 0.54). and the mean effort per individual progeny (reproductive effort/litter size) was 0.089 (SE = 0.013, range 0.053 - 0.176), or about 9% of gravid weight.

Reproductive effort was correlated with litter size ($r = 0.61$, $P<0.001$) but was not correlated with either female SVL ($r = -0.27$, $P = 0.15$) or gravid weight ($r = 0.34$, $P = 0.08$). Effort per individual progeny was negatively correlated with both litter size ($r = -0.75$, $P<0.001$) and gravid weight ($r = -0.45$, $P = 0.02$). In addition, correlations of either mean SVL or mean weights of littermates with female SVL, gravid weight, litter size, reproductive effort, or effort per individual progeny were not significant. The significance of probability values of all correlations in the matrix was verified by a multistage Bonferroni statistic (Larzelere and Mulaik, 1977).

4.2.7 Male reproductive cycle

4.2.8 Size and age at sexual maturity

Males were judged sexually mature by the presence of spermatozoa in fluid obtained from the vasa deferentia. Spermatozoa were not visible in 4 of 13 subadult males sampled (510 - 650 mm SVL). The smallest sexually mature male was 535 mm SVL and approximately three years old. That some males did not possess spermatozoa may be due to natural variability in size or age of sexual maturity, or to an artifact of the method used to assess maturity (see Methods). Cloacal smears may not always be a reliable means of detecting spermatozoa since spermatozoa were also not found in 6 of 72 larger sexually mature males (650 - 1050 mm SVL) sampled in August through October.

4.2.9 Spermatogenic cycle

The spermatogenic cycle was divided into eight stages based on the composition of cell types in the germinal epithelium of seminiferous tubules and the abundance of mature spermatozoa in the epidiymes (Table 26). The seminiferous tubules of males collected upon emergence from hibernation contained spermatogonia and some degenerating spermatocytes and spermatids. Spermatozoa were visible in the epididymis of one male collected in April but were rare or absent from the seminiferous tubules (Stage 1). By late

Table 26: Classification of the spermatogenic cycle (modified from Licht, 1967) and the phenology of spermatogenesis of *C. v. oreganus* from British Columbia.

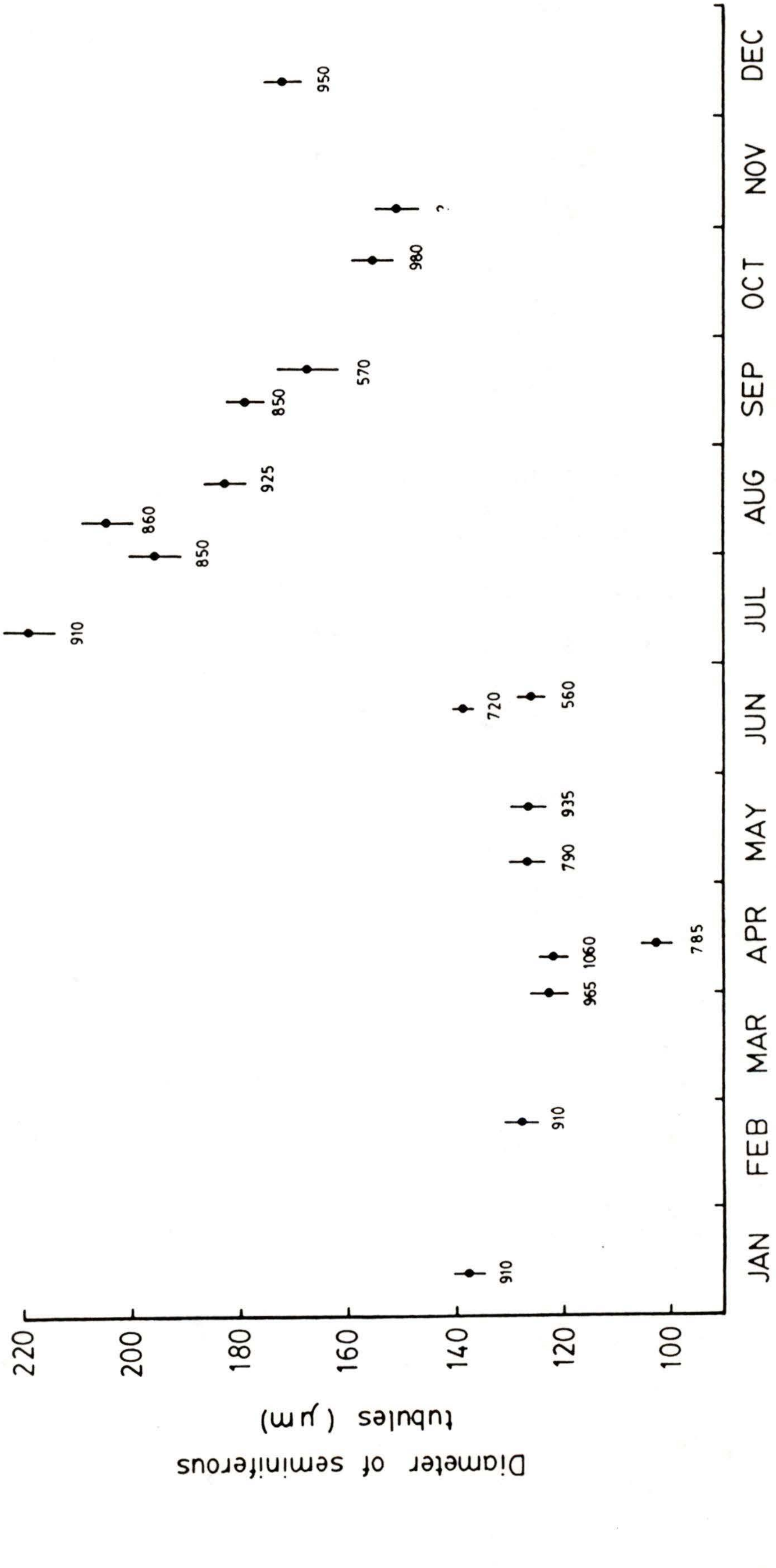
Stage	Seminiferous Tubules	Epididymes	Month
1	Involuted with mainly spermatogonia. Lumen occluded by degenerating spermatids, spermatocytes and spermatozoa.	Spermatozoa may be present.	Dec.-Apr.
2	Primary spermatocytes appearing and spermatogonia increasing.	Most empty but some spermatozoa may be present.	May
3	Primary spermatocytes dividing and some spermatids present.	Empty.	June
4	Spermatids abundant with some spermatozoa forming.	Empty.	Early July
5	Spermatids and spermatozoa abundant.	Empty.	Mid-July
6	Spermatozoa abundant (maximal level).	Spermatozoa abundant.	Late Jul.-Sept.
7	Spermatozoa abundant but spermatids and spermatocytes reduced in number.	Spermatozoa abundant.	Sept.-Nov.
8	Few germinal spermatozoa. Few spermatids and spermatocytes. Spermatozoa reduced in lumen.	Spermatozoa abundant.	Nov.-Dec.

May spermatogenesis had begun and a layer or two of primary spermatocytes were visible bordering the edge of the lumen (Stage 2). The spermatogonia of one male collected on June 18 were undergoing cell divisions but few spermatids had formed. In the same specimen some spermatozoa produced the previous year were present in the epididymis. In the tubules of a second male collected on June 21, spermatocytes and spermatids were visible; however, no spermatozoa were present in the seminiferous tubules or the epidiymis.

By early July many spermatids were present and the flagella of recently formed spermatozoa were visible projecting into the lumen of the tubules (Stage 5). Stages 4 and 5 were not distinct and the progression from one to the next was rapid as is reflected by the sudden increase in lumen diameters in July (Fig. 24). Peak sperm production occurred in late July and early August when mature sperm were abundant in seminiferous tubules and epidiymes. Stage 6 appeared to last for most of August and into September.

A reduction in the number of spermatocytes and spermatids in the germinal layer of the seminiferous tubules was observed in testes from males collected in September. Throughout the fall, spermatozoa were numerous in the epididymis but decreased in the seminiferous

Figure 24: Seasonal change in seminiferous tubule diameter in male *C. v. oreganus* ($\bar{x}$ ± 1SE, n = 20 diameters). SVL's (mm) are given below means, ? = SVL not recorded.


Diameter of seminiferous tubules (μm)
220
200
180
160
140
120
100
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
910
910
965
1060
785
790
935
720
560
910
850
860
925
850
570
980
?
950

tubules. The testis of a male dissected on November 5, one week after rattlesnakes were last seen on the surface, was almost at Stage 8. In the testes of males placed under artificial hibernation there was a progressive degeneration of the germinal layer. While spermatogonia were recognizable, the lumen of the seminiferous tubules were generally occluded by degenerating spermatocytes, spermatids and scattered germinal spermatozoa (Stage 8-Stage 1). A reduction in tubule diameter during the fall and winter reflects not only reduced spermatogenic activity but also the passage of sperm from the tubules into the epididymis and vas deferns. The vasa deferentia seem to be the major storage site for mature spermatozoa. Sperm were rare or absent from the epididymes during the spring, but were present in the vasa deferentia of males at all times of the year.

Spermatozoa were numerous in the epididymes of specimens examined in December and January, but were rare or absent from specimens examined in February and March. Motile spermatozoa found in the cloacal fluid of males dissected in January and February had a peculiar morphology. The heads of most sperm were bent back along their flagella and in many the flagellum was loosely coiled around the head.

Seasonal changes in seminiferous tubule diameters provided a corroborative index of testicular activity.

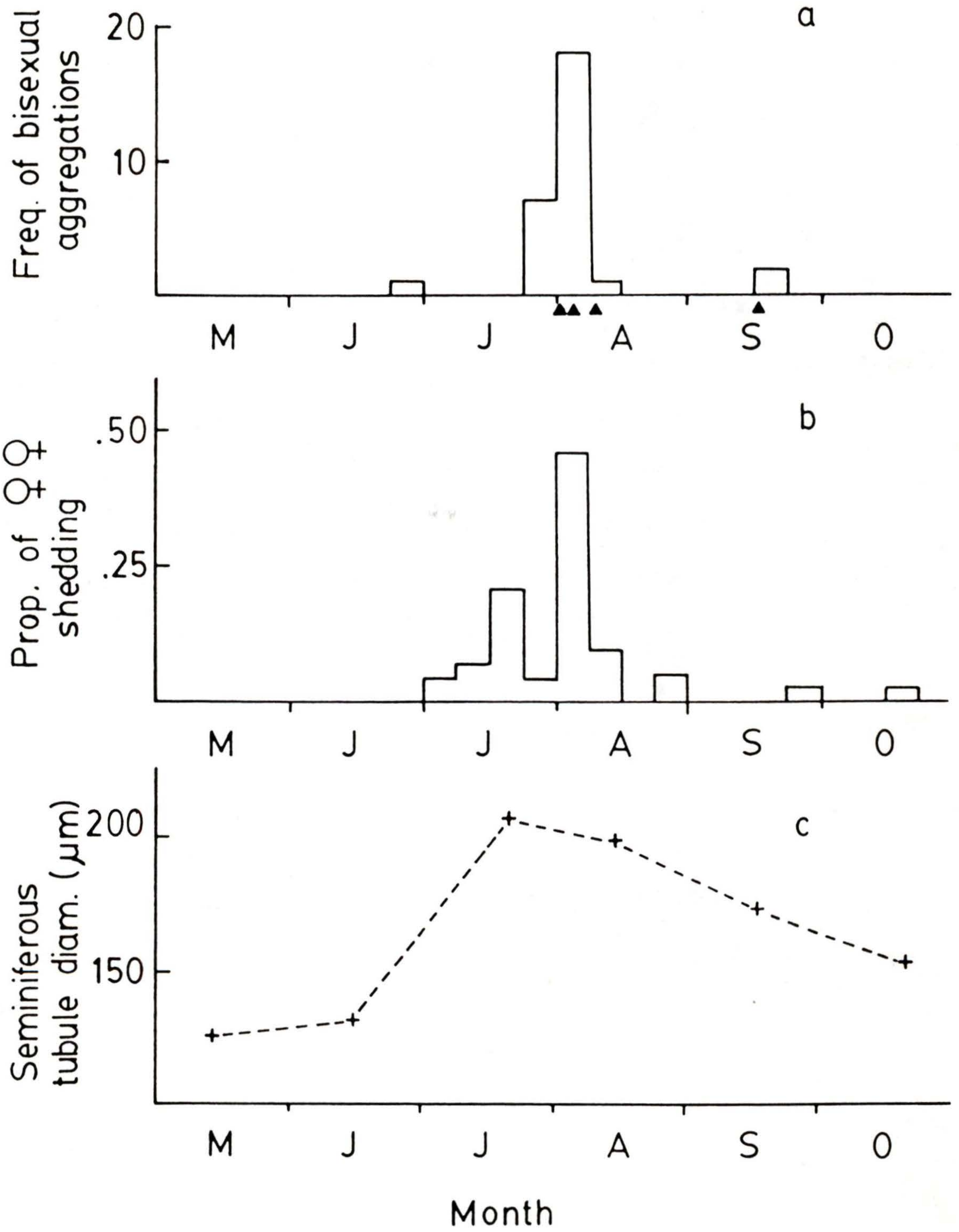
Mean tubule diameter was lowest at the time of emergence from hibernation, increased to maximum values in late summer and declined throughout the fall and winter (Fig. 24).

4.2.10 Bisexual aggregations and mating behaviour

Bisexual aggregations are defined here as groups of snakes consisting of at least one sexually mature male and one nongravid female that were located within 2 m of each other (at some shared shelter or outcrop) after spring emergence and prior to reappearance at hibernacula. The seasonal distribution of 29 bisexual aggregations pooled over 3 summers is presented in Figure 25a. Bisexual pairs or groups were most frequently encountered in late July and early August. Aggregations in which a nongravid female was undergoing or had recently completed ecdysis, comprised 21 of 26 (80%) of the observations in July and August. Shedding males were present in only three groups. Males in all other groups had shed prior to the observation judging by iridescent skin and confirmed in most cases by rattle segment gains since the last capture. Juveniles or gravid females were present in four groups.

The number of rattlesnakes involved in aggregations ranged from 2 - 8 ($\bar{x}$ = 2.8) but the majority of groups were pairs (18/29). In five groups the sex ratio in bisexual groups (>2 members) were biased towards males, towards

Figure 25: Relationship between the seasonal occurrence of bisexual aggregations, the shedding period of nongravid females and spermatogenic activity in male rattlesnakes. a) Frequency of bisexual aggregations for 1981, 1982 and 1983 combined (n = 29). Triangles = mating or courtship observed. b) The proportion of shedding nongravid females in weekly intervals during the summer. Data are pooled from observations in 1981, 1982 and 1983 (n = 42). c) Mean monthly seminiferous tubule diameters of males during the active season.


a
Freq. of bisexual aggregations
20
10
M
J
J
A
S
O
b
Prop. of ♀♀ shedding
.50
.25
M
J
J
A
S
O
c
Seminiferous tubule diam. (μm)
200
150
M
J
J
A
S
O
Month

females in three and equal in three groups. All males that were found in bisexual aggregations were at least 720 mm SVL, and most were 800 mm or greater. The number of dens represented in groups and their frequency of occurrence were: 1 den (12), 2 dens (11), 3 dens (3), 4 dens (1).

The seasonal distribution of bisexual aggregations closely overlaps the period of ecdysis of nongravid females and the peak period of spermatogenic activity in males (Fig. 25).

Copulation was witnessed in three groups and courtship behaviour was observed in another. Features common to these mating/courtship groups were: 1) that they occurred in late summer and early fall; 2) that females had usually completed ecdysis a short time prior to courtship or copulation; and 3) that enlarged follicles were absent from females at the time of mating but were usually present at emergence from hibernation the next spring (Table 27). One mating pair (group 1, Table 27) remained coupled for 105 minutes; my presence caused the interruption of copulation in two other groups (2 and 3, Table 27).

Courtship behaviours recorded in the group observed on August 3, 1983, included pressing of the chin-mental area and anterior ventral scutes along the female's head and back, alignment of the male and female bodies and cloacas, and rapid and continuous toungue flicking by the male. The

Table 27: Summary of bisexual aggregations in which courtship (CR) or copulation (CP) were observed. Shedding codes are: 1 = moist newly shed slough found at site, 2 = recently shed skin found at or near aggregation site, 3 = shed prior to formation of the group.

Group	Date D/M/Y	Time	Group Size	Behaviour observed	Members Sex, SVL, Den	Distance from den	Shedding condition	Enlarged Follicles at time of sighting	Enlarged Follicles next spring
1	09/08/81	0920	2	CP	M, 910, 16	715 m	3		
					F, 765, 11	106 m	2	absent	present
2	14/09/81	1545	2	CP	M, 950, 27	60 m	3		
					F, 890, 27	60 m	3	absent	present
3	05/08/82	1215	5		M, 810, 16	445 m	3		
					M, 890, -	-	3		
				CP	M, 845, 9	200 m	3		
					F, 715, 10	85 m	-	absent	absent
				CP	F, 849, 11	245 m	2	absent	absent
4	03/08/03	1400	5		M, 830, 17	645 m	3		
	and				M, 845, 16	1015 m	3		
	05/08/83	1430		CR	M, 990, 17	645 m	3		
				CR	M, 1020, 17	645 m	3		
				CR	F, 900,17	645 m	1	absent	present

female seldom flicked her tongue and remained relatively motionless throughout courtship except to raise her tail occasionally and expose the cloaca. Intromission was not observed after a ten minute observation period and the female was collected for weighing. The female was released at the capture site on the morning of August 5 and by mid-afternoon was again being courted, this time by the original male and a second male that was present at the site two days earlier. The original larger male aligned himself along the female's body. His position effectively prevented the smaller male from attaining close body or tail contact with the female. The trio was observed for about 20 minutes. During this time neither copulation nor male-male aggression was observed.

4.3.0 Discussion

The spermatogenic cycle of *C. v. oreganus* in British Columbia follows the aestival pattern (Saint Girons, 1982). In the aestival pattern, testicular recrudescence begins following spring emergence, spermatogenesis occurs during the summer and proceeds into the fall, and spermatozoa are stored overwinter in the epididymes or vasa deferentia. More specifically, a prenuptial aestival pattern is present because sperm production precedes the mating period. Since sperm were present in the vasa deferentia at all times of the year it is not known if sperm used in mating are those produced during the previous or current year.

An aestival spermatogenic cycle has been shown to exist in two other crotaline snakes; *C. v. viridis* (Aldridge, 1979a) and *Agkistrodon piscivorus* (Johnson *et al.*, 1982). Their cycles have phenologies similar to *C. v. oreganus* in British Columbia, but spermiogenesis begins earlier (June) in *C. v. viridis* in New Mexico. Aldridge (1975) demonstrated that temperature is the major factor responsible for initiation of testicular recrudescence and that body temperatures of 22°C or greater are required for this in *C. v. viridis*. Jacob and Painter (1980) have suggested that by basking at dens in November and December, *C. v. viridis* in New Mexico may be able to initiate the cycle prior to ingress into hibernation. A shorter autumnal active period and lower spring temperatures would explain the later onset of spermiogenesis in northern rattlesnakes.

In this study the age at sexual maturity for male *C. v. oreganus* was estimated at 3 years of age (possibly 4). This is consistent with estimates for males of other North American or European viperids (Table 28). Sexual maturity of male *C. v. oreganus* in Idaho populations is reached at SVL's between 460-520 mm and at an age of 2 or 3 years (Diller and Wallace, 1984). Males in British Columbia

Table 28: A summary of age at sexual maturity in male viperid snakes.

Species	Location	Age at sexual maturity	Authority
Crotalus v. oreganus	British Columbia	3 - 4	present study
" " "	Idaho	2 - 3	Diller and Wallace, 1984
" " "	California	2	Fitch, 1949*
Crotalus horridus	South Carolina	4	Gibbons, 1972
Agkistrodon contortrix	Kansas	2	Fitch,1960
Agkistrodon piscivorus	Florida	2	Wharton, 1966
Vipera berus	Denmark	3 - 4	Volsøe, 1944
" "	England	2 - 3	Prestt, 1971

* - see discussion for determination of age

mature at similar sizes but 1-2 years of age later than rattlesnakes in Idaho. The age at sexual maturation of males in southern populations is unknown; however, if males in central California attain sexual maturity at SVL's comparable to northern males, then a male would mature in its second year (Fitch, 1949). There is therefore a trend within this subspecies for delayed sexual maturity of males with increasing latitude.

The size distribution of male rattlesnakes present in bisexual aggregations did not include any males less than 720 mm SVL and most were considerably larger. Thus, although males mature at a small size and early age, they may not become sexually competent (i.e. participate in courtship activities) until a much greater size or age is attained.

The age at which female *C. v. oreganus* in British Columbia attain sexual maturity and produce their first litter is greater than has been reported for females of other species and subspecies of North American or European viperids (Table 28). Diller and Wallace (1984) estimated that female *C. v. oreganus* in Idaho attain sexual maturity between 4 and 6 years of age and between 580 and 600 mm SVL. In California populations, the smallest female with enlarged ova (>1.9 cm) in the spring was 737 mm SVL (Fitch, 1949) and the smallest female with developing embryos was

Table 29: A summary of the reproductive frequency and age at sexual maturity in female viperids.

Reproductive frequency codes: 1 = annual, 2 = biennial and 3 = triennial or longer cycles.

Species / subspecies	Location	Reproductive frequency	Age at sexual maturity	Authority
Crotalus v. oreganus	British Columbia	2 - 3	7 - 8	present study
" " "	Idaho	1 - 2	4 - 6	Diller and Wallace, 1984
" " "	California	1 - 2	3 - 4	Fitch, 1949*
Crotalus v. viridis	Saskatchewan	2	3	Gannon and Secoy, 1984*
" " "	Colorado	2	3	Klauber, 1972
" " "	Wyoming	2	-	Rahn, 1942
Crotalus v. lutosus	Utah	2	3 - 4	Glissmeyer, 1951
Crotalus v. helleri	California	-	2 - 3	Klauber, 1936
Crotalus atrox	Texas	2	3	Tinkle, 1962
Crotalus horridus	Wisconsin	2	4 - 5	Keenlyne, 1978
" "	Pennsylvania	2	5	Galligan and Dunson, 1979
" "	South Carolina	2	6	Gibbons, 1972
Agkistrodon contortrix	Kansas	2	3	Fitch, 1960
Agkistrodon piscivorus	Virginia	1	-	Blem, 1981
" "	Louisiana	1	-	Kofron, 1979
" "	Florida	2	3	Wharton, 1966
Sistrurus catenatus	Wisconsin	1	3	Keenlyne, 1978
" "	Pennsylvania	2	-	Reinert, 1981
Vipera berus	Finland	2	-	Vainio, 1931; Viitanen, 1967
" "	Sweden	2	-	Nilson, 1981
" "	Denmark	1	5	Volsøe, 1944
" "	England	2	3	Prestt, 1971
" "	Switzerland	2	-	Saint Girons and Kramer, 1963
Vipera aspis	France (northwest)	2 - 3	-	Saint Girons, 1957
" "	France (Pyrenees)	2	-	Saint Girons, 1972

* - see discussion for determination of age

720 mm SVL (Fitch and Glading, 1947). Fitch (1949) estimated that four years were required for a rattlesnake to reach adult length of 800 mm. Thus female *C. v. oreganus* in California are probably sexually mature in their third year.

The size at which females attain sexual maturity in British Columbia is comparable to that of California females and both are much larger than reported for Idaho. Delayed maturation in Okanagan populations (relative to California) probably results from slower annual growth due to a shorter growing season. Growth rates of rattlesnakes in Idaho are very similar to those experienced by snakes in British Columbia and the earlier maturation in Idaho females may be related to the overall smaller size of rattlesnakes in that population.

Female reproductive cycles of north temperate zone viperids have been described as either: 1) primarily annual 2) primarily biennial or 3) both biennial and triennial (Table 28). Biennial cycles appear to be the prevalent cycle in most populations and species of viperid snakes. Triennial cycles have not been documented for any crotaline genera although they were expected to occur infrequently in *A. contortrix* (Fitch, 1960) and *C. horridus* (Galligan and Dunson, 1979; Gibbons, 1972). The populations of *C. v. oreganus* in British Columbia are therefore unique among crotaline snakes in that many females follow a triennial or longer cycle.

Vainio (1931) originally postulated a biennial cycle in *V. berus* based on observations that about half of the females from his summer collections were gravid. Researchers have since considered cycles to be biennial if if the ratio of gravid to nongravid females is not different from 1:1, and presumed an annual cycle if the majority of females (say 80%) in a sample are gravid. Blem (1983) has pointed out that in many studies statistical analysis of the gravid : nongravid female ratio is questionable or lacking. Another problem, seldom acknowledged, stems from the fact that determination of reproductive status is generally made only upon dissection of females collected at various times in a single season or from such data pooled over several years. Reproductive frequency determined by this method has the disadvantage that proportions of gravid to nongravid females in a sample may more accurately reflect differences in seasonal activities or ease of capture of the two reproductive classes, than reproductive frequency. Researchers postulating a predominantly annual cycle based on a majority of gravid females present in their sample often fail to recognize (or ignore) the possibility that a biennial cycle could equally apply if the ratio of gravid to nongravid females is reversed in alternate years

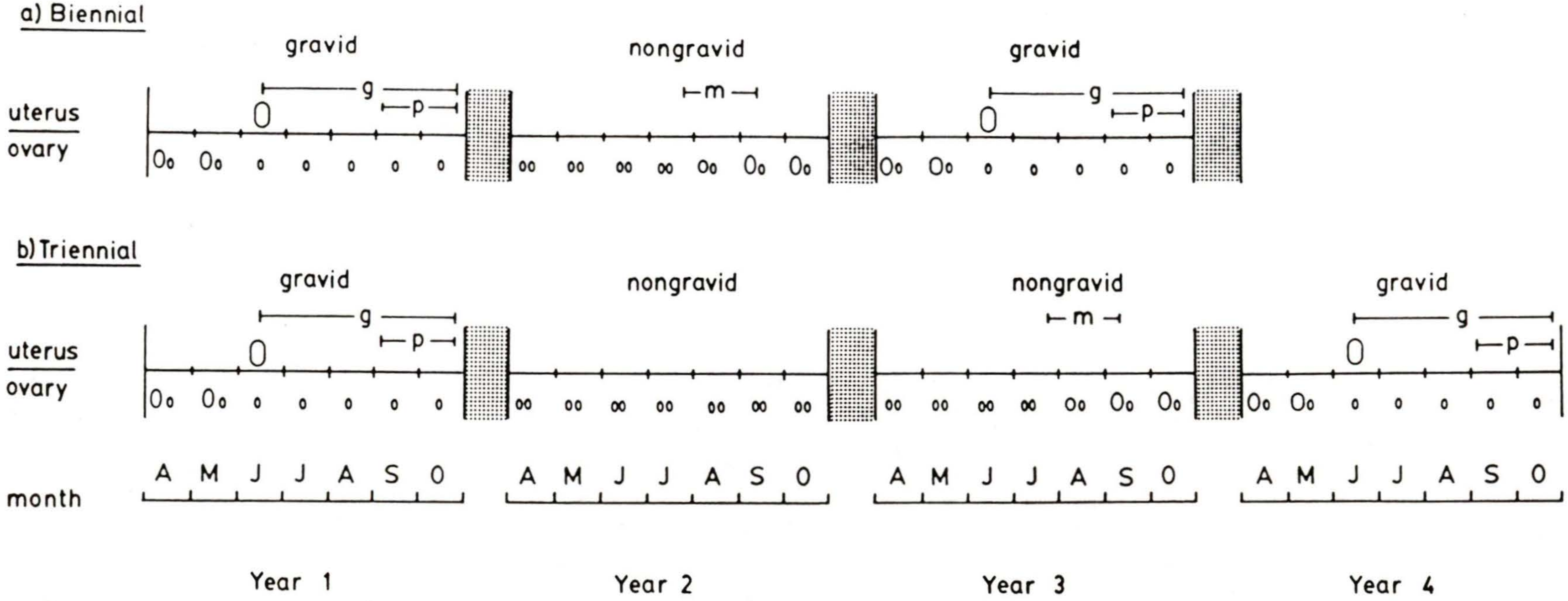
(Tinkle, 1962). Thus investigations that rely on dissection of single or pooled samples may be subject to sampling bias and ignore the dynamic nature of reproductive cycles.

The issue may be further complicated in two ways: 1) all females in a population may not follow the same cycle as was evident in this study, and 2) gravid and nongravid females might reasonably be expected to experience differential survivorship since the sedentary habits of gravid females may result in less exposure to predators (and *vice versa*). For all of the reasons just mentioned, studies which have relied on the relative proportions of gravid to nongravid females (in the absence of other data) may provide only a general indication of the frequency of reproduction or may be entirely misleading. Triennial cycles may be present in populations of other rattlesnake species but the data from previous short-term, dissection-oriented, field studies may have been insufficient to confirm their existence.

The only reliable means for ascertaining the frequency of reproduction is to determine the reproductive status of individuals over several years through studies involving mark-recapture. In only a few studies has the determination of reproductive frequency, based on the proportion of gravid to nongravid females, been corroborated by mark-recapture (e.g. Saint Girons, 1957; Fitch, 1960; Prestt, 1971; Hasegawa, 1984; Gannon and Secoy, 1984). Saint Girons (1957) found a 1:2 ratio of gravid to nongravid females in a population of *V. aspis* in which a triennial cycle prevailed. This was also the case in Okanagan populations for in each year there was about twice as many nongravid as gravid females captured. This was not the result of collecting bias since most of the sampling was conducted at dens and, at other times of the year, gravid females were much easier to locate than nongravid females.

The ovarian cycle determined for *C. v. oreganus* in this study was in nearly all respects the same as described for biennial cycles in *C. atrox* (Tinkle, 1962) and *C. v. viridis* (Rahn, 1942; Aldridge, 1979b) and for triennial cycles in *V. aspis* (Saint Girons, 1957). Patterns of follicular development in biennial and triennial reproductive cycles are illustrated in Figure 26. In females that follow a biennial cycle, the anestrous follicles present in ovaries during pregnancy undergo secondary vitellogensis (Aldridge, 1979b) toward the end of the next active season, approximately 10-12 months after parturition. Vitellogenic follicles undergo litte or no growth during the overwintering period, but receive additional yolk during the spring. Ovulation and fertilization probably occur in June judging by the level

Figure 26: Suggested patterns of follicle development in *C. v. oreganus*: a) Biennial cycle; b) Triennial cycle. Shaded boxes represent the overwintering period. g = gestation, p = parturition and m = mating period.


a) Biennial
gravid
nongravid
gravid
g
m
g
p
p
uterus
ovary
b) Triennial
gravid
nongravid
nongravid
gravid
g
m
g
p
p
uterus
ovary
A M J J A S O
A M J J A S O
A M J J A S O
A M J J A S O
month
Year 1
Year 2
Year 3
Year 4

of development achieved by embryos removed from a gravid female (snake 11, Table 23) and by the fact that enlarged follicles were still contained within the ovaries of a partially decomposed gravid female (790 mm SVL) examined in mid-May.

By comparison, in a triennial cycle, the anestrous follicles of gravid females probably remain relatively unaltered during the first nongravid (low weight gain) year and do not yolk up until the fall of the second nonreproductive year (Fig. 26). A triennial cycle in which vitellogenesis does not proceed until the end of the second nongravid year would explain the occurrence of nongravid females which lack enlarged follicles in fall or spring samples.

The amount of body mass and the rapidity with which it can be accrued by postpartum females appear to be important determinants of reproductive frequency. Females lose on average, 6% of their weight during gestation, 37% through parturition and an additional 5-7% of their postpartum weight during hibernation. Therefore, to ensure reproduction in alternate years, they must regain this lost mass and more. Females that are unable to double their postpartum weight in the next summer do not initiate vitellogenesis in that summer and do not produce a litter in the next year. Vitellogensis appears to be inhibited for even longer periods if females continue to show poor weight gains resulting in quadrennial or longer cycles. Individual variation in foraging success and year-to-year variability in prey abundance and length of time available for foraging (dictated by the weather) will determine ultimately whether a female will follow the minimum cycle (biennial) or reproduce less frequently. Body size may also affect reproductive frequency indirectly because smaller females may 1) suffer greater depletion of fat reserves in embryo production and/or 2) be less efficient foragers or unable to include larger prey in their diet and thus regain lost weight less rapidly than larger females.

Differences in the length of the growing season, whether due to latitudinal or altitudinal differences are frequently invoked to explain intraspecific variation in reproductive frequency in reptiles (e.g. Fitch, 1970; Christiansen and Moll, 1973). There are, however, a few examples from the literature on reproductive frequency in viperids of closely situated populations with different cycles (*V. aspis*, Saint Girons, 1957) and examples of northern populations in which females are believed to reproduce with greater frequency than conspecific southern populations (e.g. *A. piscivorus*, see Wharton, 1966; Blem, 1981, Table 27). Differences in the length of the active period does not seem to provide an an entirely adequate explanation in these cases. While length of the active season is certainly important, the accumlated warmth during the active season and nutritional status of individuals are also important at the local level as was suggested in this study and by others (Saint Girons, 1957; Wharton, 1966; Gregory, 1982; Diller and Wallace, 1984).

In order to compare reproductive frequency of northern versus southern populations of *C. v. oreganus* it is necessary to first review and clarify the cycles present in populations studied by Fitch and coworkers in central California. Fitch (1949) concluded that *C. v. oreganus* followed a biennial cycle based on the presence of enlarged follicles in 16 of 33 females dissected in a spring sample. Upon emergence, however, all adults had only anestrous follicles (10 - 12 mm) and follicular enlargement was not noticeable until nearly mid-June. The inconsistency of these findings with those of Rahn (1942) on the seasonal development of follicles in a biennial cycle for *C. v. viridis* was brought to light by Fitch (1970). The absence of two distinct follicle classes in early spring samples suggests that secondary vitellogenesis begins in the spring rather than late summer or early fall. I support the view that females in California may follow a potentially annual cycle in which anestrous follicles present in postpartum females in autumn do not undergo secondary vitellogenesis until the following spring (Type I vitellogenesis, Aldridge, 1979b). Although hibernation begins shortly after parturition in California (Fitch and Glading, 1947), emergence occurs in early March and females feed during the two month spring mating season (Fitch and Twining, 1946). A postpartum female may therefore be able to restore depleted fat reserves during spring feeding bouts and reproduce in successive years. Females with poor foraging success may be unable to initiate vitellogenesis in some years and reproduce biennially.

Aldridge (1979b) described a second pattern of vitellogenesis based on dissections of *C. v. viridis* in New Mexico (Type II). He alluded to a potentially annual cycle in that subspecies if females are able to initiate vitellogenesis immediately following parturition, but he was unable to provide solid evidence for this. Type II vitellogenesis is shown by both biennial and triennial females in British Columbia populations. Evidence for an annual cycle using Type II vitellogenesis was found in *C. v. oreganus* in Idaho (Diller and Wallace, 1984). They noted that some 30% of females in their spring collections contained both remnants of incubation chambers in the uteri and enlarged follicles in the ovaries, and suggested that postpartum females that had large fat reserves could undergo vitellogenesis immediately and thereby have enlarged follicles by the next spring. The predominant cycle in that population was believed to be biennial.

In British Columbia, females did not begin vitellogenesis immediately after giving birth. Fat reserves at parturition were virtually depleted and in most instances birth occurred so late in the season that females had no time to recuperate body mass by feeding prior to hibernation. In addition, most females did not feed during the gravid year, although a few were able to lessen the burden on fat reserves by feeding early in the spring of the gravid year.

Derickson (1976) has suggested that follicular development in reptiles and amphibians is related to the amount of lipids stored in the body. Numerous studies have shown that abdominal fat body weights in viperids are highest in females that are in preovulatory condition (i.e. initiating vitellogenesis). These weights diminish prior to ovulation and during gestation, and are lowest at parturition (Vainio, 1931; Tinkle, 1962; Wharton, 1966; Gibbons, 1972; Nilson, 1981; Diller and Wallace, 1984). Saint Girons (1957) found that reproductive females had fat body weights equivalent to 12% of their body mass and that females with < 10% prior to hibernation did not reproduce the following year. The fat body cycles depicted for *V. berus* in biennial or triennial cycles (Saint Girons, 1957) correspond closely to the pattern of weight change exhibited by biennially and triennially reproducing females in this study. Thus, although fat body weights were seldom measured here, the relative increase in female body mass during nonreproductive years should also reflect a relative increase in fat stores.

The importance of lipid reserves to the ovarian cycle of reptiles has been demonstrated experimentally by Hahn and Tinkle (1965) for the lizard *Uta stansburiana*. Removal of fat bodies in pre-estrous females delayed or inhibited follicular growth. Similarly, ovarectomized females did not display the rapid lipid mobilization from fat bodies (to the ovaries) that was observed in sham operated females.

In this study, vitellogenesis was only initiated if females experienced large weight gains in the summer. Mating occurs in late summer or early fall at a time when only small follicles are present in the ovaries. Since small follicles were also present in the ovaries of females that were not destined to reproduce the next year (i.e. those which exhibited only small weight gains and did not undergo vitellogenesis), there appears to be a connection between the ability to accrue body mass, female attractiveness or receptivity to mating and vitellogenesis.

The sexual attractiveness pheromone may be the lipoprotein precursor of yolk, vitellogenin, or a compound carried by it and secreted through the skin as in garter snakes (Garstka and Crews, 1981; Garstka *et al.*, 1982). In garter snakes mating is believed to stimulate the pituitary to release gonadotropins which trigger follicles to release estrogen which in turn stimulates the liver to synthesize vitellogenin (Crews and Garstka, 1982). In the subtropical garter snake *Thamnophis melanogaster*, sexual attractiveness has been induced by placing females on heavy feeding regimes (Garstka and Crews, 1982). They suggested that heavy feeding may promote binding of circulating estradiol to the liver and stimulate the production of vitellogenin without the prerequisite of estrogen release from follicles. A mechanism such a this occurring in *C. v. oreganus* could explain why only females that have had good foraging success and have rapidly gained weight become sexually attractive and are mated prior to obvious follicular enlargement.

My only gauge of follicular growth was by palpation and small increases in follicular size that may accompany the onset of secondary vitellogenesis would not have been detected using this method. Thus it is unclear whether females that gain weight rapidly become sexually attractive or receptive and, following mating, initiate vitellogenesis, or if sexual attractiveness and mating occur only after secondary vitellogenesis has started. Copulation appears to be an important prerequisite for the initiation of vitellogenesis in *T. sirtalis* (Bona-Gallo and Licht, 1983). Evidence for mating as a prerequisite for vitellogenesis in *C. v. oreganus* is sketchy. The female from one mating pair that was disrupted (group 3, Table 25) did not undergo vitellogenesis. The rapidity with which the female uncoupled from the male suggested that intromission had occurred just prior to the disruption. The length of coupling observed in another pair was 105 minutes and copulation in rattlesnakes normally lasts between 6 and 12 hours (Klauber, 1972). Sufficient stimulus for gonadotropin release by the pituitary may not have been achieved with the short copulation period of the disrupted pair.

Gabe and Saint Girons (1962) also noted that follicular enlargement in *V. aspis* coincided with fall matings but a causal relationship was not ascertained. Female *V. berus* reproduce biennially in Sweden and initiate vitellogenesis in the fall, but mating does not occur until the spring (Nilson, 1981). While mating is not required for vitellogenesis, Nilson (1981) provided evidence that mating is necessary for ovulation to occur. In that species the timing of the mating period is male dependent because spermiogenesis does not begin until after hibernation and is completed just prior to the spring mating period (Nilson, 1980).

Testosterone has been implicated in the timing and control of mating behaviour in many reptile species (see review in Weil and Aldridge, 1981). Testosterone levels in *A. piscivorus*, which has a spermatogenic cycle similar in phenology to *C. v. oreganus*, have been found to parallel spermatogenic activity and are highest during the period of maximum spermiogenesis (Johnson *et al.*, 1982). High testosterone levels accompanying the period of spermiogenesis in *C. v. oreganus* (July-August) in British Columbia may be the stimulus for summer mating.

The mating period also overlapped with the period of ecdysis in nongravid females. In three of four mating groups observed in this study, the courted or mated females had shed very recently. In addition, a high proportion of bisexual groups included females that were undergoing or had just completed ecdysis. Kubie *et al.*, (1978b) demonstrated that sexual attractiveness of estradiol-treated female garter snakes was markedly enhanced following ecdydsis. Their explanation for this effect is that vitellogenin is concentrated between the old and new skin prior to ecdysis and is present in abundance after shedding. In *V. berus* an increase in courtship activity and male-male interactions follows ecdysis (Andrén, 1982). The vomeronasal organs have been shown to play an essential role in communication between sexes during courtship in *T. sirtalis* (Kubie *et al.*, 1978a) and for the determination of sex and reproductive status during courtship and male combat dances in *V. berus* (Andrén, 1982). Male *C. v.*

viridis have been observed to trail females during the mating season (Duvall *et al.*, 1985). Shedding of nongravid female *C. v. oreganus* may therefore be an important cue to mating by signalling to males the sexual receptivity of females and by inducing sexual excitement in male snakes (e.g. Burchfield, 1982). Pheromones of integumentary origin have also been implicated in the formation of aggregations in snakes (Noble and Clausen, 1936; Heller and Halpern, 1982a, 1982b) and probably function in the formation of bisexual aggregations at shedding sites during the mating season by enabling the sexes to locate each other.

In central California, *C. v. oreganus* mate during an eight week period in early spring and females are able to complete the entire reproductive cycle (anestrous follicles to viable young) in one active season (Fitch, 1949). In British Columbia mating was only recorded in late summer and early fall. Considering the intensity with which the dens and surrounding areas were searched during the spring, it is highly probable that should spring mating be common or occur at all, it would have been observed. Males have the capacity to contribute sperm at all times of the year; however, females appear unable to complete the entire ovarian cycle in one active season. Sperm from summer matings may be stored for up to 10 months in the uteri until released for fertilization. A testable hypothesis to explain summer versus spring mating is that copulation is a required stimulus for females to initiate vitellogenesis prior to the year in which young are born.

The annual reproductive cycle shown by some females in Idaho is intreging from the standpoint of such a hypothesis. Diller and Wallace (1984) did not observe mating; however, if mating is a prerequisite for vitellogensis in *C. v. oreganus* as suggested in this study, then this would mean that females in Idaho would have to mate when they are gravid or postpartum for annual reproduction to occur. Based on the relationship between fat reserves and sexual attractiveness that I have proposed, it seems unlikely that males would be attracted to and mate with gravid or postpartum females. Experiments need to be conducted to examine the interrelationship between weight gains, ecdysis, female attractiveness, mating and vitellogenesis in order to answer some of the questions raised by this study.

The mean litter size based on counts of developing ova, oviducal eggs and fetuses for Idaho rattlesnakes was 5.5 (Diller and Wallace, 1984). Since their counts also included nonviable fetuses (12.2% of all fetuses), their actual litter size would approximate 4.8 young, which is not appreciably different from the mean litter size of 4.6 for females in this study. Mean litter size reported for females in California were 9.9 (based on egg counts including anestrous follicles, Fitch, 1949) and 7.6 (based on embryo counts, Fitch and Glading, 1947). Diller and Wallace (1984) suggested that smaller litter size in Idaho compared to California may be related to smaller overall size of rattlesnakes in Idaho. It is difficult to provide an adequate explanation for why the litter size of the larger British Columbia females is somewhat lower than for the considerably smaller adult females in Idaho. Neonates in Idaho (n = 19, $\bar{x}$SVL = 293 mm, $\bar{x}$weight = 18.1 g, Diller and Wallace, 1984) are only slightly larger than in the Okanagan. Therefore the production of many small young versus few large young does not explain differences in litter size. There is in fact little difference in the size of newborn rattlesnakes among British Columbia, Idaho or California (≅ 280 mm SVL, 20 g , Fitch, 1949) populations.

Values for mean reproductive effort are 0.5 in Idaho and 0.37 in British Columbia. Differences are probably not related to different methods used to calculate reproductive effort. Diller and Wallace (1984) used average caloric content of a clutch/average caloric content of females; the same constant for converting wet weight to calories was applied to both neonates and adults. If anything, my use of total weight loss at parturition should elevate the value of reproductive effort. Idaho females allocate a greater proportion of resources (body mass or fat reserves) to reproduction than do British Columbia females. Measures of reproductive effort are not available for California rattlesnakes. The magnitude of reproductive effort reported for *C. v. oreganus* falls within the range of values (0.137 - 0.409) known for other viperids (Seigel and Fitch, 1984).

The large size of neonates appears to be one phylogenetic constraint affecting the reproductive frequency in rattlesnake populations in British Columbia. A lengthy period for completion of the entire processes of vitellogenesis and embryonic development and a considerable amount of energy are required to produce young. The short active season lengthens the absolute period of time for development of young and reduces the amount of time available for recuperation of energy reserves necessary for future reproductive efforts. Given these phylogenetic, energetic and environmental constraints, *C. v. oreganus* should not be thought of simply as an iteroparous animal that skips opportunities for reproduction (Shine and Bull, 1979). Rather, infrequent reproduction should be viewed as an obligatory modification of a life history trait to enable existence of rattlesnake populations in cold, northern climates.

5.0 POPULATION DYNAMICS

5.1.0 Methods

The Jolly-Seber (Seber, 1982) open population mulitple sample mark-recapture model was used to estimate den population sizes by considering each fall and spring season as a sampling period. This method was used only for those dens which were intensively sampled a minimum of four periods. Obtaining sufficiently large sample sizes to yield meaningful estimates necessitated the inclusion of all members of a den population regardless of sex or age. Sex related bias in catchability of marked animals was assessed by comparing the distribuiton of recapture frequencies between males and females using all recapture records from all dens (snakes first caught in the last sampling period were not considered in this analysis). Equal catchability of marked individuals was tested using Leslie's (1958) method. Unequal catchability due to animals switching from den to den during years, was assessed by the percentage of snakes that returned to the same den each year.

The Jolly-Seber method also estimates probabilities of survivorship between sampling periods and their variances; however, because these estimates would apply to the entire population and not provide information on age-specific survivorship they were not calculated. Instead, minimum annual survivorship estimates ($\hat{S}_m$) were calculated for size classes (corresponding approximately to known age groups) of males and females for 1981 and 1982. These estimates were the proportion of animals captured in one fall that were recaptured (or known to have been alive through subsequent recaptures) in the fall of the next year and were based on recapture records of snakes from all dens that were intensively sampled in each spring and fall period.

Analysis of composition of den populations was based on size-frequency distributions obtained for each sex in each spring and fall season. Snakes first marked during the summer (June-August) were included in a den's spring population if they were collected near the den prior to the end of June, and then only if they were subsequently recaptured at the same den, thereby confirming their membership in the den population. Snakes caught at a den in the spring were also included in the population for the previous fall, even if they had not been seen during that period. Similarly, snakes that were collected at dens in the fall, not seen the following spring, but known to have been alive through subsequent recaptures, were included in a spring sample.

The densities of rattlesnakes at Sites A and B were estimated by dividing the total number of snakes marked on each site by the total area used by snakes on each site. The approximate boundaries of the total summer range were drawn on an aerial photograph and the areas determined by the dot-grid method (Avery, 1977).

5.2.0 Results

5.2.1 Population estimates

For the Jolly-Seber method to provide an accurate estimate of population size the major assumptions of equal probability of capture for marked and unmarked snakes and equal probability of survival of marked animals in the population must be met. The validity of these assumptions could not be tested directly; however, indirect assessments were made. The frequency distributions of recapture of males and females were not significantly different (Kolmogorov-Smirnov two sample test, $D = 0.08 < D_{0.05} = 0.09$, $n_1 = 498$, $n_2 = 480$), therefore, sex did not appear to influence an individual's probability of capture. Leslie's (1958) test of equal catchability of marked individuals was performed on a block of snakes (n = 23) from den 27 that were alive from spring 1981 until spring 1983. This group included about equal numbers of adults (n = 11) and juveniles (n=12) and about equal numbers of males (n = 12) and females (n = 11). It was not possible to reject the null hypothesis of equal catchability ($0.50 < P(\chi^2_{22} > 21.3) < 0.75$).

Fencing may increase the likelihood of achieving equal catchability, and since all other dens were sampled by hand collecting, Leslie's test was performed on a second block of snakes ($n = 24$) from den 11 that were alive during the same time interval. About two-thirds of these snakes were adults. However, in both age classes the sex ratios were close to 1:1. This sample was considered to be representative of the population structure of most of the larger dens. The null hypothesis also was not rejected in this unfenced population ($0.25 < P(\chi^2_{23} > 23.3) < 0.50$).

When at dens, small snakes were no more difficult to locate or capture than larger snakes because even well camouflaged, snakes invariably revealed their position by rattling. Bright dorsal markings and a habit of basking in the open made newborn snakes conspicuous to the trained eye, despite their small size and absence of sound-producing rattles.

The assumptions of equal catchability were probably little affected by individuals leaving den populations temporarily and therefore being uncatchable during their absence. Den fidelity was about 93% over all sites and years and most recorded intances of den switches were apparently permanent.

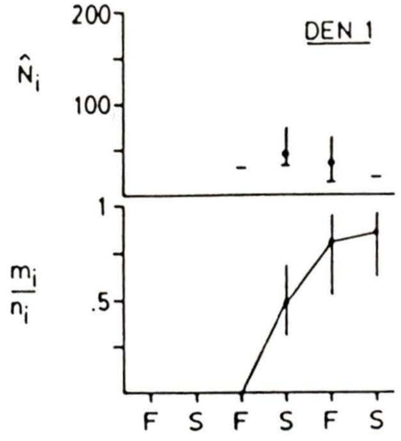
The assumption of equal probability of survival of marked snakes may have been violated because the population to be estimated included both juveniles and adults, and as shall be shown, survivorship increases with age. The mark itself should not have affected survivorship, since it is inconspicuous and did not appear to impair the snakes in any way. Seber (1982) suggested methods for testing equal probability of survival; however, he pointed out that if survival is independent of mark status and the probability of capture is independent of age (size), then Jolly-Seber estimates will not be greatly affected by age-dependent mortality.

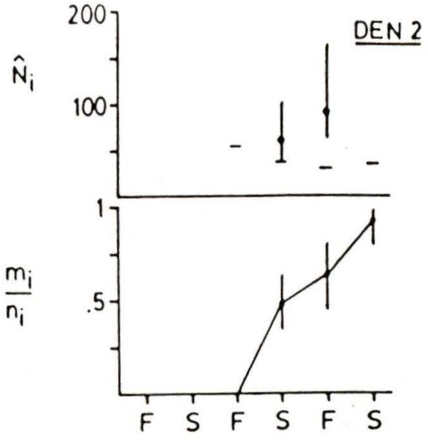
Estimates of den population size ($\hat{N}_i$) were calculated for all dens that were discovered and intensively sampled prior to and including the fall of 1981 and until the spring of 1983. $\hat{N}_i$ was also calculated for each den sampled in only three intervals (spring and fall 1982 and spring 1983); however, the level of sampling provided few recaptures and yielded largely meaningless estimates for dens 3, 14, 15, 23 and 28.

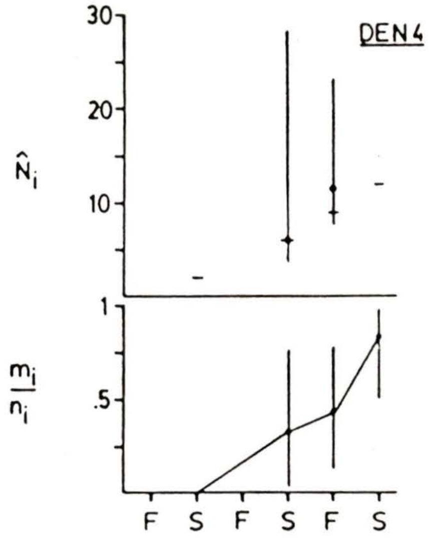
Population size estimates are displayed in Figure 27 for five dens on Site A and in Figure 28 for five dens on Site B and den 27 on Site C. Plotted below $\hat{N}_i$ in these figures are the proportion of marked individuals (m_i/n_i) in each sampling interval. The denominator in the expression m_i/n_i

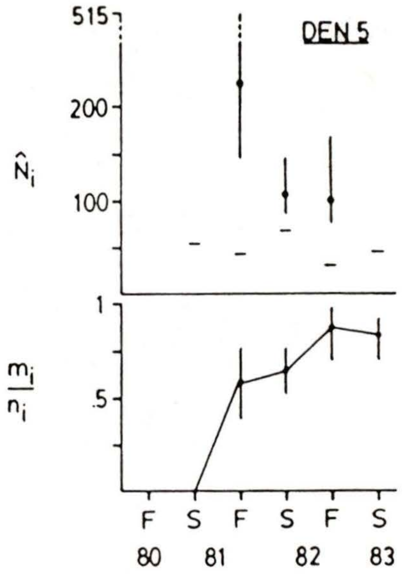
Figure 27: Population size estimates for five dens on Site A. Upper figures show Jolly-Seber estimates of population size $\hat{N}_i$ and 95% confidence intervals. Horizontal bar = number of rattlesnakes collected during a sampling interval (F=fall, S=spring).

Lower figures are the proportion of marked animals in each sample (m_i/n_i) and 95% binomial confidence intervals (Neave, 1978). In fall samples n_i does not include newborn snakes because these individuals could not have been marked in a previous interval.


DEN 1
$\hat{N}_i$
200
100
$\frac{m_i}{n_i}$
1
.5
F S F S F S


DEN 2
$\hat{N}_i$
200
100
$\frac{m_i}{n_i}$
1
.5
F S F S F S


DEN 4
$\hat{N}_i$
30
20
10
$\frac{m_i}{n_i}$
1
.5
F S F S F S


DEN 5
$\hat{N}_i$
515
200
100
$\frac{m_i}{n_i}$
1
.5
F S F S F S
80 81 82 83

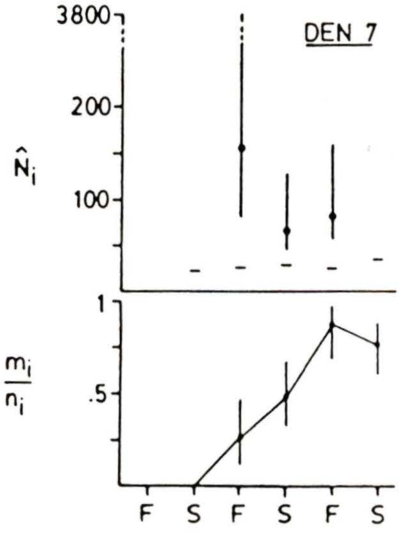
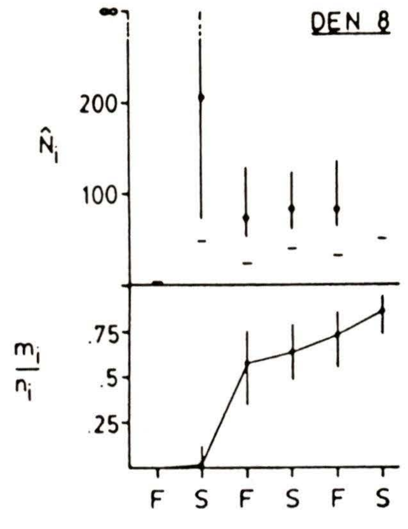
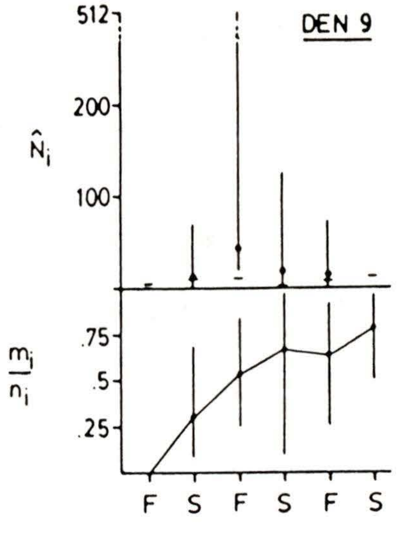
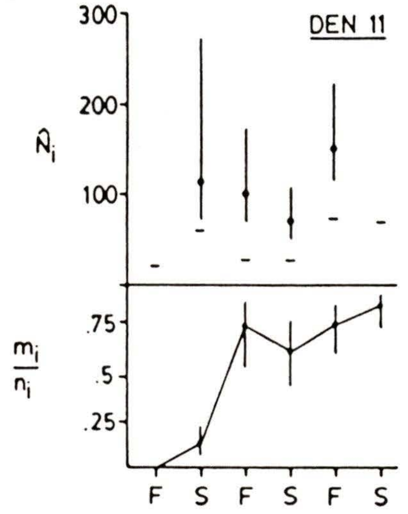
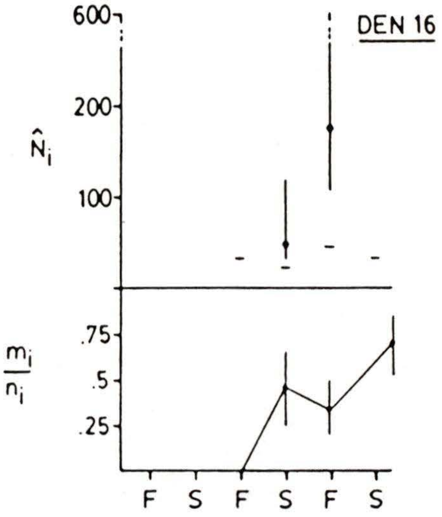

DEN 7
$\hat{N}_i$
3800
200
100
$\frac{m_i}{n_i}$
1
.5
F S F S F S

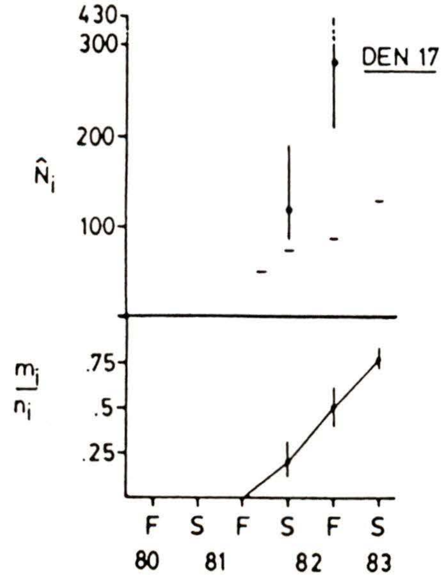
Figure 28: Population size estimates for five dens on Site B and den 27 on Site C. Explanation of figures as in Figure 27.

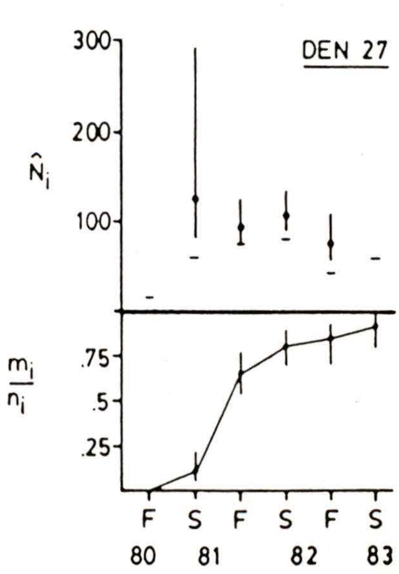

DEN 8
∞
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S


DEN 9
512
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S


DEN 11
300
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S


DEN 16
600
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S


DEN 17
430
300
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S
80 81 82 83


DEN 27
300
200
100
$\hat{N}_i$
.75
.5
.25
$\frac{m_i}{n_i}$
F S F S F S
80 81 82 83

did not include newborn snakes in fall samples since they were not available for marking in previous intervals. These were excluded to provide a better representation of the sampling intensity of the marked population in any season. The proportion of marked animals in samples at most dens increased to between .75 and .95 by the end of the study. In calculating $\hat{N}_i$, however, the newborn snakes were included in the sample (n_i). The precision of $\hat{N}_i$ is dependent on sampling intensity and sample size: as the proportion of marked animals increases and/or when n_i approaches $\hat{N}_i$, the variance about $\hat{N}_i$ decreases (Seber, 1982). For dens sampled over the maximum number of intervals (6) the estimates of the three most recent intervals were fairly consistent (dens 8, 9, 11, 27, Fig. 28). Similarly, the last two estimates for dens sampled from spring 1981 to spring 1983 were comparable (dens 5, 7, Fig. 27). Large increases in $\hat{N}_i$ and little overlap of confidence intervals between spring and fall periods shown by dens 16 and 17 (Fig. 28) reflect increases in sample size and/or lower proportion of marked snakes. The numbers of snakes using these two dens probably lie somewhere between two estimates.

There was considerable inter-den variation in population size. Using the total number of marked snakes at a den as an approximate measure of population size, the 15 dens on Site A were utilized by 8 to 133 individuals, while the seven dens on Site B contained between 12 and 226 individuals. There was no observable relationship between the size of a den population and external features of the hibernaculum (e.g. the size of the outcrop, its position on the slope, the number of entrances. etc.). Dens with few members (<40) were in some instances located in close proximity to dens with moderate to large numbers of snakes. For example, dens 23 and 24 located about 50 m above and below den 2, den 13 near den 8, and den 9 near den 11. On Site A small dens were often clustered together (e.g. dens 25 and 26, dens 21 and 22). Hibernacula with moderate to large populations (>70 snakes) were usually greater than 400 m from the nearest large denning population (e.g. dens 8, 11, 15, 16, 17, 5 and 7). Site A contained numerous dens of moderate to small size while Site B contained a few, very large dens (> 100 snakes) and a few, very small dens.

5.2.2 Population densities

On Site A, a total marked population of 836 snakes ranged over an area of approximately 524 ha, a density of about 1.6 rattlesnakes/ha. The summer range used by 659 rattlesnakes on Site B was approximately 264 ha, yielding a density of 2.5 rattlesnakes/ha. Summer movements on Sites C and D were not sufficiently documented to provide accurate estimates of density.

5.2.3 Population age/size composition

Size-frequency histograms illustrating the population composition for each fall and spring sampling period are presented in Figures 29 and 30 for selected dens on Sites A, C and D, and in Figures 31 and 32 for dens on Site B. In these figures the four smallest size classes are juveniles and the size classes starting at 650 mm SVL are adults. Temporal changes in a populations structure are difficult to interpret because the additions or losses of individuals into and from size classes due to growth into a larger size class, mortality and recruitment may be partially obscured by incomplete sampling of individuals in any given season. Immigration and emigration were rare events and therefore did not markedly affect changes in a populations structure. In most den populations, the size class distribution of adults changed little, due mainly to growth of subadults into adult size classes. Overt changes in population structure occurred mainly within the juvenile classes, and short term changes in the proportion of adults to juvenile in a population appear to be due mainly to year to year variability in recruitment. For example, at den 27 (Fig. 30), poor reproductive success in 1981 and 1982, and growth of juvenile into larger size classes, shifted the balance in this population towards adults by spring 1983. A similar shift towards a largely adult population was seen at den 11 (Fig. 31) in the fall of 1981; however, in 1982 several females were gravid and high recruitment shifted the balance again to a greater proportion of juveniles. Den 7 (Fig. 30) and den 8 (Fig. 31) showed only minor changes in population structure, apparently because of relatively constant, but low recruitment in each year.

There was no clear relationship between population size and structure. Moderate to large den populations often had a buildup of adults, e.g. dens 2, 8, 11, 17, 27. Small dens typically had few adult females and a somewhat greater proportion of juveniles than adults (e.g. dens 1, 4, 9, 26). There was considerable inter-den variability in population structure and no single size-frequency histogram which could be said to be representitive of rattlesnake populations in the Okanagan.

5.2.4 Sex ratio

In this study 851 males and 842 females were marked on all sites. The sex ratio within size classes did not differ markedly from a 1:1 ratio, except in size classes greater than the asymptotic lengths attained by females (Table 30). Among dens on all sites, the estimated proportion of males in a population was 0.50 (SE = 0.018, n = 24, cluster sampling, Cochran, 1963). The proportion of males in a den population ranged from 0.25 to 0.68. Sex ratios in juvenile classes at nearly all dens showed only minor fluctuations from equality over time. Adult males

Figure 29: Population composition for dens 1, 2, 3, and 4 on the east end of Rattlesnake Hill (Site A); males above, females below. S=spring, F=fall. For females the open rectangles = nongravid females, black rectangles = gravid females, stippled rectangles = postpartum females. Note that postpartum females that did not survive the winter (i.e. were never recaptured) are classified as postpartum (rather than gravid) in fall periods; postpartum females that survived the winter are classed as postpartum in the spring periods to distinguish them from other nongravid females.

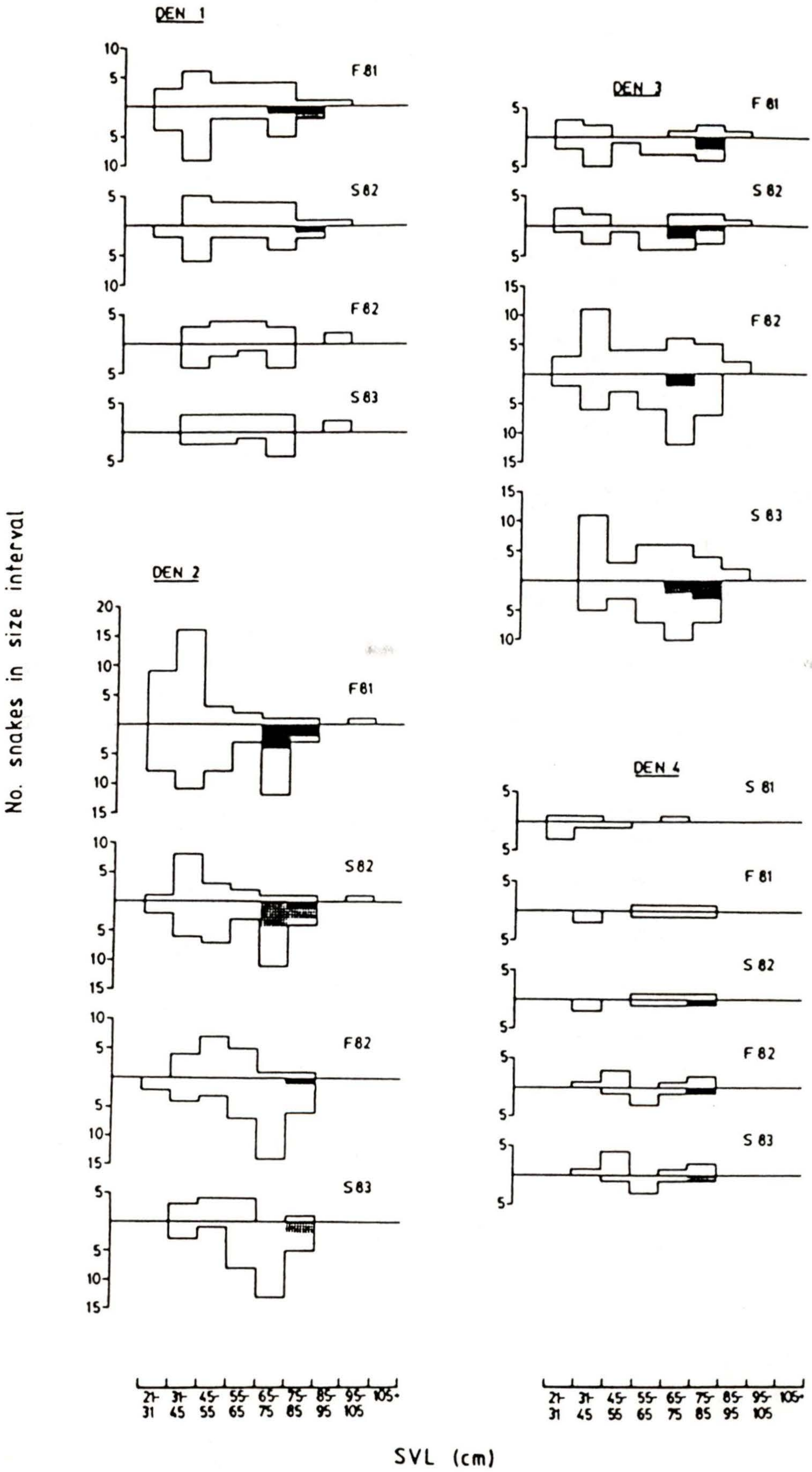

DEN 1
F 81
S 82
F 82
S 83
DEN 2
F81
S82
F82
S83
DEN 3
F 81
S 82
F 82
S 83
DEN 4
S 81
F 81
S 82
F 82
S 83
No. snakes in size interval
21- 31
31- 45
45- 55
55- 65
65- 75
75- 85
85- 95
95- 105
105+
SVL (cm)

Figure 30: Population composition for dens 7 and 26 on Site A, den 27 on Site C and den 28 on Site D. Symbols as in Figure 29.

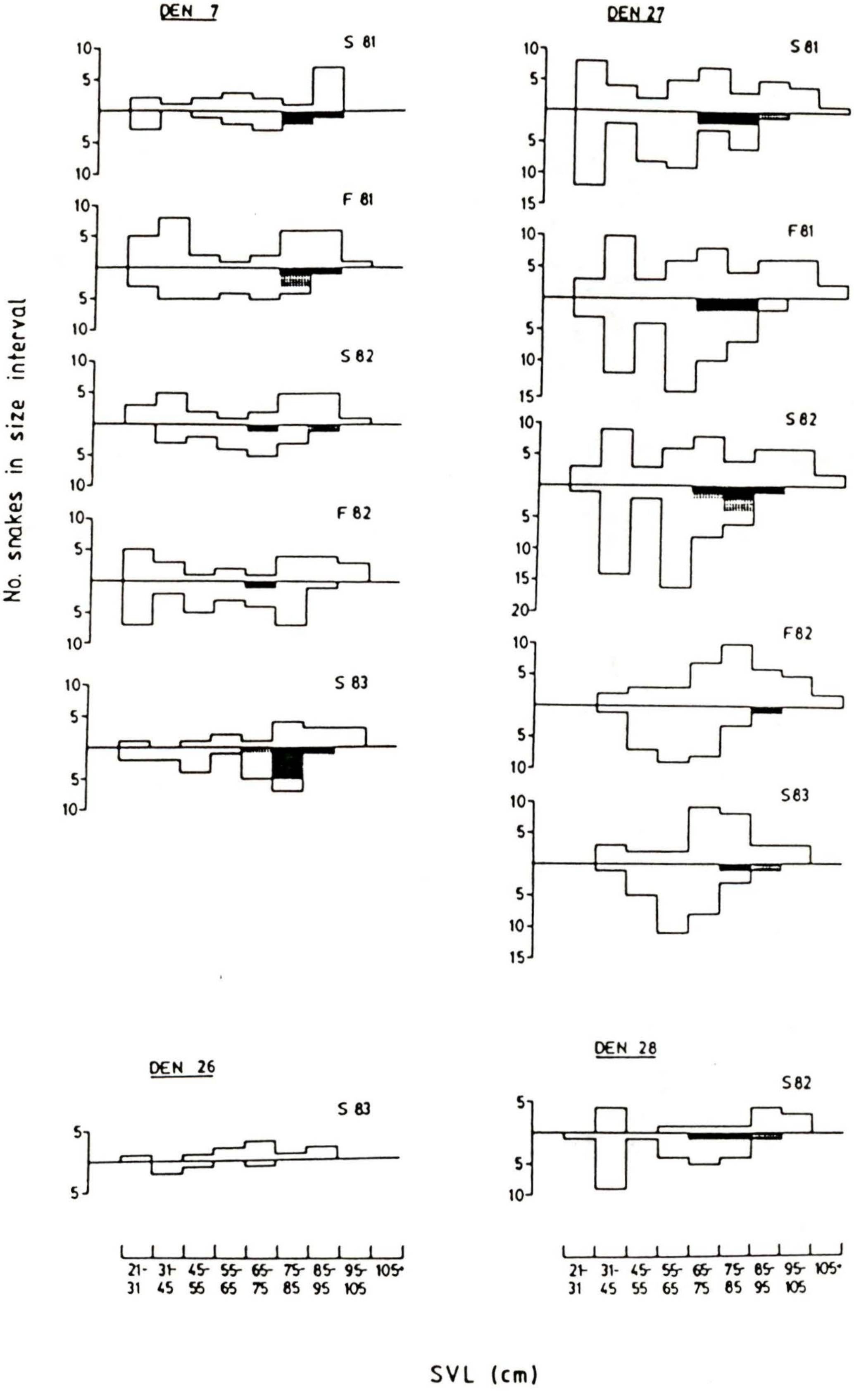

DEN 7
DEN 27
DEN 26
DEN 28
S 81
F 81
S 82
F 82
S 83
10
5
15
20
No. snakes in size interval
21- 31- 45- 55- 65- 75- 85- 95- 105+
31 45 55 65 75 85 95 105
SVL (cm)

Figure 31: Population composition for dens 8, 10, 11 and 13 on the western end of Deep Lake ridge (Site B). Symbols as in Figure 29.

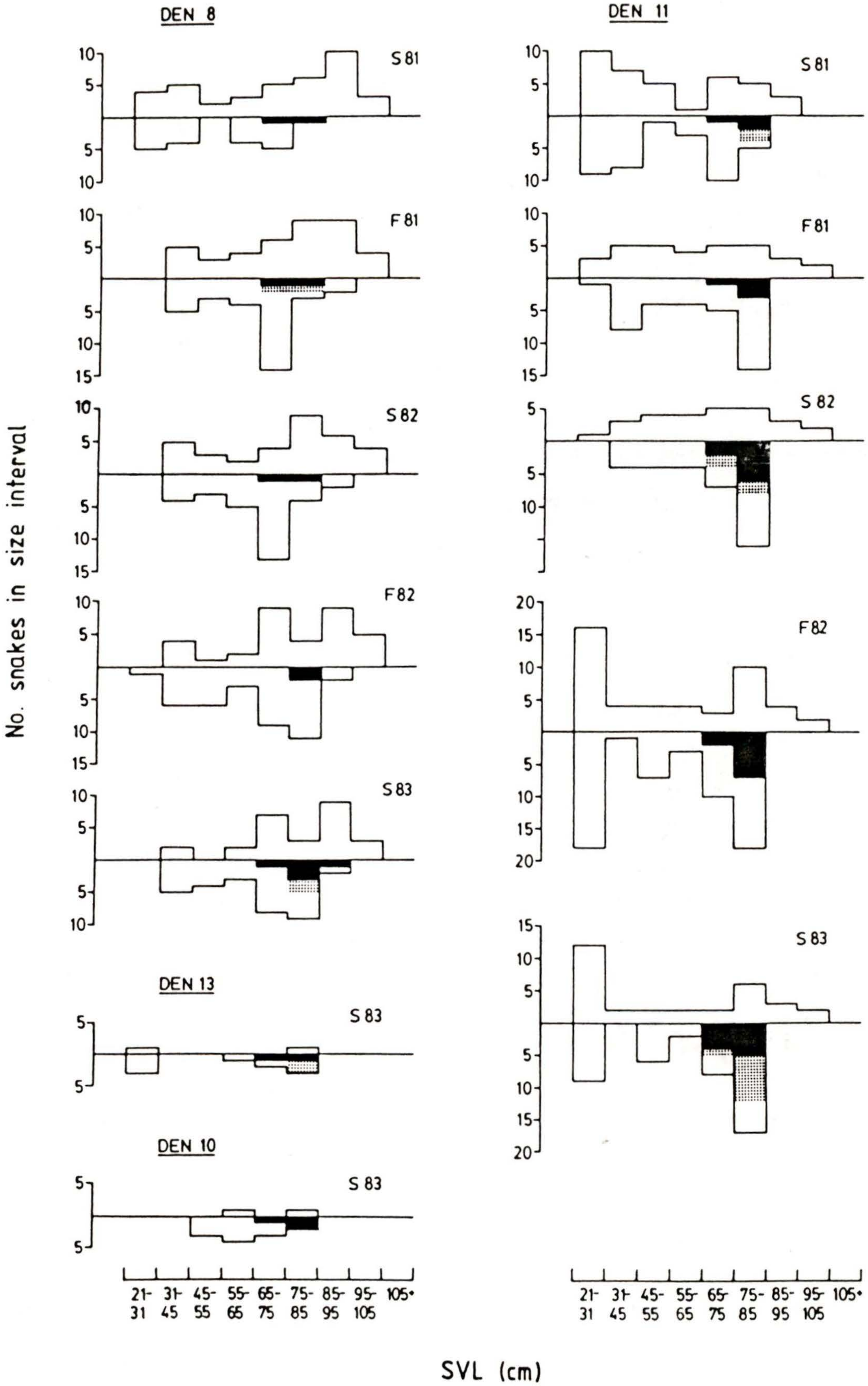
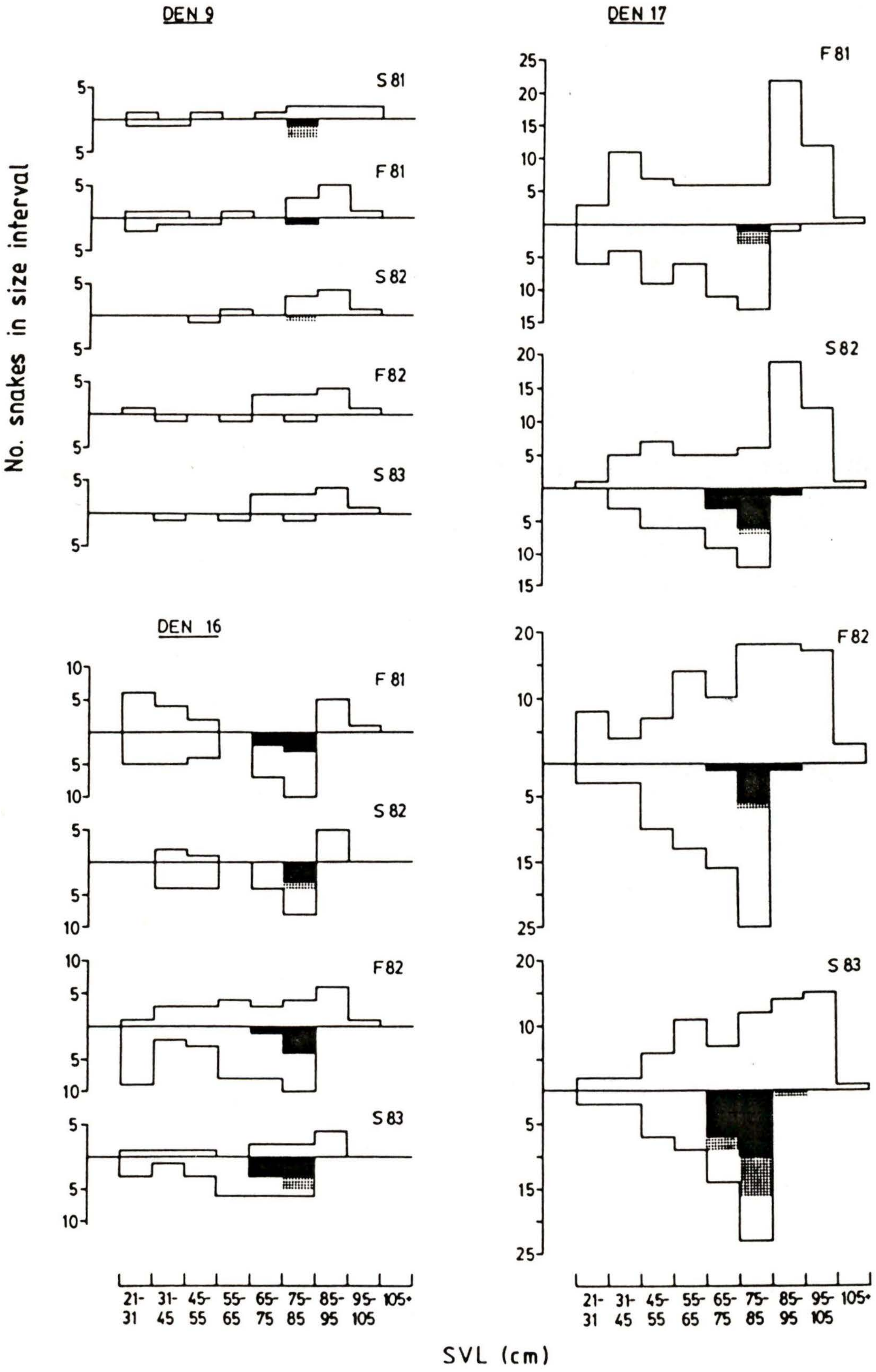

DEN 8
DEN 11
S 81
F 81
S 82
F 82
S 83
DEN 13
S 83
DEN 10
S 83
No. snakes in size interval
21-31
31-45
45-55
55-65
65-75
75-85
85-95
95-105
105+
SVL (cm)
5
10
15
20

Figure 32: Changes in population composition for dens 9, 16 and 17 on Site B. Symbols as in Figure 29.


DEN 9
S 81
F 81
S 82
F 82
S 83
DEN 16
F 81
S 82
F 82
S 83
DEN 17
F 81
S 82
F 82
S 83
No. snakes in size interval
5
10
15
20
25
21- 31
31- 45
45- 55
55- 65
65- 75
75- 85
85- 95
95- 105
105+
SVL (cm)

consistenly outnumbered adult females at dens 8, 9, 15, 17, 23, 24 and 27, while the reverse was true at dens 2, 3, 11 and 16.

5.2.5 Overwintering survivorship

The most reliable estimates of overwintering survivorship were obtained for the fenced population on Site C during the winter of 1981-82. In this population, 67 of 73 rattlesnakes (91.8%) that were alive prior to hibernation in the fall of 1981 survived the winter. In all but the yearling class (n = 1), winter survival in males was 100% (Table 31). There was some mortality in females in the subadult size classes, resulting in slightly lower average survivorship in females than males. Sample sizes were too few from this den to yield realistic estimates of neonate survival during their first hibernation. Minimum survivorship of newborn rattlesnakes from dens sampled by hand was 22.6% for males (n = 31) and 21.6% for females (n = 37) during the 1981-82 winter (data from seven dens combined). In the 1982-83 overwintering period, minimum neonate survivorship was 41.0% for males (n = 39) and 25.6% for females (n = 43, data from ten dens combined). Highest values for overwintering neonate survivorship were 60% and 50% for males (n = 10) and females (n = 8) respectively at den 5 in 1981-82, and 76.5% and 58.3% for males (n = 17) and females (n = 12)

Table 30: Sex ratios in juvenile and adult size classes of *C. v. oreganus* based on the initial SVL of all individuals marked during this study.

Size class (mm SVL)	Male	Female	Sex ratio males:females
210-310	133	149	1:1.1
315-450	147	149	1:1.0
455-550	88	101	1:1.4
555-650	96	125	1:1.3
655-750	122	171	1:1.4
755-850	105	133	1:1.3
855-950	115	14	1:0.12
955-1050	40	0	
1050 +	5	0	
Total	851	842	1.01:1

Table 31: Overwintering survivorship of *C. v. oreganus* at den 27 during the winter of 1981-82.

Size Class (mm SVL)	Male n	Male % survival	Female n	Female % survival
210-310	0	-	1	0
315-365	1	0	5	100
370-515	2	100	6	100
520-615	6	100	9	100
620-715	4	100	12	75
720-815	5	100	5	80
820-915	2	100	4	100
920-1015	7	100	-	-
1020 +	4	100	-	-
Total	31	96.8	42	85.7

respectively at den 11 in 1982-83. In 4 of 7 dens in 1981 and 5 of 10 dens in 1982, overwintering mortality of neonate rattlesnakes was estimated to be 100% (i.e. none were ever recaptured).

5.2.6 Annual survivorship

Estimates of annual survivorship ($\hat{S}_m$) for 1981 and 1982 are presented for males in Table 32 and for females in Table 33. These estimates are considered to be minimum values because of the possibilty of missing animals that were alive in a given sampling period. In 1981, $\hat{S}_m$ was based primarily on recaptures of animals first marked in the spring of 1981 (only 49 rattlesnakes were marked at four dens in the fall of 1980). Therefore, estimates may be upwardly biased because the inclusion of mainly spring collected animals ignores possible mortality during the winter of 1980-81. This bias, however, is probably small because average winter survivorship was greater than 95% in most size classes. Survivorship estimates for 1982 were expected to be lower than in 1981 for 2 reasons: 1) winter mortality is incorporated in the 1982 $\hat{S}_m$ and 2) live snakes missed in the fall of 1981 could be recaptured during 1982 and spring 1983; however, snakes alive but not captured in the fall of 1982 could only be recaptured in spring 1983, the last sampling period during this study. As a result a better estimate of minimum annual survivorship probably

Table 32: Minimum annual survivorship ($\hat{S}m$) of male *C. v. oreganus* in 1981 and 1982. Chi-square with Yates correction = 3.814, values greater than this indicate a significant between year difference in survivorship for individuals in the same size class. NC = number captured at the beginning of the season, NR = number recaptured.

	1981			1982				
Size Class	NC	NR	$\hat{S}m$	NC	NR	$\hat{S}m$	Chi-square	$\hat{S}m$ Pooled
210 - 310	38	9	0.24	40	7	0.18	0.27	0.20
315 - 365	15	10	0.67	50	19	0.38	2.76	0.45
370 - 515	21	18	0.86	56	34	0.61	3.28	0.68
520 - 615	14	12	0.86	40	29	0.73	0.40	0.76
620 - 715	32	23	0.72	39	26	0.67	0.04	0.69
720 - 765	11	11	1.00	33	27	0.82	1.00	0.84
770 - 815	12	10	0.83	23	20	0.87	0.05	0.85
820 - 865	14	9	0.64	20	15	0.75	0.08	0.71
870 - 915	18	18	1.00	28	24	0.86	1.30	0.91
920 - 965	20	19	0.95	32	28	0.88	0.17	0.90
970 - 1015	7	7	1.00	14	12	0.86	0.07	0.90
> 1020	3	3	1.00	10	7	0.70	0.09	0.77
Total	205	159	0.77	385	248	0.64		0.69

Table 33: Minimum annual survivorship ($\hat{S}m$) of female *C. v. oreganus* in 1981 and 1982. Chi-square with Yates correction = 3.814, values greater than this indicate a significant between year difference in survivorship for individuals in the same size class. NC = number captured at beginning of the season, NR = number recaptured.

	1981			1982				
Size Class	NC	NR	$\hat{S}m$	NC	NR	$\hat{S}m$	Chi-square	$\hat{S}m$ Pooled
210 - 310	48	22	0.46	32	2	0.06	14.3	0.30
315 - 365	9	3	0.33	52	21	0.40	0.001	0.39
370 - 515	14	12	0.86	52	23	0.44	6.05	0.53
520 - 615	22	21	0.95	43	29	0.67	4.95	0.77
620 - 715	20	17	0.85	56	47	0.84	0.06	0.84
720 - 765 GV	13	12	0.92	14	13	0.92	0.46	0.93
" - " NGV	15	9	0.60	46	35	0.76	0.76	0.72
770 - 815 GV	7	7	1.00	14	12	0.85	0.07	0.90
" - " NGV	7	5	0.71	39	30	0.77	0.03	0.76
> 820 GV	5	4	0.80	7	6	0.85	0.27	0.83
" NGV	3	3	1.00	16	9	0.56	0.62	0.63
Total	163	115	0.70	371	227	0.61		0.64

lies somewhere between the 1981 and 1982 estimates.

There were no significant differences between the 1981 and 1982 estimates of $\hat{S}_m$ within any size class of males; however, survivorship was slightly lower in all but two size classes in 1982 (Table 32). Pooled survivorship was lowest in the young of the year and increased with size and averaged about 84% for adult males (>720 mm).

Significant differences in $\hat{S}_m$ were found in three juvenile female size classes, survivorship being lower in 1982 (Table 33). As in males, pooled survivorship increases with increasing size in females. Survivorship of adult females averaged slightly lower than for adult males.

Nongravid females (postpartum or with no enlarged follicles in the fall) were treated separately from gravid females (enlarged follicles in the fall) in calculating $\hat{S}_m$. In all but the largest female size class in 1981, gravid females experienced higher survival than nongravid females. There were no significant between year differences in survivorship for either reproductive class in any of the size classes (Table 33). The size classes were homogeneous with respect to the survivorship of gravid and nongravid females (1981-1982 data pooled, heterogeneity chi-square, $0.95 < P(\chi^2_2 > 0.51) < 0.975$). The null hypothesis of survival independent of reproductive condition was rejected using data pooled across size classes ($P(\chi^2_2 > 6.47) <$

Table 34: Age-specific survivorship and fecundity of female *C. v. oreganus*. l_x = survivorship to age x, m_x = number of female young born by a female of age x. See text for assumptions.

Size Class (mm SVL)	x (years)	$\hat{S}_m$	l_x	m_x	$l_x m_x$
210 - 310	0	.46	1.00	0	
315 - 365	1	.39	.460	0	
370 - 515	2	.86	.179	0	
" "	3	.86	.155	0	
520 - 615	4	.95	.133	0	
" "	5	.95	.126	0	
620 - 715	6	.84	.120	0	
" "	7	.84	.100	2.0	.200
720 +	8	.78	.084	0	0
	9	.78	.066	0	0
	10	.78	.051	2.5	.128
	11	.78	.040	0	0
	12	.78	.031	0	0
	13	.78	.024	3.0	.072
	14	.78	.019	0	0
	15	.78	.015	3.0	.045
	16	.78	.012	0	0
	17	.78	.009	3.0	.027
	18	.78	.007	0	0
	19	.78	.005	3.0	.015
	20	.78	.004	0	0
	21	.78	.003	3.0	.009

$R_o = \Sigma\, l_x m_x = .496$

0.01).

This relationship was examined in finer detail. Postpartum females (n = 41) experienced 73% overwintering survivorship while 98% of females (nonparturient females with small or enlarged follicles, n = 52) survived the winter of 1981-82. Survivorship for the 1981 and 1982 active seasons combined was 78.4% for postpartum females (n = 37), 91.8% for females with small follicles (n = 72) and 89.7% for gravid females (n = 53). Adult females therefore experience the highest mortality during the hibernating period and summer immediately following parturition.

5.2.7 Life table

A reproductive life table for female *C. v. oreganus* was constructed based on age-specific survivorship corresponding to minimum annual survivorship estimates for size classes as follows: first year = 210-310 mm, second year = 315-365 mm, third and fourth years = 370-515 mm, and fifth and sixth years = 520-615 mm SVL (see Table 31). Juvenile survivorship was based on pooled $\hat{S}_m$ unless significant between year differences were found in which case the highest $\hat{S}_m$ was used. For adult females, $\hat{S}_m$ of 0.78 was obtained from data pooled across years and size classes.

Additional parameters were : 1) a 1:1 sex ratio at birth, 2) first litter at 7 years of age, 3) reproduction on a triennial basis following the first two litters and biennial thereafter, and 4) litter size of 4 at first reproduction, 5 at the second and 6 thereafter. The resulting life table gives a total net reproductive rate (R_O) of 0.496, indicating a population in decline (Table 34).

5.3.0 Discussion

Denning populations of *C. v. oreganus* in the Okanagan vary emormously in size and composition; however, within a single den, population size and composition were relatively stable during the short time frame of this study. Compositional changes occurred mainly within the juvenile segment of the population through annual variability in recruitment, combined with the diluting effects of low yearling survivorship, rapid juvenile growth and to a lesser extent emigration. Adults represent a stable element, largely because annual survivorship and den fidelity are high and growth rates low. A build up of adults and strong representation in most juvenile size classes were characteristic of most of the larger dens. Smaller dens had few adults and often a greater proportion of juveniles than adults. Recruitment at a few dens was relatively constant between years while in other dens the reproductive cycles of adult females apparently achieved some synchrony which resulted in recruitment occuring in pulses.

Skewed adult sex ratios in den populations are probably of little demographic consequence since females have access to and breed with males from neighbouring dens. The absolute number of adult females is of greater importance in terms of long term maintenance of a constant population size (compare population size and recruitment of dens 2 (many adult females, few adult males) and den 9 (few adult females, many adult males). Since emigration from other dens is rare and recruitment comes only from females within the den population, dens with few adult females are unable to exhibit the same level of population growth as are larger dens.

The sex ratio of *C. v. oreganus* remains roughly equal throughout life and this is apparently typical in most species of snakes (Turner, 1977). The slight excess of females in most size classes (Table 30) is probably due to the fact that females do not grow as rapidly or to as large a size as males. Skewed sex ratios in favour of males have been noted previously for rattlesnakes (Fitch, 1949; Woodbury and Hansen, 1950; Julian, 1951; Klauber, 1936, 1972; Galligan and Dunson, 1979) but Turner (1977) suggested these results are largely due to collecting biases. Diller and Wallace (1984) also recognized a bias but towards females; in their unbiased collections of *C. v. oreganus* in Idaho the sex ratio did not differ from 1:1. Klauber (1936) and Julian (1951) reported higher proportions of adult males than adult females, which they believed was due to higher mortality among females. In the Okanagan population, the excess of adult males (about 18% more than adult females) and higher minimum survivorship in adult males supports such an inference.

Inter-den variability in size and structure have not been reported for rattlesnake populations since most investigators have focussed on a single den. One of the major differences between the composition of rattlesnake populations in the Okanagan and those studied elsewhere is that juveniles are well represented in most denning populations. The among den variability in population structure documented here is also of interest because it illustrates how erroneous it may be to infer growth rates on the basis of apparently discrete size classes from a single size frequency histogram of a single population (e.g. Gannon and Secoy, 1984). Given relatively constant age-specific growth rates, a lack of individuals of a given size class (particularily juveniles) may indicate that recruitment was low in (a) previous year(s), not that snakes grow so rapidly as to pass completely through a vacant size class. Size frequency distributions have been used successfully for estimating growth rates in snakes but only when they are based on large samples and are compared on a seasonal basis (e.g. Voris and Jayne, 1979) and/or in conjunction with other indicators of age (e.g. rattle numbers, Fitch, 1949; Klauber, 1937).

Survivorship in snakes has been estimated using mark-recapture models (Gregory, 1977) but more commonly it has been based on disappearance rates among marked snakes (Hirth, 1966a; Prestt, 1971; Parker and Brown, 1973, 1974, 1980). Hirth (1966a) reported overwinter survivorship of 75% for adults (n = 16), 50% for juveniles (n = 8) and 64% for neonates (n = 11) for a population of *C. v. lutosus* in Utah. Parker and Brown's (1974) estimate for winter survivorship of adults at the same den was 96.4%. Similar high overwintering survival rates were recorded for both juveniles and adult *C. v. oreganus* in this study. For neonates, values as high as reported by Hirth (1966a) were found at some dens, but in general, neonate mortality was high during hibernation. Overwintering mortality has been considered as the major source of mortality in neonates of other rattlesnake species (Fitch, 1949; Galligan and Dunson, 1979; Gannon and Secoy, 1984). Other potential causes of mortality (e.g. starvation, predation) have been mentioned in previous chapters and further studies are needed to elucidate the relative contributions of each factor during the critical first year of a rattlesnake's life.

Parker and Brown's (1974) estimate of annual survivorship in adult C. v. *lutosus* of 85.4% (recalculated by Turner (1977) to be 82.6%) agrees with estimates obtained in this study. Near total depletion of fat reserves during gestation, leading to starvation in some females, may account for the 6-10% higher level of winter mortality for postpartum females in this study. Lower summer survivorship of postpartum versus non-postpartum females (gravid females and females in the second year of a triennial cycle) may also reflect differences in activity patterns which expose females in the former group to a higher risk of predation. Nonfeeding gravid females are relatively sedentary and remain under cover or rely on crypsis to avoid predation. Postpartum females presumably make more extensive summer movements in search of prey than other nongravid females and therefore may be more conspicuous to predators.

In his review of population dynamics of reptiles, Turner (1977) critically examined and reanalyzed much of the demographic data pertaining to snakes. He dismissed the data presented in virtually all of the early studies as inadequate for the purposes of demography, mainly on the basis of procedural problems (inefficient sampling and faulty data analysis). Most of the recent rattlesnake studies have included some data on population size and composition, growth rates and reproduction (Sehman, 1977: Galligan and Dunson, 1979; Gannon and Secoy, 1984; Diller and Wallace, 1984), but none has squarely addressed demography. Parker and Brown (1974) and Vial *et al.*, (1977) have constructed life tables for 2 species of crotaline snakes. Obtaining estimates of survivorship, particularly for neonates and juveniles, appears to be one of the major stumbling blocks to deriving life tables for snakes.

In this study juveniles were sufficiently represented to enable minimum survivorship estimates to be obtained through mark-recapture. The life table for *C. v. oreganus* suggests that Okanagan populations are declining. Since l_x values were based on minimum survivorship, R_o is almost certainly not as low as calculated here. R_o could also be increased by some females reproducing at age 6 and/ or following a biennial reproductive cycle for the first two reproductive efforts. However, since small adult females tend to reproduce with lower frequency than large females, the hypothetical reproductive schedule for an average female is probably reasonable. Given this schedule of births and fecundity, at least 20% of females must survive to sexual maturity and live to about 20 years of age for long term equilibrium to be achieved ($R_o \cong 1$). This could occur if survivorship during the second year was 78%. In view of the trend for survivorship to increase with size, it is not unreasonable to suspect that survivorship during the second year is greater than for neonates and approaches that of two year old snakes (i.e. between 0.46 and 0.86). Juvenile survivorship may be higher at some dens or in some years than others; thus it would be premature to suggest these populations are facing imminent extinction based on data from 2 years only. On a cautionary note, however, even with greater juvenile survivorship, rattlesnake populations are likely to grow very slowly.

While it is tempting to speculate that the number of snakes at a den may be related, in part, to recency of colonization, support for this idea is not available. It is possible however, to make statements about recolonization of dens after severe human disturbance because many of the dens studied on Sites A and B were hunted to virtual extinction during the 1930's to the late 1950's by Rev. A. C. Mackie of Vernon, British Columbia. Mackie kept records of the numbers of snakes he destroyed annually at 12 dens on Site A and 5 dens on Site B between 1930 and 1960. Information essential to matching dens known today to those he began hunting 40 to 50 years ago are, for the most part, lost. However, using his unpublished manuscript (Mackie, 1944), diaries and maps I was able to identify 3 dens and piece together information on historical levels for 2 dens on Site B. Between 1930 and 1958 Mackie removed 183 rattlesnakes (138 of them between 1930-1934) at den 9 (his Whittall den). At present, about 30 rattlesnakes utilize the den. Current use of this den is far below historical levels, possibly for two reasons. First, Mackie dynamited (date unknown) about 1.5 m of solid rock from the face of this den in a futile attempt to examine the internal structure of a hibernaculum. The explosion may have caused structural damage which reduced the den's insulative capacity; however, high overwintering survivorship in this den indicates that this is not a valid explanation for the low present day use. An alternative reason is that rather than repopulating this den, rattlesnakes may have colonized an outcrop 40 m below den 9 which today serves as den 11. During Mackie's time, this outcrop did not appear to be utilized as a hibernacula for he made no mention of a den near den 9 in his manuscript, diaries or maps. A total of 150 rattlesnakes were marked at den 11 during this study.

Den 16 (Mackie's Austen den) has a present population of about double the number of snakes that Mackie removed (99 today versus 54 killed at the den between 1935 and 1957). Although other dens cannot be positively matched by name to Mackie's , the presence of old .22 caliber shells, cemented entrances, placement of flat rocks at entrances ("sun parlors") and rock cairns at some dens are evidence that many of the dens I studied were originally known to him.

The current rattlesnake population on Site B of between 650 and 700 is well above the total number of about 400 rattlesnakes killed by Mackie between 1930 and 1960 on this hillside. On this basis it is safe to assume that the population has recovered from the decimation it suffered in the past, but whether populations today are increasing, declining, or unchanging is not known.

6.0 GENERAL DISCUSSION AND CONCLUDING REMARKS

At the outset of this study I expected to find differences in ecological and life-history parameters among populations of *Crotalus viridis*, and predicted that these should vary along a latitudinal gradient. In this thesis I have equated a latitudinal gradient with a climatic gradient, namely a reduction in the length of the active season with increasing latitude. In comparing the life-history of *C. v. oreganus* in British Columbia with conspecific populations from southern and central areas of the species' range two trends were evident. These were: 1) a reduction in annual growth of juvenile rattlesnakes, which resulted in delayed attainment of sexual maturity of both sexes; and 2) a decrease in the frequency of reproduction in British Columbia populations.

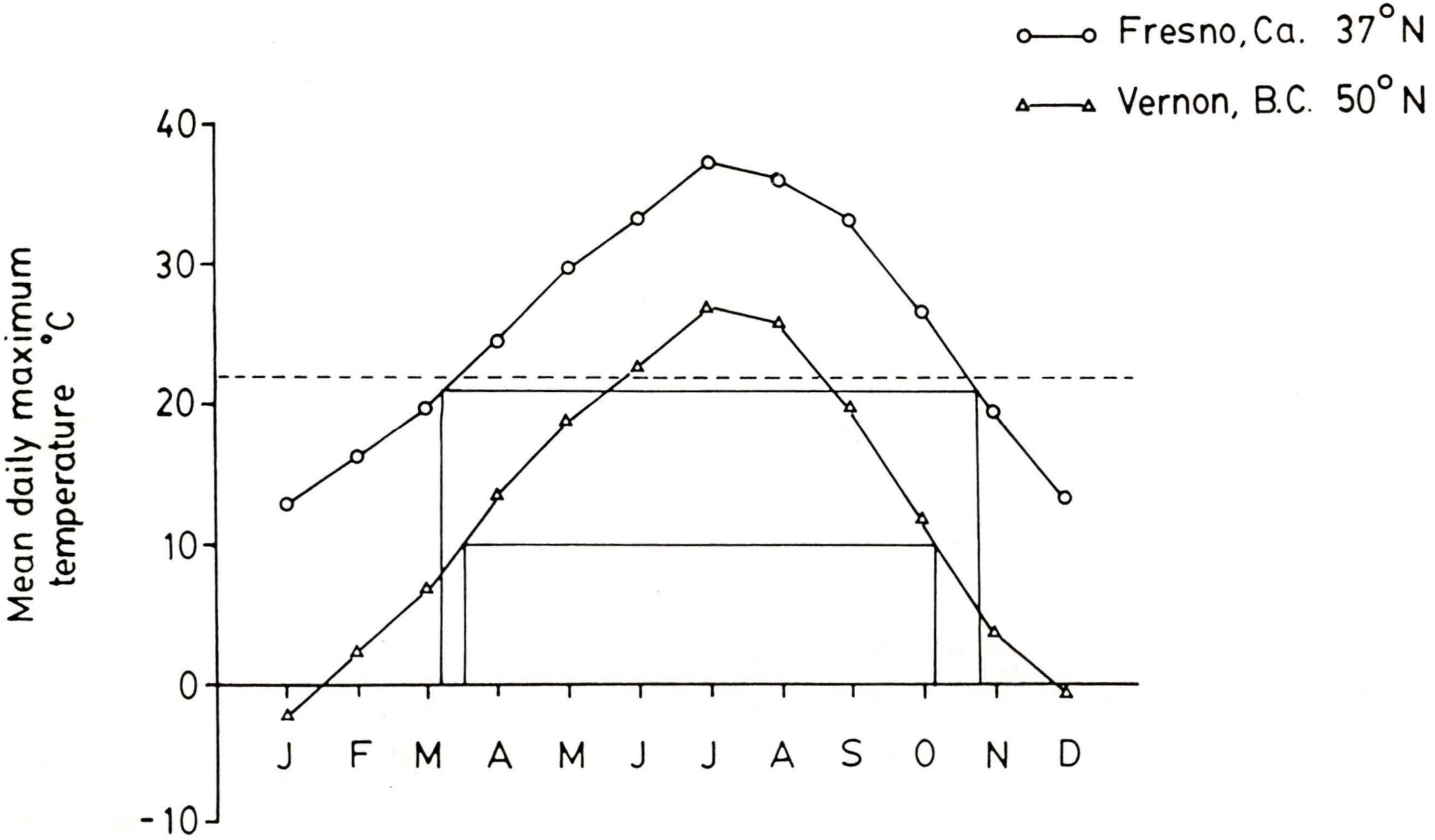
Differences in growth rates and reproductive frequency among populations of *C. viridis* are probably influenced by factors additional to differences in the actual length of the active season. For example, in British Columbia, dietary restrictions on neonates are severe and growth is slow until a body size of about 450 mm SVL is attained. Diets of juveniles in California are not constrained to the same degree because small ectothermic prey are available. The length of the active season in northern and central portions of the range varies little (April to October in most locations), and is one to two months shorter than in California. Two reasons for comparable periods of activity were suggested: 1) populations of *C. viridis* studied in the central portion of the range were generally located at high elevation sites and therefore subjected to climates similar to more northerly, low elevation sites; and 2) rattlesnakes in northern areas appear to be active at lower temperatures than those from southern areas (e.g. spring emergence occurs at 10°C in British Columbia, at 15.5°C in Utah and 21°C in California). Thus, differences in the lengths of the active periods do not necessarily vary in a linear fashion with latitude.

Nonetheless, the length of the active period is expected to have a major influence on growth rates and reproduction in rattlesnakes. In order to relate variation in life-histories of rattlesnakes to climatic differences it is important to distinguish between the length and quality of the active season defined in physical terms (e.g. number of frost-free days, etc.), and defined in biological terms (e.g. the number of days during the year on which the temperature is high enough to allow rattlesnakes to forage, or which are suitable for promoting embryonic development, etc.) By knowing the temperatures at which snakes emerge from and enter into hibernation, we can begin to relate the length and quality of the active season from both perspectives.

Figure 33 illustrates this more clearly. Here I have plotted the mean daily maximum temperatures by month for Fresno, California (close to the site of Fitch's 1949 study) and for Vernon, British Columbia, and for each location, delineated an area under the temperature curve according to the threshold emergence temperature of rattlesnakes at each site (10°C in British Columbia and 21°C in California). The area under the curve represents the thermal regime available to rattlesnakes over the course of the active season. Note that the lengths of the active seasons, expressed in months on the ordinate, correspond closely to the actual active periods of rattlesnakes at each site. The area under the curve is only slightly larger in California than in British Columbia.

The critical difference between these two areas is their position relative to one another; the mean difference between maximum daily temperatures at the two sites over the 12 month period is about 12°C. Because of this difference, the period available for activities which are facilitated by or dependent on high temperatures (e.g. foraging, digestion and gestation) will be shorter in the north than in the south. For example, suppose that rattlesnakes at both sites are only able to forage when daily temperatures equal or exceed 22°C (dashed line Fig. 33). The foraging period for rattlesnakes in British

Figure 33: A comparison of the length and thermal quality of the active season experienced rattlesnakes in British Columbia and California (climate data for Fresno, Ca. from Anonymous, 1974).


Fresno, Ca. 37°N
Vernon, B.C. 50°N
Mean daily maximum temperature °C
40
30
20
10
0
-10
J
F
M
A
M
J
J
A
S
O
N
D

Columbia would be reduced to about 1/2 of the total active period, whereas in California, foraging would be possible for most of the active season. This example is, of course, simplistic and I have ignored the fact that snakes can exert some control over their body temperatures by thermoregulating, and that temperate reptiles may possess physiological adaptations to cold temperatures (Davies *et al.*, 1981). However, the example serves to illustrate how climatic regimes may affect activity periods of rattlesnakes in different geographic locations. A reduction in annual energy intake as a result of a shorter active season can lead to reduced annual growth, delayed sexual maturity, and infrequent reproduction as was found in this study.

This study provides at least partial answers to the question of what limits the northern distribution of *C. v. oreganus*. The availabilty of overwintering sites may be the proximal cause for the present distribution of rattlesnakes in this province, as is the case for *C. v. viridis* in Saskatchewan (Gannon, 1980). However, given that hibernacula are not limiting, a further reduction in the quality of the environment, i.e. a shorter active season, lower prey abundance etc., would result in slower growth, extremely delayed sexual maturity and reproduction so infrequent that a viable population could not be maintained.

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7.0 APPENDIX I

7.1.0 Incidence of injury in rattlesnakes

Scars and/or recent injuries were observed on 123 of 1596 (7.7%) rattlesnakes examined in this study (neonates excluded). These disfigurements consisted of slash-like wounds or circular puncture wounds (85.4%), spinal injuries (9.7%) and deformed or missing tails (4.9%). Scars were most frequently distributed on the head and dorso-lateral surfaces of the anterior and posterior thirds of the body. Spinal injuries were usually confined to the posterior half of the body, and nearly all tail injuries had resulted in the loss of the rattle and distal portion of the tail. The physical nature of scars or deformations may be used to infer the manner in which an injury was sustained. For example, small circular scars or slash-like scars were probably caused by teeth, talons or claws of a variety of small predators. Broken or missing ribs underlying larger circular scars suggest a deeper and more powerful impact as would be produced by talons of large raptors. Damage to tails and spinal column could have been sustained when a predator grabbed the snake as it sought to escape head first under cover. Other scenarios are conceivable; however, it is likely that predators are the only injury producing agent encountered by rattlesnakes. Human activities resulted in the death of two snakes at two dens. A greater proportion of adults had injuries than juveniles, however, within both age classes males and females had nearly identical levels of injury (Table 35).

Table 35: The proportion of juvenile and adult rattlesnakes with scars or injuries (neonates excluded).

Sex / Age	n	Scars	Spinal injuries	Missing tails	Total number of snakes examined	Proportion scarred or injured
Males						
Juveniles	16	14	2	0	438	.036
Adults	49	46	2	1	368	.133
Females						
Juveniles	19	17	2	0	490	.039
Adults	39	28	6	5	300	.130
Population total	123	105	12	6	1596	.077

8.0 APPENDIX II

8.1.0 Thermoregulation

8.1.1 Methods

The body temperatures (T_B) of an adult male and a gravid female were monitored by telemetry over a 30 hr period on a hot day and clear night in mid-June to study thermoregulation. Temperature sensing transmitters (Model SM1, AVM Instrument Co.) were calibrated in a circulating water bath (0 - 40°C) against a digital thermometer. The time required to complete 30 pulses was recorded at 1°C increments and calibration curves were plotted for each transmitter. The implantation procedure was the same as described previously (see Methods in Annual Cycle). Transmitters were recalibrated after removal from the snakes. For each transmitter the two curves were essentially identical; therefore compensation for shifts in the calibration curve was not required. Temperatures determined from the curves were considered to be accurate to within ± 0.2°C.

The following ambient temperatures were recorded as close as possible to the snake: air temperature (T_A), measured 2 cm above the ground in the shade; shaded substrate temperature (T_S); and insolated substrate temperature (T_{SI}). In addition, the activity/position of a snake was noted at each recording using the activity categories of Parker and Brown (1980). These included: thermoregulating with >50% of the body exposed to the sun (R1); thermoregulating with < 50% of the body exposed to the sun (R2); thermoregulating during cloudy weather (R); underground or under rocks (UR) and moving (M). Temperature readings were made at 30 - 45 minute intervals.

9.2.0 Results and Discussion

The overnight site of the adult male (Fig. 34) was a west facing outcrop on the north face of Rattlesnake Hill. Shortly after the sun struck the outcrop at 1030 h the male emerged into the vegetation at the base of the outcrop. T_B rose rapidly form 21.5 to 30.0°C in 30 min. This snake remained in a looped posture within the sun-shade mosaic provided by the vegetation until 1500 h when it moved into complete shade of an overhanging ledge and coiled up. This move occurred when T_{SI} and T_A approached their maximum daytime values of 55°C and 35°C respectively. Between 1100 h and sundown at 2040 h, T_B was maintained within a narrow range of 29.5-31.5°C, and in general closely approximated T_S. After the snake retreated into the outcrop its T_B dropped at a rate of 0.7°C/h and reached a low of 21.5°C at

0830 h. Emergence occurred at approximately the same time as on the previous day.

The thermoregulatory behaviour of a gravid female monitored the same day, in many ways paralleled that of the male. Her overnight site was in a burrow beneath a large table rock located on the upper regions of the south face of Rattlesnake Hill. This site received sun at 0705 h. The female emerged briefly and exposed about 1/4 of her body to the sun at 0930 h, but on each subsequent visit during the day she could be seen coiled up in the shade about 25 cm inside the burrow entrance. Changes in T_B followed the same pattern as T_A and T_S, rising slowly and peaking in mid-afternoon (Fig. 35). T_B ranged between 30.7 and 33.0°C and T_A and T_S were generally 2-5°C warmer. A high and fairly constant T_B was maintained during twilight and throughout the night by retreating progessively deeper into the burrow. Beginning at 2200 h, I attempted to measure T_A and T_S as close as possible to the snake. These proved to be only slightly cooler than T_B. T_{SI} (which was the exposed ground temperature during the night) dropped to 12.7°C or about 17°C below the female's T_B inside the burrow.

Data collected on radiotracked rattlesnakes were not sufficient to draw broad conclusions concerning thermoregulation in *C. v. oreganus* Details on the thermal

Figure 34: Thermoregulatory behaviour of an adult male monitored over a 30 h period on a hot day and clear night in June, 1982. For an explanation of activity codes see text. SO = sun on the outcrop, SD = sun down on outcrop.

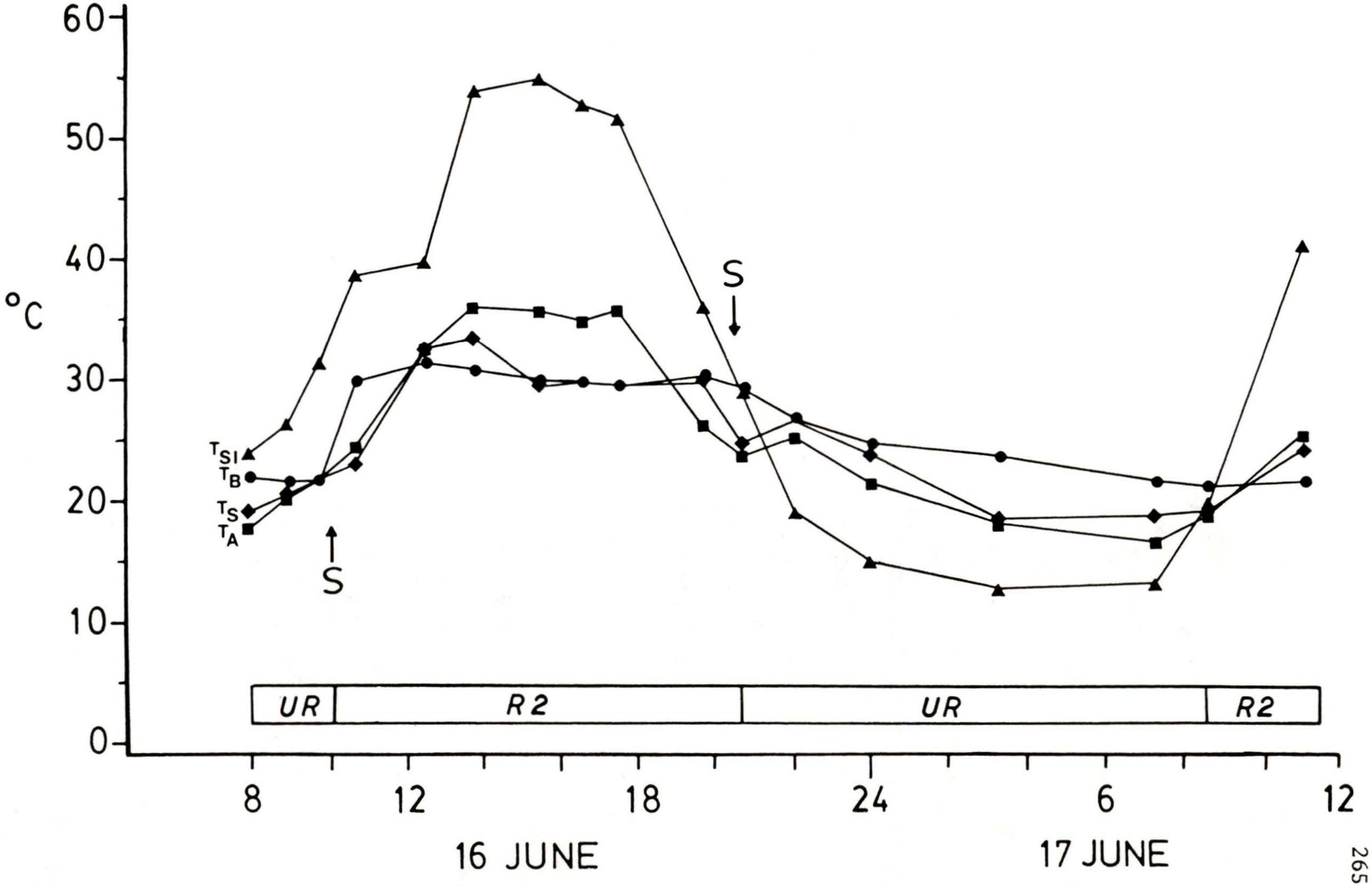
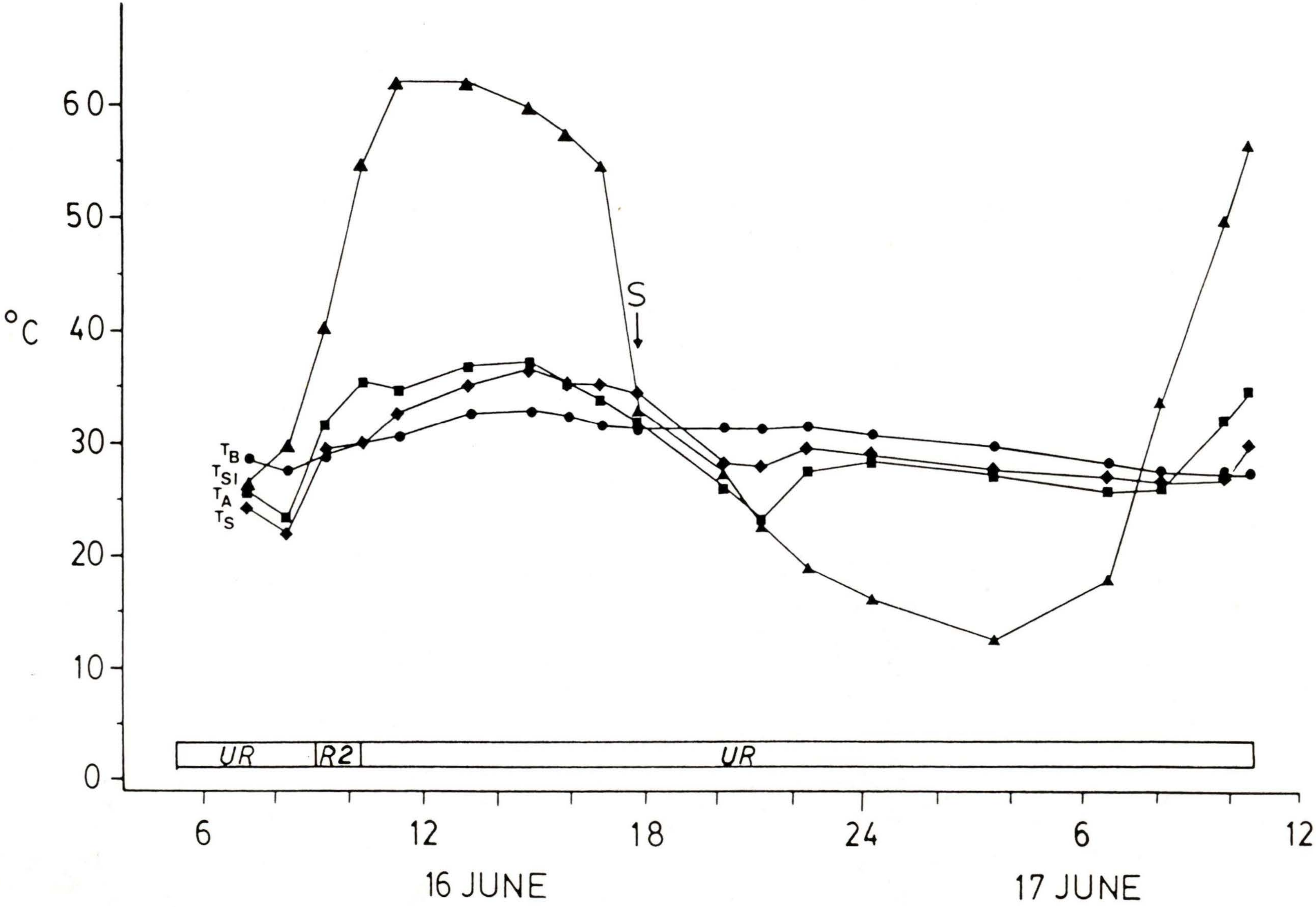

60
50
40
30
20
10
0
°C
T_SI
T_B
T_S
T_A
S
S
UR
R2
UR
R2
8
12
18
24
6
12
16 JUNE
17 JUNE

Figure 35: Thermoregulatory behaviour of a gravid female monitored during a hot day and clear night in June. Activity codes explained in text. Sun on outcrop until sundown (S).



60
50
40
30
20
10
0
°C
S
T_B
T_SI
T_A
T_S
UR
R2
UR
6
12
18
24
6
12
16 JUNE
17 JUNE

biology of *C. viridis* are provided by Cunningham (1966), Sehman (1977) and Gannon and Secoy (1985). A comparison between the male and gravid female monitored over the same 30 h period in June provides insights on the preference for inhabiting the north versus south-facing slopes during the summer. The table rock used by the gravid female fulfilled the requirements of protection from predators and from daily temperature extremes during the gestation period. Rookeries situated on the south face receive sunlight 3 to 4 h earlier, but also lose it earlier than sites on the north face. Sites on the south face are therefore beneficial for rapid warming, whereas sites on the north face enable greater surface activity during the day and early evening.

9.0 APPENDIX III

9.1.0 Overwintering thermal biology

9.1.1 Methods

As an adjunct to the examination of ecological aspects of hibernation, I collected data on the thermal biology of overwintering rattlesnakes. Little is known about the temperatures at which snakes hibernate and even less is known about the possible cues to emergence from hibernacula in the spring. To this end, I wanted to monitor body temperatures and movements of hibernating snakes and examine the hypothesis that entrance to and emergence from hibernacula are mediated by seasonal reversals of the surface to subsurface temperature gradient inside natural hibernacula (Viitanen, 1967).

During the 1982-1983 overwintering period the surface to subsurface temperature gradient inside den 14 (Site A) was monitored. Den 14 is a south facing rock outcrop about 9 m wide and 4 m high. The main entrance, located on the lower east side of the den, leads downward (at an angle of about 45^{o}) in a westerly direction into the rock. A second entrance was beneath some broken rock on the center of outcrop approximately 2.5 m west from the main entrance.

To measure internal temperatures, a 3 m long cable containing 5 thermistors, spaced at 0.5 m intervals, was inserted into the main entrance. The position of the distal thermistor was about 1.6 m below (vertical distance) the base of the outcrop while the fifth thermistor lay at the surface, just inside the main entrance. Resistance was measured with a digital multimeter and temperature was determined from a thermistor specific conversion table.

Body temperatures of rattlesnakes overwintering in the den were monitored by radiotelemetry. On October 10, 1982 five adult rattlesnakes were implanted with temperature sensing transmitters (see Appendix II for details). These snakes were released on October 16 to the den. Den 14 was visited and temperatures were recorded every second day between October 16 - 30, 1982, weekly until March 18, 1983 and thereafter every second day until May 12, 1983. On each visit the external air temperature (shaded, 10 cm above ground), shaded and insolated soil temperature (recorded about 1m from the den entrance) and snow depth (on a level patch of ground 10 m upslope from the den) were also measured. Recordings were taken between 1000 and 1300 h. Diel change in the gradient was examined by taking readings at four hour intervals over a 20 h period on April 12-13, 1983.

The position of each snake relative to the den entrances was determined by locating the source of the strongest transmitted signal along the face of the den. Overwintering body temperatures were also monitored for an adult male rattlesnake that hibernated in den 24 during the same winter. This snake had been radiotracked during the summer of 1982 and entered hibernation in late August before it could be recaptured for transmitter removal. No internal or external temperatures were recorded at den 24 during the winter.

9.2.0 Results

9.2.1 Overwintering den temperatures

Inside den 14, a surface to subsurface temperature gradient was present throughout the fall and winter. The magnitude of the gradient (temperature difference between probe 1 at 1.6 m and probe 5 at the surface) varied inversely with the external air temperature (Fig. 36). A negative gradient (surface cooler than subsurface) was established in the fall and maintained throughout the winter. Progressively cooler air temperatures during the fall resulted in a gradual decrease in the core temperature (approximated by the temperature at probe 1) and a decline in temperatures at all depths. The core temperature cooled at an overall rate of 1.0°C/week between October 15 and November 15 and dropped a further 4°C the following week in tandem with the first snow producing weather system (Fig. 36). Once snow persisted on the ground the core temperature decreased less rapidly (0.04°C/week) and was little affected by fluctuations in the external temperature. Core temperature varied between 3-5°C during the period of mid-November to mid-January. A warm spell in early February diminished the gradient and marked the beginning of a gradual increase in core temperature which continued into late spring. A partial reversal of the gradient occurred after snow had melted in mid-March. The gradient never completely reversed; instead it collapsed and underwent a uniform warming at all depths below the surface at an overall rate of about 0.6°C/week until mid-May.

9.2.2 Temperatures and movements of snakes during hibernation

Of five rattlesnakes from den 14 that were fitted with transmitters in October, only one was monitored until spring emergence. One female was found dead on the surface in mid-November. The signals from two other transmitter grew faint and were lost in early winter. Another transmitter lost its temperature sensing capacity in late February; however, it continued to give a constant audible pulse until May. The snake bearing this transmitter was known to be alive after the last temperature reading because a shift in the signal source indicated a 2.5 m lateral movement in early March. This snake did not emerge and was presumed to have died inside the den.

The overwintering temperatures of two snakes are shown in relation to the den temperature gradient in Figure 37. Both snakes emerged to bask on sunny days in late October when T_A exceeded 10°C, and were able to raise their T_B's 10-15°C above the air temperature. Body temperatures on the days after their final appearance on the surface were warmer than the temperature at the lowest probe, suggesting that these snakes were located at deeper or more insulated sites inside the den.

Possible movements by both snakes during the first weeks of hibernation were suggested by changes in their body temperatures which were more pronounced than the gradual decrease in temperature at probe 1. Between November 21 an November 29 the body temperatures of both snakes decreased while the temperature at probe 1 remained virtually unchanged. These decreases could be interpreted as upward movements, possibly in response to a narrowing of the gradient. More likely, the decreases were due to a slower rate of cooling of the snakes situated at lower depths in the den and probably represent a lag behind the temperature decline at sites nearer to the surface, rather than movements. Movements to deeper (or warmer) sites in the

Figure 36: The temperature gradient profile in den 14 between October 1982 and May 1983. A = air temperature, numbers 1-5 are temperatures recorded at 0.5 m intervals from the surface (probe 5) to the deepest position inside the den (probe 1). SF = first persisting snowfall, SM = snow completely melted.

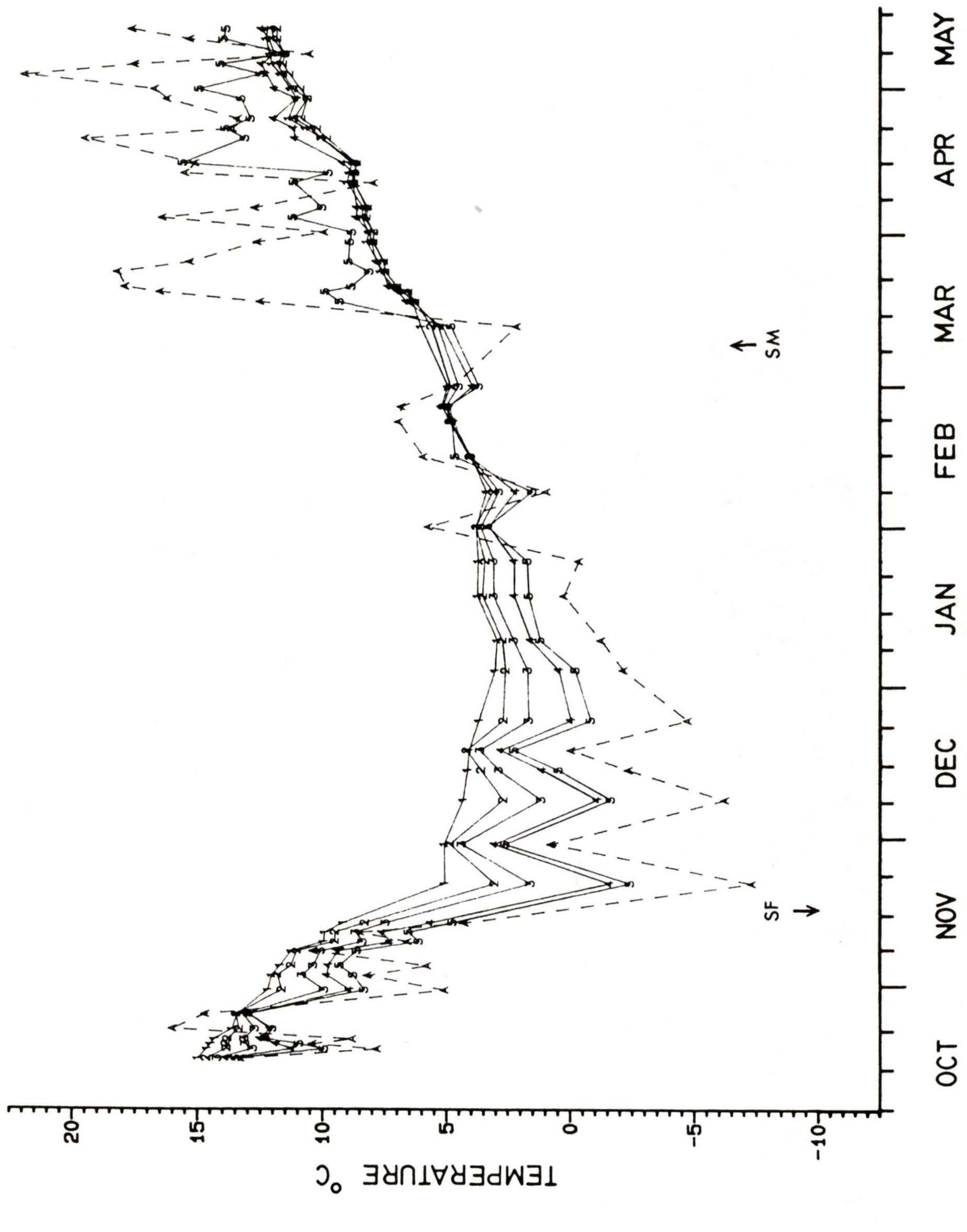
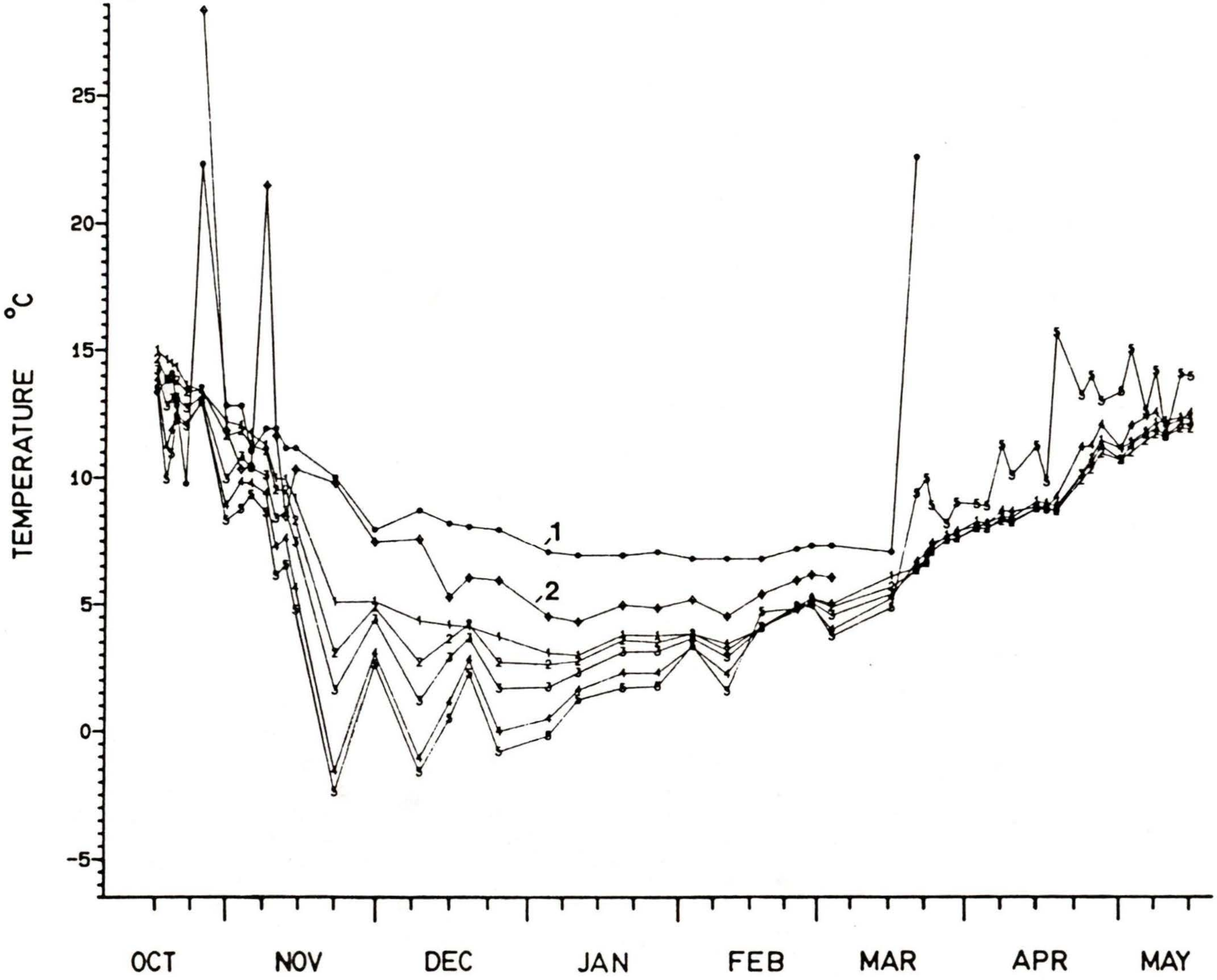

TEMPERATURE °C
20
15
10
5
0
-5
-10
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
SF
SM

Figure 37: Body temperatures of two snakes in relation to the internal temperature gradient during hibernation. Symbols as in Figure 36.


TEMPERATURE °C
25
20
15
10
5
0
-5
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1
2

den were inferred by the increase in temperature noted for both snakes by the next visit on December 7 (Fig. 37). Another decrease in temperature followed by an increase in mid-December suggested a second downward movement by snake 2. Thereafter their body temperatures exhibited a pattern of change which closely paralleled the change in temperature at probe 1. This indicated that snakes remained relatively stationary for the duration of the overwintering period. Between January 9 and February 25, body temperatures were their coolest, averaging 6.9°C (SE = 0.03) and 4.8°C (SE = 0.16) for snakes 1 and 2 respectively.

The rattlesnake monitored in den 24 entered hibernation sometime between August 25-30, 1982 and emerged on April 15, 1983. Its body temperature dropped from 21.7 to 6.3°C between August 30, 1982 and January 3, 1983, at an overall rate of 0.86°C/week. Between January 9 and February 15 the T_B averaged 5.7°C (SE = 0.06).

Both snakes 1 and 2 made lateral movements within the den during the beginning and end of the hibernation period. Six days after its release to the main entrance snake 1 was seen at the second entrance, and on the next visit was again in the main entrance. The source of the signal was strongest from an area 2 m below and west of the second entrance until the end of hibernation. Snake 2 was last seen basking at the second entrance in early November and until late February the signal was strongest from just below that area. In early March the signal shifted about 1.5 m east of the second entrance. A permanent shift of 2.5 m east to the rock face above the main entrance occurred in mid-March.

The source of the signal from the snake in den 24 was noted on fall and spring visits. In the fall, the signal emanated from an area about 4 m east along the rock face from the entrance and was also strongest from that position on the first spring visit. From April 4 until emergence on April 15 the signal was strongest from the near the den entrance, and a body temperature of 15°C on April 4 suggested that the the snake was indeed very near the entrance.

9.2.3 Emergence in relation to the den temperature gradient

As previously stated, the surface to subsurface gradient never reversed completely, instead there was a uniform warming at all subsurface locations. Temperature differences between probes 1 and 4 in early spring were usually less than 1°C. During the month prior to emergence snake 1's temperature increased only slightly in unison with a small increase in core temperature. Snake 1 emerged sometime between March 14-17 and was found 4 m from the den on March 18.

Figure 38: The emergence of rattlesnakes from den 14 in relation to the internal temperature gradient and air temperature. Symbols for gradient as in Figure 36. Sex, age and reproductive classes in the histogram as in Figure 2.

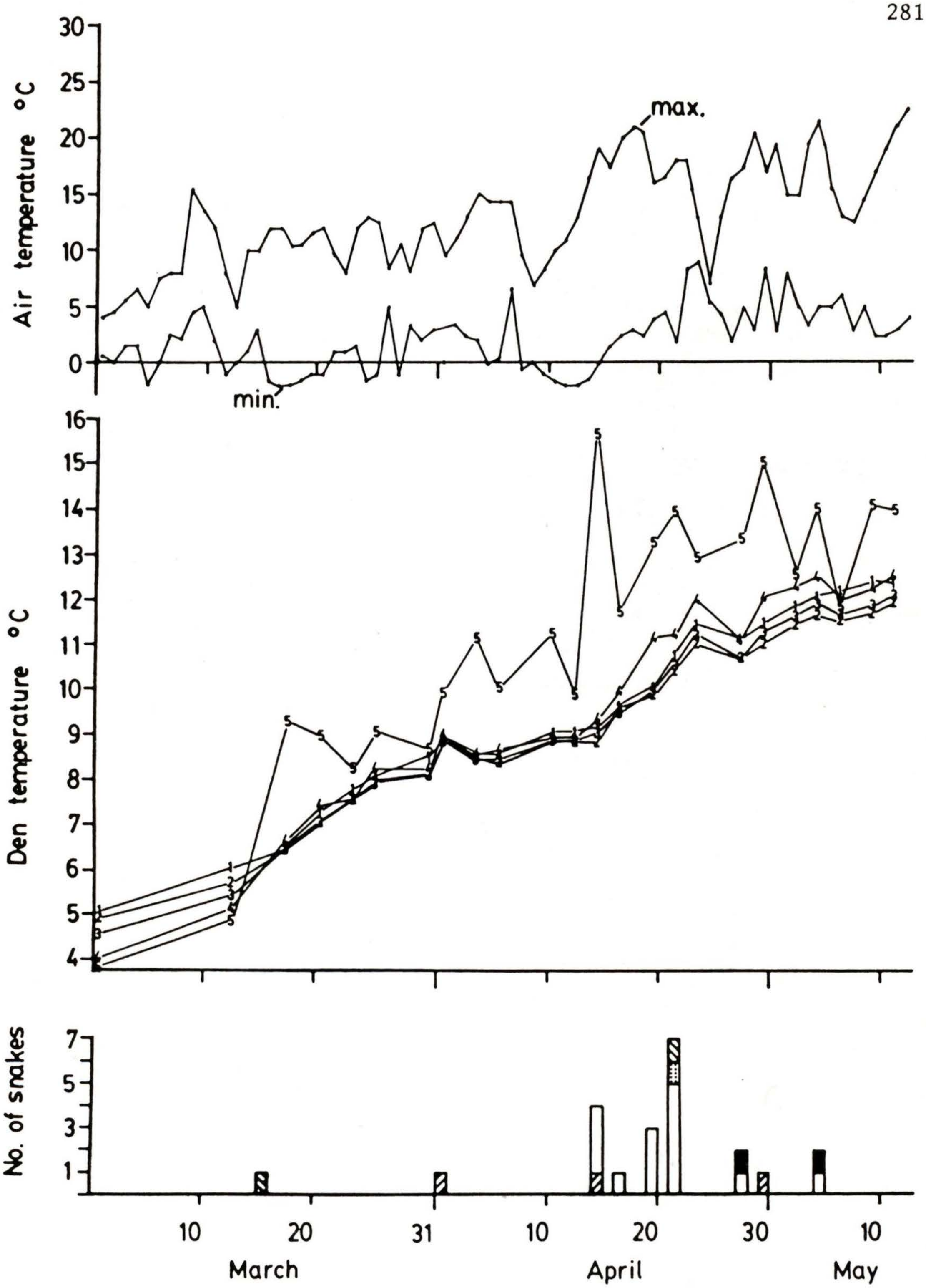

Air temperature °C
30
25
20
15
10
5
0
max.
min.
Den temperature °C
16
15
14
13
12
11
10
9
8
7
6
5
4
No. of snakes
7
5
3
1
10
20
31
10
20
30
10
March
April
May

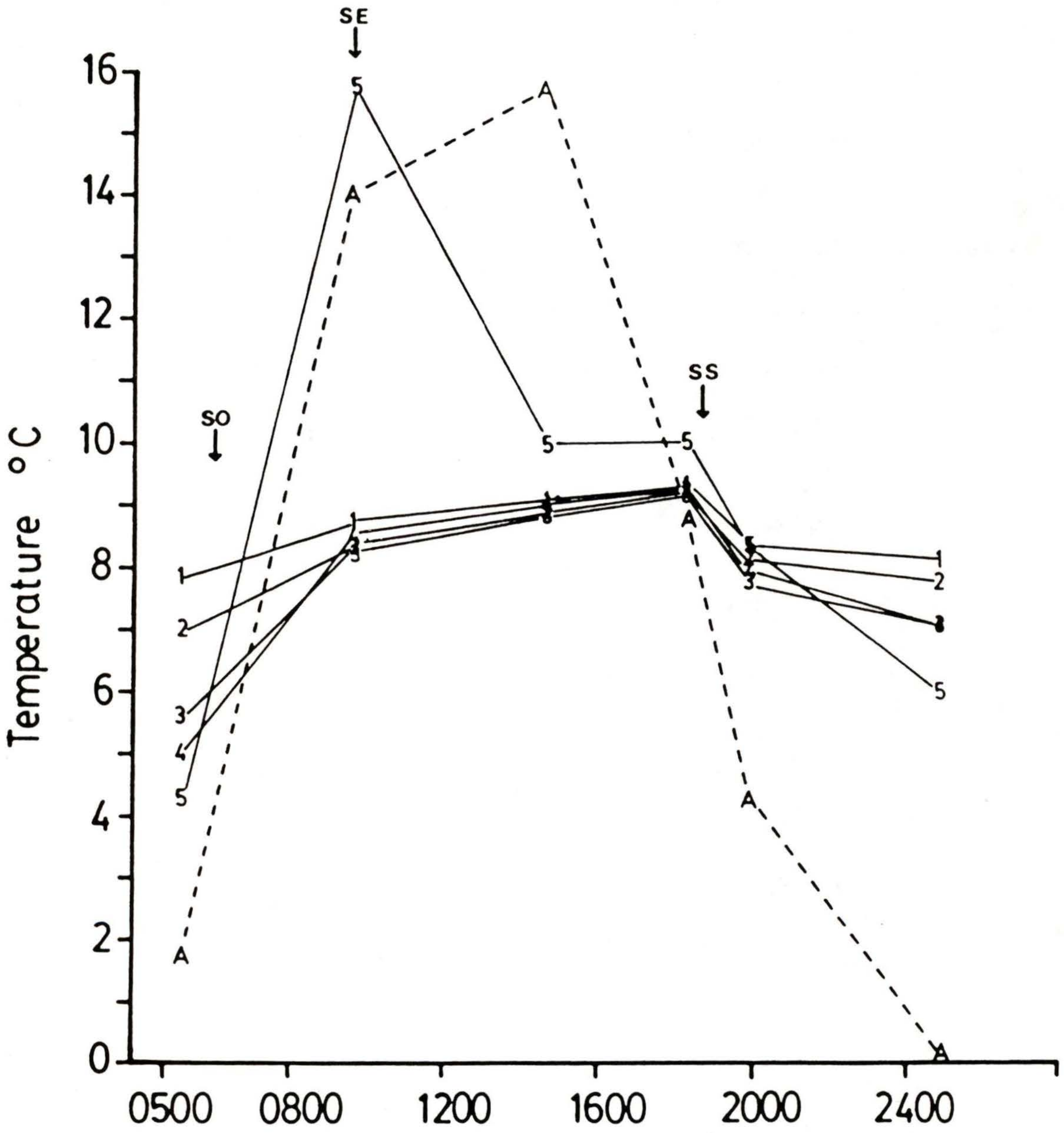
Figure 38 illustrates the date of emergence of snakes from den 14 in relation to the gradient and external temperatures. The core temperature warmed by nearly 3°C before the next snake appeared on the surface on April 1. Overcast conditions during the previous 10 day period prevented rapid nightime cooling and facilitated the daily warming inside the den. The peak emergence occurred between April 15-22, a week of 15°C + temperatures, which coincided with a second period of rapid internal warming. By April 24 the internal temperatures reached 11°C and snakes emerged thereafter on virtually any warm (15°C +), precipitation free day.

The male hibernating in den 24 warmed at a rate of 0.5°C/week between February 15 and March 26, reaching 8.5°C on the last visit prior to its move to near the den entrance on April 4. A period of rainy weather delayed emergence of this snake until April 15.

Snakes emerged both during the morning and the afternoon, depending mainly on the daily weather. Cloacal temperatures were recorded for 23 rattlesnakes pulled from the entrances of several dens during late March and early April of 1982. Temperatures of emerging snakes averaged 8.0°C (SE = 0.4, range 5.5 - 12.8).

The diel change in the gradient during a clear day in April is shown in Figure 39. The negative gradient

Figure 39: Changes in the internal den gradient during a clear spring day (April 13-14, 1983). A = air temperature, SO = sun on den, SE = sun shining directly into main entrance, SS = sunset. Symbols for the gradient as in Figure 36.


SE
SO
SS
Temperature °C
16
14
12
10
8
6
4
2
0
0500
0800
1200
1600
2000
2400
1
2
3
4
5
A

established during the night diminished by midmorning. Throughout the day temperatures below the surface were within 0.5°C and increased only about 1°C by the late afternoon. The negative gradient was restablished late in the evening. Thus warmth penetrates into the den each day and is lost again at night.

9.3.0 Discussion

Until recently information on temperature and spatial arrangements of overwintering snakes has been mainly collected by excavating hibernacula (see summary tables in Brown *et al.*, 1974; Jacob and Painter, 1980) and from semi-natural or man-made hibernacula (Gillingham and Carpenter, 1978; Sexton and Hunt, 1980). The consensus from such studies is that snakes hibernate singly or in small clusters within the den, body temperatures are usually within 1°C of the substrate temperature at the same depth (ranging from 0-10°C, averaging 6°C), and that snakes are capable of moving at these low temperatures. Overwintering body temperatures of snakes have been monitored only recently with the advent of miniaturized temperature sensing radiotransmitters (Jacob and Painter, 1980; Sanders and Jacob, 1981; Brown, 1982). Viitanen's (1967) hypothesis that entrance and emergence may be related to seasonal reversals of the surface-subsurface temperature gradient has received empirical support from studies by Lang (1971) and Sexton and Hunt (1980). Sexton and Marion (1981) provided corroborative data through experimental manipulations of the temperature gradient in artificial hibernacula. They were able to demonstrate that *C. v. viridis* selected the warmer portions of the reversing gradient and that snakes made exploratory movements in response to changes in the gradient as a unit and not to a localized warming of regions within the artificial den.

In field situations our knowledge of movements of snakes with respect to the gradient is less certain because: 1) it has been difficult to measure the temperature profile within a hibernaculum and 2) a snake's position cannot be observed and must be inferred from its temperature relative to the temperature inside the den. Jacob and Painter (1980) measured the soil temperature gradient adjacent to a den in which body temperatures of *C. v. viridis* were monitored by telemetry; however, because the snakes hibernated at depths well below the deepest probe, their movements in relation to the gradient could not be determined. Brown (1982) monitored overwintering body temperatures of *C. horridus* during hibernation but was unable to measure subsurface soil temperatures. Both of these studies revealed that snakes overwinter at a wider range of temperatures than had previously been known. As was also found in this study, body temperatures of hibernating snakes decline gradually during the fall, stabilize in late winter and warm gradually prior to emergence.

The present study is apparently the first to monitor simultaneously body temperatures of snakes in relation to the temperature gradient inside a natural hibernaculum. Brekenridge and Tester (1961) were able to determine movements of toads (*Bufo hemiophrys*) in hibernation with respect to the soil temperature gradient using radio-isotope tagging. Toads made downward movements just in advance of the downward movement of the 0°C isotherm during the winter and emerged only after the 0°C isotherm became vertical. In this study I have evaluated movements of hibernating rattlesnakes with some caution because the probes presumably did not quite reach the positions/depths of hibernating rattlesnakes. As interpreted they provide field evidence for selection of warmer regions within the den as the temperature declines during the early winter.

There are some consistencies in the pattern of the gradient change during the period of spring emergence between this and previous studies. The most notable is that upon warming at the surface in early spring the gradient diminishes, becoming nearly isothermal, and even when partial or complete reversal is attained in late spring, there is usually less than 2-3°C difference between the deepest and shallowest subsurface temperature (or the rear versus front in artificial dens). In effect there is virtually no gradient to speak of during the emergence period unless one were to compare only the temperatures of the deepest region to the insolated surface. The warming to a uniform temperature at all subsurface depths occurs on a daily cycle; therefore warm air appears to penetrate the den entrance during the day, but the gradient does not reverse. Viitanen (1967) has suggested, to which my data add support, that it is the downward passage of warming temperatures during the spring that activates snakes to begin movements to the surface.

One of the major problems in assessing the validity of the reversing gradient hypothesis as the stimulus for emergence from hibernation, is that it is not possible to separate the confounding effects of the gradient's reversal and the concomitant warming at all depths within the den during the spring. Snakes may make use of a temperature gradient to orient and navigate their way out of the den, but the gradient is so weak that it is doubtful whether they would be capable of detecting minute changes in the gradient unless they made extensive movements within the den. In natural dens, movements may be greatly hindered by narrow passage ways, some of which may be blocked by fellow hibernators. In addition, there is no evidence to support the idea that snakes actually require a thermal gradient to direct them to the surface. Other sensory abilities such as olfaction may be more valuable in this respect. Scent trails laid down along passage ways may provide far better direction within dens than minute changes in temperature. Once near the surface, light intensity and increasing air temperature during the day are likely to provide the impetus for emergence onto the surface.

Earlier emergence has been correlated with shallower depths of hibernation (Carpenter, 1953; Lang, 1971; Etheridge *et al.*, 1983); i.e. snakes which hibernate at lower depths emerge later than snakes hibernating nearer the surface. This hypothesis remained unanswered in this study because the three other snakes which hibernated in den 14 were not recaptured and their emergence dates relative to the depth/temperature during hibernation could not be examined. Sex related differences in temperatures at which snakes are stimulated to begin movements to the surface may explain an earlier emergence of one sex, as in the lizard *Cnemidophorus sexlineatus* (males emerge at 19.6°C while females emerge at 27°C, even though both hibernate at the same level underground, Etheridge *et al.*, 1983).

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Macartney, J.M. and P.T. Gregory. 1981. Differential susceptibility of sympatric garter snake species to amphibian skin secretions. Am. Midl. Nat. 106:271-281

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Crotalus viridis oreganus, IN BRITISH COLUMBIA.

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