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Life History Traits of the Western Diamondback Rattlesnake (*Crotalus atrox*) Studied from Roundup Samples in Oklahoma

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ABSTRACT In 1987, 1988, and 1989, 1011 live *Crotalus atrox* were examined at the Waynoka, Okeene, Apache, Waurika, and Mangum rattlesnake roundups in Oklahoma. Males are the more numerous in each local sample. At birth, the average size of males exceeds that of females and the differential increases with age, with adult males being about 10% larger than females. Young thought to have been born in August or early September increased in size nearly 54% by the following April (the time of the roundups) and added another rattle segment to the natal button; those thought to be second-year young were 168% larger than neonates and had six rattle segments. Sexual maturity evidently is attained in the third year when most females longer than 900 mm were fecund, and breeding seems to be annual. There is an average of 13 (4–24) yolked follicles and the number is proportional to female size. The average diameter of the natal button is 6.8 mm. Although successive rattle segments may increase slightly in size, after a snake acquires 10 segments (usually in the fourth year), there seems to be little growth between successive sloughs. Occasional reduction in the size of the proximal segments of rattle strings of medium-sized to large adults may indicate undernourishment. The largest and oldest snakes were probably between 10 and 15 yr old and represented 4.2% of the sample. Slightly more than half of the snakes were second-year young and young adults thought to be 3 or 4 yr old. Annual adult mortality is estimated at 20%. Subtle differences in sizes and proportions distinguish each of the five roundup populations.

Key words: Rattlesnake roundups, *Crotalus atrox*, basal rattle segments, Oklahoma.

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Since Klauber's (1956) landmark investigations, many excellent field studies of rattlesnakes have been made and knowledge of rattlesnake ecology has progressed significantly. The common and wide-ranging *Crotalus horridus* and *C. viridis* have been especially well studied at several sites in their extensive ranges (Brown, 1991; Brown et al., 1991; Diller and Wallace, 1984; Duval et al., 1985; Galligan and Dunson, 1979; Gannon and Secoy, 1984; Golan et al., 1982; Martin, 1982; McCartney, 1989; McCartney and Gregory, 1988; Reinert and Zappalorti, 1988; Wallace and Diller, 1990). No comparable studies have been made on *Crotalus atrox*, although it also is wide-ranging and ecologically significant as a dominant predator. The "rattlesnake roundups" that are held annually at many places within the range of *C. atrox* yield harvests of thousands of snakes that are a potential source of demographic and life-history information. However, the opportunity to obtain such information largely has been neglected because conservationists and herpetologists generally deplore the roundups and tend to avoid them.

We were contracted by the Non-Game Program of the Oklahoma Department of Conservation to investigate five annual rattlesnake roundups (Waynoka, Okeene, Apache, Waurika, and Mangum) to gather information concerning economics and sociology of the roundups and the effects of such roundups on local wildlife, including prey populations of rodent pests. With cooperation of the roundup leaders and organizers, we examined large samples of live snakes and snake viscera that were discarded at the roundup butcher shops. Our objective was to investigate growth, rattle development, longevity, reproduction, food habits, and population structure in the snakes examined. The formal roundups are held on spring weekends (mainly in April) when the snakes have recently emerged from nearby hibernacula. Many snakes are captured by local hunters on warm days in March and kept several weeks until the local roundup when they are sold for the "snake pit" displays or for their hides and meat. Data presented herein apply specifically to snakes at the beginning of their season of activity; the condition of their gonads, fat bodies, and rattle development differ at other times of year and are relatively poorly known. Those aspects of this study concerned with food habits and endoparasites were reported by Pisani and Stephenson (1991) and Stephenson and Pisani (1991), respectively.

MATERIALS AND METHODS

Eight roundups were attended, as follow: Waynoka (1987, GRP; 1988, HSF & GRP); Waurika (1988, HSF & GRP); Okeene (1988, HSF & GRP; 1989, HSF); Apache (1988, HSF; 1989, HSF); and Mangum (1988, HSF). Waynoka and Okeene are in northern Oklahoma in the Cimarron River drainage, whereas Waurika, Apache, and Mangum are in the southern part of the state in the Red River drainage. Snakes were chilled by immersion in ice water for several minutes; when they were immobilized so that they could be handled with relative efficiency and safety, they were removed. After examination, the snakes were returned to holding boxes; usually, they recovered to full activity within 45 min.

Data recorded from the live snakes include sex, snout-vent length (SVL), tail length, rattle-string length, number of rattle segments, vertical diameter of each segment, number of tail bands, and weight. All measurements are in millimeters and grams. Numbered plastic tags were inserted into the gullets of many live snakes (1988) or tied to their rattles (1989) and retrieved at the time of butchering; in this way, the viscera could be associated with individuals for which data had been recorded in life. At each roundup, snakes were collected mainly within a 40-km (25-mi) radius of the sponsoring town, but others that were captured earlier were brought from more remote areas. The Oklahoma roundups were held on successive weekends over a 4-wk period; snakes from earlier roundups were shipped to, and displayed at, later roundups. Western Diamondback Rattlesnakes from Texas, which emerge earlier than those from Oklahoma, may have been represented at any or all of the Oklahoma events. However, we used only snakes from separately crated lots that were identified by hunters as having been collected locally.

Although we attempted to obtain representative samples of each population, the snakes that we examined may already have been subject to selection, some of it subtle. For example, these collections lacked an adequate representation of first-year snakes. According to collectors' statements, young frequently were encountered in the field, but usually were "left for seed" because their monetary value was negligible. Dealers who purchased the snakes paid by the pound and the larger the snake, the greater its value. At the butcher shops, large snakes were preferred. Whenever feasible, we examined lots of snakes that were destined for immediate butchering so that we could collect their viscera; this may have resulted in some bias in the sex ratio of our sample. However, we found males to be more numerous even in the smaller size classes. Butchering was conducted sporadically at the roundups; its timing seemed to be correlated first, with the objective of providing fresh meat and skins for immediate sale and, second, with the aim of collecting admission fees from spectators. Statistical tests follow Sokal and Rohlf (1969).

RESULTS AND DISCUSSION

Sex Ratios and Sizes

Males always were more numerous than females in the live samples; the ratio was 57.5% males to 42.5% females (1.4:1, $n = 1011$, $P < 0.05$). The percentages of males at different roundups differed slightly, as follows:

Waynoka, 52.1%; Waurika, 55.6%; Okeene, 57.4%; Mangum, 60.3%; and Apache, 60.4%. It is unclear whether males actually were more numerous than females or, instead, more easily found. Males may emerge from hibernacula a little earlier than females, but this possibility seems to be contraindicated by the fact that relatively fewer males were encountered in samples from early roundups (Waurika, Waynoka) than from later ones (Apache, Mangum). Perhaps males, motivated by sexual search, are more inclined to travel and to rattle when disturbed and, therefore, are found more easily. Our procedure of processing batches of snakes that were about to be butchered also may have biased sex ratios, because large snakes were preferred for butchering.

As measured by snout-vent length (SVL) and weight, male *Crotalus atrox* are substantially larger in average and maximum sizes than females (Figs. 1–2). Moreover, males have longer tails than females and there is scarcely any overlap between the sexes in relative tail length (Fig. 3). The wide range of variance in tail length in each sex reflects individual variation and allometric changes during growth.

Mature female *Crotalus atrox* possessing enlarged follicles range in size from 840 mm SVL (live weight, 440 g) to 1300 mm SVL (live weight, 1416 g). The longest male is 1520 mm SVL (live weight 2776 g). Our findings corroborate Klauber's (1956) report that male *C. atrox* are 10.3% longer than are females on an average. The sponsors of the Waynoka event have recorded the total lengths of the two longest snakes captured there each year since 1950. The approximate snout-vent lengths of these record snakes (presumed to be males) were estimated by subtracting the sum of 8.04% of the total length (≅ tail length) plus 49 mm (average length of a rattle string). The mean total length and snout-vent length of the 37 longest snakes are 1844 (range = 1473–2032) and 1647 (range = 1307–1820) mm, respectively. The means and ranges for the 37 runners-up are 1727 (1467–2007) mm total length and 1540 (1300–1792) mm SVL.

Growth and Rattle Development

Each snake retaining an intact rattle string carries a record of its growth from the time of birth. There is a high correlation (± 94%) between the size of the basal rattle segment and SVL (Fig. 4). In the smallest snakes, the average diameter of the basal rattle segment is approximately 1.8% SVL, but owing to allometric growth, the relative size of the basal rattle segment decreases with respect to snout-vent length in larger and older individuals. Thus, it is about 1.6% SVL in young adults, 1.55% in 18 large adults 1200–1299 mm SVL, 1.45% in four individuals 1300–1399 mm SVL, and 1.40% in four individuals that exceed 1400 mm SVL. In our composite pooled sample representing both sexes and all five localities, the average diameter of the natal button is 6.8 mm; the average sizes of successive rattles are 8.2, 9.5, 11.1, 12.3, 13.7, 14.3, 15.0, 15.6, 15.8, and 16.3.

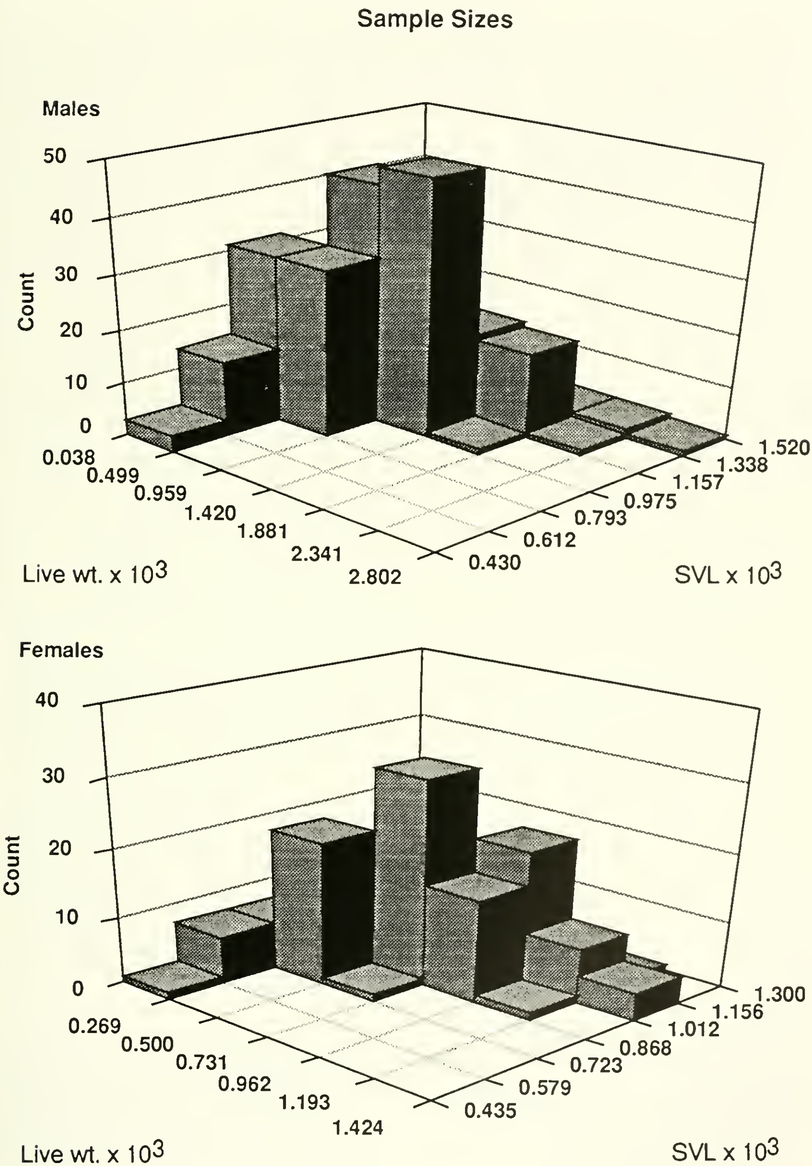


Fig. 1. The relationship between snout-vent length (SVL) and weight in samples of *Crotalus atrox* from Oklahoma.

At birth, the snout-vent length and rattle diameter of males exceed those of females and the disparity increases with age (Table 1). From the sizes of successive rattle segments, percentages of gains between successive sloughs (after the postnatal slough) are: 20.6, 15.9, 16.9, 10.8, 11.4, 4.4, 4.9, 2.0, 2.0, and 1.3. These measurements demonstrate that growth slows markedly after the third slough and even more after the fifth. In all snakes having incomplete, but tapered, rattle strings, the number of missing segments was estimated from the size (diameter) of the terminal segment. For instance, if the diameter of the terminal segment is 13.7 mm or nearer this figure than to the means for the next smaller or larger segments (12.3 and 14.3, respectively), it was assumed that three more distal segments had been lost, because 13.7 mm is the mean for the fourth segment (counting inward from the tip toward the base) in intact strings. Thus, the growth rate postulated here and implied in Table 1 is inferred and is based on the following assumptions. (1) Large snakes produce larger rattles than smaller snakes and the diameter of the basal rattle segment is proportional to the snout-vent length of the snake. (2) Neonates of *Crotalus atrox* from Oklahoma conform with Klauber's (1956) findings for the species; born in late summer, they have mean overall length of 330 mm (ca. 302 mm SVL). (3) The smallest snakes in our sample that are recognizable as a distinct cohort are first-year young, which are about 7 mo old. These snakes are 50% longer than neonates and possess one additional rattle segment. (4) Young too large to belong to the first-year cohort are concentrated in a second-year cohort; these individuals range between 800–900 mm SVL and usually possess strings of six rattle segments (having gained four segments in their first full growing season). (5) Under natural conditions during their season of activity, adult wild *C. atrox* shed with the same frequency as individuals thriving in captivity—i.e., about three times in 2 yr (with an 8-mo growing season).

First-year young comprise a recognizable cohort, distinct from second-year young. There are only 20 first-year snakes in our entire sample, but the snake-catchers indicated that they were relatively numerous in the field. The average snout-vent length of snakes in our sample is 465 mm (range = 430–582). Seventeen of these snakes had added one rattle segment to the original button; two had added two segments and one still had only the button.

Klauber (1956) reported the average total length of newborn *Crotalus atrox* to be 330 mm; if one allows 28 mm for the tail and button, the average snout-vent length of these neonates, born primarily in August, would be 302 mm. We obtained no data for neonates because the youngest snakes were already about 7 mo old at the time of the roundups and had been active for at least 2.5 mo. Based on Klauber's (1956) figures for *C. atrox* neonates, we deduced that, on the average, the first-year young in our sample had increased 162 mm in SVL and gained one rattle segment in the interval since birth. Although the rate of development of first-year young provides clues as to the stage of development to be expected in second-year young, presumably there is progressive diminution in length gains and

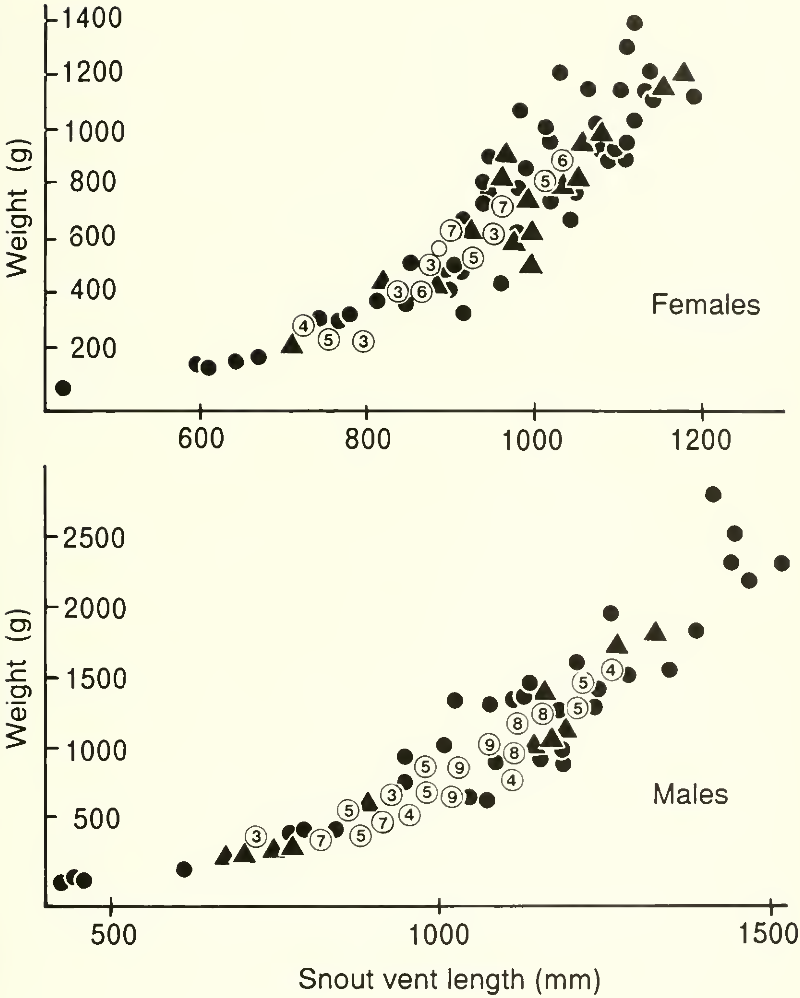


Fig. 2. The relationships between length and weight in female (**upper**) and male (**lower**) *Crotalus atrox* from Oklahoma. Circles represent one record, whereas triangles represent two records; multiple records greater than two are indicated by numbers enclosed in open circles.

rattle gains as growth proceeds. The first-year snakes in our sample probably had been active through September and most of October; thus, in only 8–10 wk, they became 54% longer and added one rattle segment. The average diameter of the new rattle segment is 1.3 mm (19%) larger than the natal button; probably most of the young snakes grew after the slough that produced this second rattle segment.

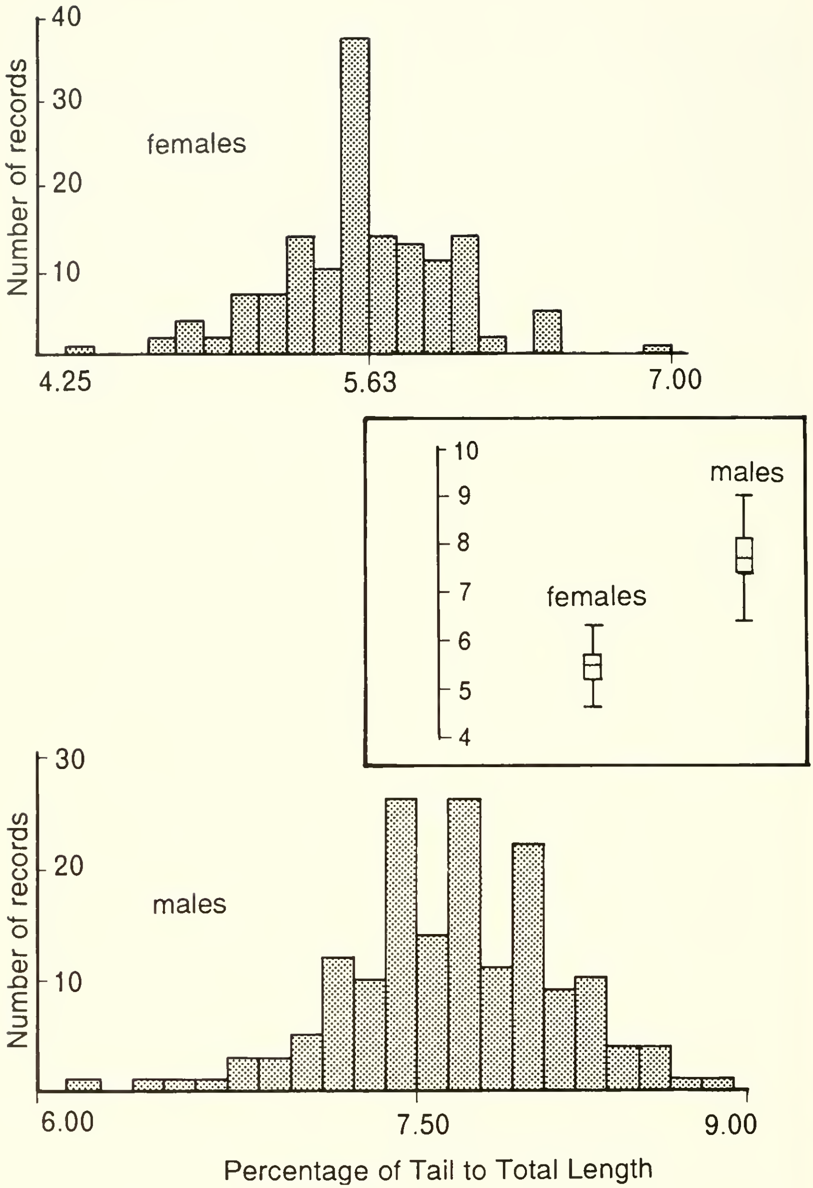


Fig. 3. Relative tail length in male and female *Crotalus atrox* from Oklahoma.

Only four snakes in our sample possess two or three rattle segments in addition to the natal button; apparently most reached these stages at times of year other than the spring, when roundups were held. In contrast, 39

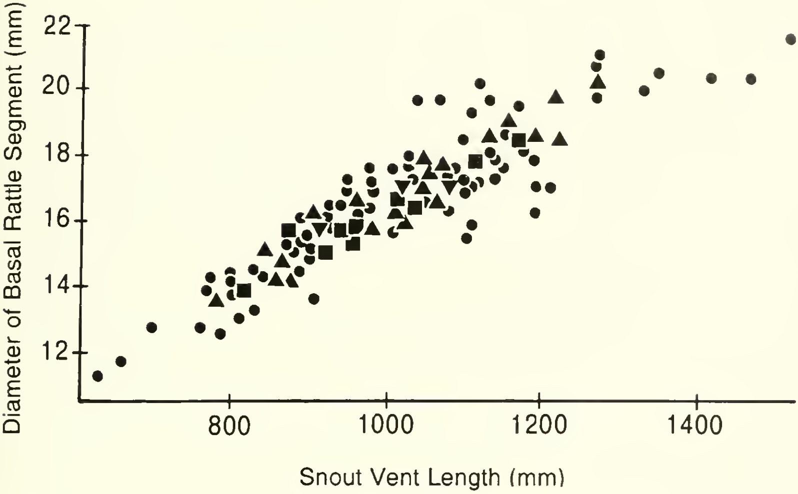


Fig. 4. The correlation between the diameter of the basal rattle segment and snout-vent length in *Crotalus atrox*. Circles represent one record, whereas triangles represent two records; squares represent three records and inverted triangles four records.

immature snakes have four segments plus button, whereas 55 others have five rattle segments plus the button and 51 possess six segments plus button. Each of the three latter groups is assumed to represent second-year young. The average snout-vent length of these snakes, 810 mm (813 in 82 males; 806 in 62 females), indicates that they are about 74% longer than their first-year counterparts. In the 1-yr period, these snakes gained an average of four rattle segments and the diameter of basal rattle segment increased from 8.16 to 13.7 mm, about 65%.

Correlations among numbers of rattle segments (in intact strings), size of rattle (diameter of basal segment), and body size (SVL) of *Crotalus atrox* are shown in Table 1 and Figure 4. For each rattle segment, beginning with the button, there is a wide range in rattle diameter and body length. The body size and the diameter of the basal rattle segment increase relatively rapidly as the first six segments develop during the fall period after birth and the first full growing season following hibernation; however, growth diminishes abruptly when the snakes reach adolescent size. Body sizes and sizes of new rattle segments continue to increase gradually in medium- and large-sized adults. The snakes acquire rattle segments 9–14 as young adults, evidently in their third, fourth, and fifth full growing seasons (April–October). At these ages, males are notably larger than females, but this sexual dimorphism is not as extreme as it is in old adults. After a snake has gained its tenth segment, size gains between sloughs

Table 1. Correlation between number of rattle segments, sizes of segments, and snout-vent lengths in male and female *Crotalus atrox*.

Sex	Number of rattle segments	Diameter of rattle segment			Snout-vent length of snake		
		$\bar{x}$	Range	n	$\bar{x} \pm$ SE	Range	n
Male	1	6.83	6.0 – 7.4	120	...	...	...
	2	8.32	7.3 – 9.9	164	467.60 ± 11.4	410 – 530	10
	3	9.47	8.5 – 10.8	195	509	...	1
	4	11.34	10.2 – 12.9	242	654	603 – 710	4
	5	12.35	11.5 – 14.8	289	706.04 ± 10.8	640 – 872	24
	6	13.74	11.5 – 16.2	277	823.97 ± 12.6	720 – 1065	38
	7	14.07	12.2 – 16.8	195	892.03 ± 19.4	755 – 1040	40
	8	15.34	12.7 – 16.8	195	937.70 ± 12.2	710 – 1080	57
	9	16.02	12.8 – 18.1	114	996.16 ± 10.4	815 – 1133	51
	10	16.54	13.1 – 19.8	77	1034.92 ± 13.0	865 – 1292	49
	11	16.35	14.6 – 18.7	21	1071.00 ± 12.4	882 – 1318	43
	12	16.71	14.3 – 18.7	22	1092.13 ± 17.5	942 – 1270	24
	13	17.13	15.1 – 18.7	13	1154.88 ± 12.3	946 – 1290	64
	14	17.34	16.0 – 19.0	11	1130.00 ± 15.1	970 – 1290	28
	15	17.54	13.8 – 18.1	5	1153.64 ± 14.0	1105 – 1280	14
Female	1	6.75	6.2 – 7.6	125	435	...	1
	2	8.00	7.2 – 9.3	139	445.38 ± 13.6	408 – 531	8
	3	9.46	8.4 – 11.7	161	537	492 – 582	2
	4	10.87	10.0 – 12.7	224	619.20 ± 14.2	588 – 595	5
	5	12.19	11.0 – 15.0	247	696.19 ± 14.4	572 – 850	21

Table 1. Continued.

Sex	Number of rattle segments	Diameter of rattle segment			Snout-vent length of snake		
		$\bar{x}$	Range	n	$\bar{x} \pm$ SE	Range	n
Female	6	13.66	11.2 – 16.2	228	807.97 ± 13.1	710 – 1010	34
	7	14.55	12.6 – 16.4	185	843.77 ± 19.6	700 – 1002	31
	8	14.56	11.2 – 16.8	117	910.14 ± 43.8	752 – 1040	36
	9	14.98	11.0 – 17.0	55	915.59 ± 11.1	752 – 1040	34
	10	15.08	12.8 – 18.3	37	987.46 ± 14.0	837 – 1093	21
	11	15.33	13.3 – 16.9	42	954.96 ± 13.1	800 – 1143	48
	12	15.08	12.8 – 16.7	16	979.22 ± 14.2	860 – 1140	36
	13	15.39	14.1 – 16.7	16	1006.04 ± 14.6	893 – 1105	24
	14	15.46	14.3 – 17.1	14	1018.42 ± 14.5	926 – 1100	12
	15	16.01	15.8 – 17.6	11	1035.54 ± 12.8	930 – 1066	13

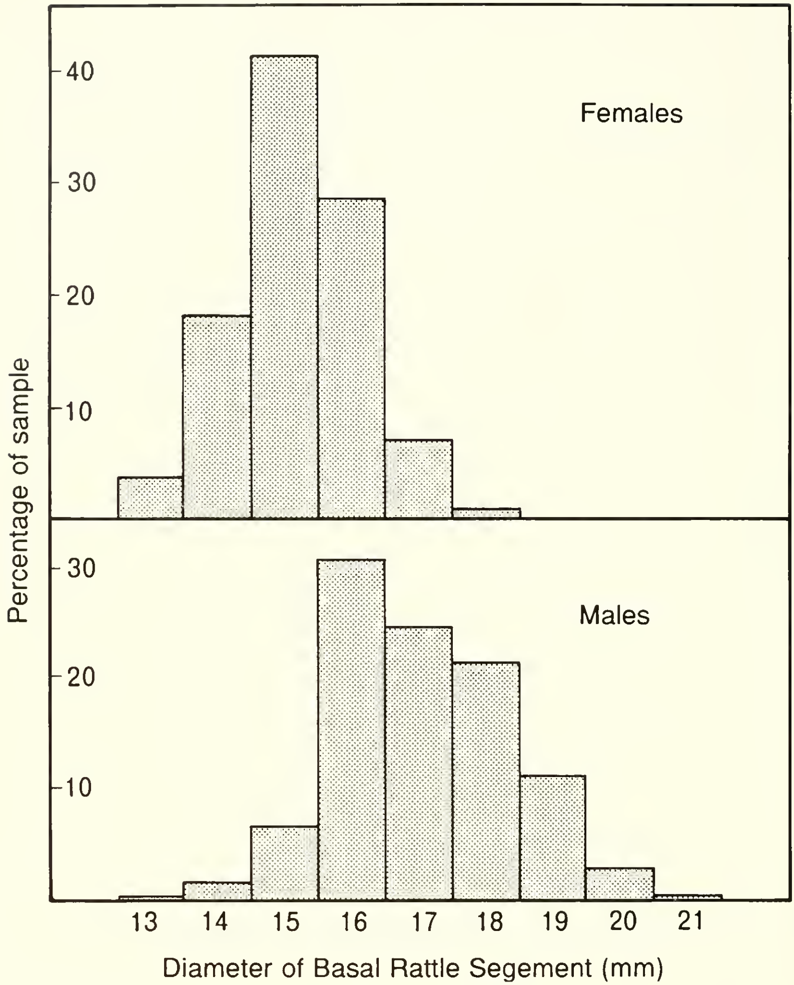


Fig. 5. Diameter of basal rattle segments in adult male and female *Crotalus atrox*.

usually are relatively small. The diameters of basal rattle segments in 645 fully adult snakes (413 males and 232 females) are shown in Figure 5. The basal rattle segment of most females is 15–16 mm in diameter, whereas the basal segments of most males are 16–17 mm in diameter. The largest snake examined (SVL 1520 mm, weight 2.78 kg) had a string of eight rattle segments, each of which was 21.5 mm in diameter.

Table 1 is based on the records of all snakes having complete or nearly complete strings that are tapered. Although some strings lack one or more

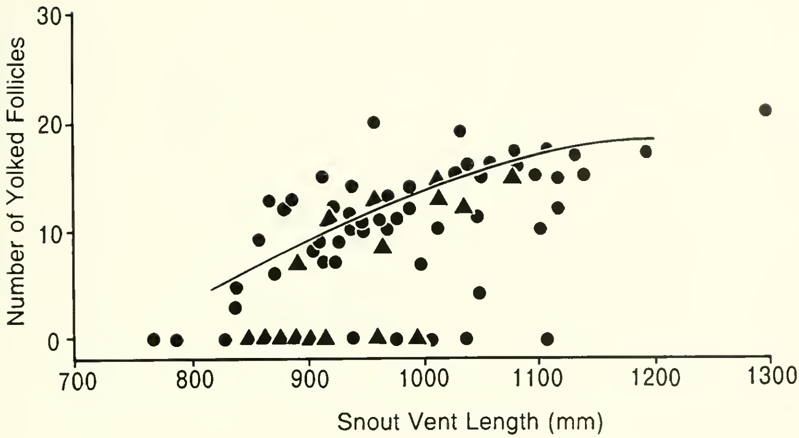
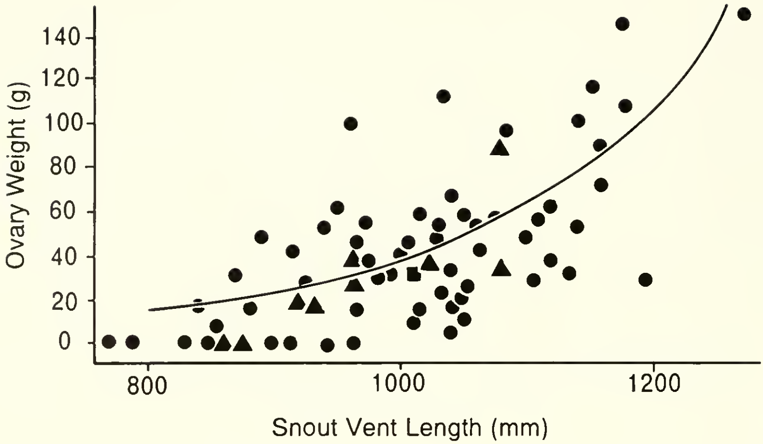


Fig. 6. Numbers of yolked follicles and snout-vent length in female *Crotalus atrox*. There is no reproductive activity in females with snout-vent lengths less than 800 mm. Reproductive activity is variable in females with snout-vent lengths between 800 and 1000 mm, whereas nearly all those longer than 1000 mm are reproductively active. Small closed circles represent one record and triangles represent two records.

terminal segments, the number of missing segments could be extrapolated. The longest intact rattle strings have 11 segments plus the button, and each of 15 incomplete strings has 13 segments. Based on measurements of basal rattle segments of primarily immature or adolescent *Crotalus atrox* that possessed complete strings, we calculated the average diameters of the button and each of the successive segments up to the tenth segment. Snakes having incomplete but tapered strings then were added. This permits projection of the pattern to adults that had produced as many as 16 rattle segments, even though they had lost one or more terminal segments.

Examination of Table 1 reveals several irregularities—e.g., some females are larger than their male counterparts, and there is a cohort that is older but slightly smaller than a younger cohort. These anomalies doubtless result from the heterogeneity of the sample with respect to differing rates of development in different areas (notably between northern and southern Oklahoma) or between years. Forty-three of the largest and presumably the oldest snakes (4.7% of the total sample) have untapered strings of large rattle segments. Untapered rattle strings indicate loss of the tapered rattle segments acquired during growth and, in some, loss of additional segments that the snakes acquired as adults.

In Table 1, snakes with one, two or three rattle segments are considered to be first-year young, whereas most of those with four (probably), five, six, or seven segments are considered to be in their second year. Klauber (1956)



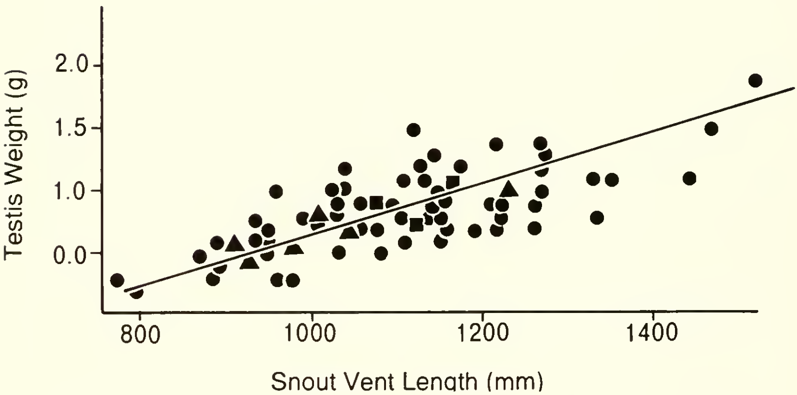


Fig. 7. Gonad weight and snout-vent length in *Crotalus atrox*. **Upper:** Ovary weight in female *Crotalus atrox*. **Lower:** Testes weight in male *C. atrox*. Circles represent one record, whereas triangles represent two records and squares represent three records.

recorded a total of 118 sloughs in a combined total of 50 "snake-years" in four captive *Crotalus atrox* kept active year-round; this amounts to an average of 2.3 sloughs per snake per year. Given an activity season of about 8 mo in Oklahoma, an adult diamondback might be expected to slough about 1.5 times each growing season or three times in 2 yr; thus, the 15 sloughs tabulated in Table 1, might represent the first 4–5 yr of the snake's life.

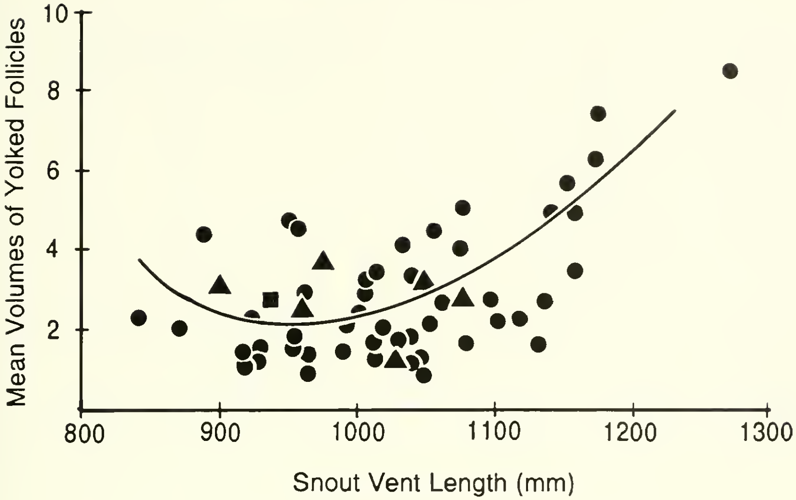


Fig. 8. Mean volume of yolked follicles correlated with snout-vent length in female *Crotalus atrox*. Circles represent one record, whereas triangles represent two records and squares represent three records

Reproduction

Most of the adult females that we examined had yolked follicles that were not fully grown, but that presumably would have matured to be ovulated later in the spring. In this respect, *Crotalus atrox* differs from species such as *C. horridus* and *C. viridis*, both of which emerge from hibernation with fully mature follicles that are ready to be ovulated (Fitch, 1985). Most ovarian follicles of *C. atrox* collected in April were about 30 × 10 mm, but some, especially those from large females, were considerably larger and others from relatively small females were smaller. Of the 59 female snakes examined that were longer than 900 mm (SVL), 54 (91.5%) were ovigerous; in contrast, of the 11 individuals that were less than 900 mm in length, only four (36.5%) were ovigerous (Fig. 6). Probably most females in the 800–899-mm size range and some of those in the 900–999-mm size range were immature second-year young. The correlation between ovary weight (and testis weights for males) and snout-vent length is graphically depicted in Figure 7. All ovaries of adult females (n = 25) longer than 1050 mm SVL had yolked follicles. We conclude that *C. atrox* bear litters annually in Oklahoma and that most individuals mature and produce their first litters as 3-year-olds. (See Growth and Rattle Development, above). Recent studies support the idea that rattlesnakes are highly efficient sit-and-wait predators that convert the prey into their own biomass (Derickson, 1976; Ford and Seigel, 1990; Gibson et al., 1990; Secor, 1990).

Table 2. Composition of population sample of *Crotalus atrox* according to sex (females represented by boldfaced numbers), length, number of rattle segments[1], and estimated age. Indet. = indeterminate age.

	Rattle segments (estimated years of age)																	
SVL	1–3 (1)		4–7 (2)		8–10 (3 & 4)		11–13 (5 & 6)		14–16 (7 & 8)		17–19 (9 & 10)		20–22 (11 & 12)		23–25 (13 & 14)		Indet.	
400–499	8	**7**																
500–599	5	...	...	**4**														
600–699	...	...	12	**16**														
700–799	...	...	33	**35**	6	**4**												
800–899	...	...	35	**29**	26	**30**	...	**11**	...	**2**								
900–999	...	...	24	**14**	62	**59**	10	**51**	4	**14**	...	**6**	...	**2**				
1000–1099	...	...	3	**3**	59	**29**	37	**24**	14	**11**	6	**16**	1	**3**				
1100–1199	...	...	...	...	16	...	40	**5**	39	**4**	22	**5**	5	**2**				
1200–1299	...	...	...	...	3	...	8	...	13	...	13	...	2	...	3	...	10	...
1300–1399	...	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	10	...
1400–1499	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	5	...
1500–1599	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...

[1]Value extrapolated for those individuals with incomplete but tapered strings.

Table 3. Lengths, weights, and numbers and sizes of rattle segments in largest and oldest *Crotalus atrox* of sample.

			Rattles			
				Diameter		
SVL	Weight (g)	Source	No. segments	Basal segment	Terminal segment	Probable age (yr)
1520	2776	Waurika, 1988	8	21.5	21.5	12
1450	3042	Waurika, 1988	12	21.3	21.6	14
1414	2466	Okeene, 1989	13	18.3	19.0	13
1400	2110	Mangum, 1988	8	20.4	20.6	11
1330	2152	Waurika, 1988	9	19.4	10.9	11
1310	1550	Okeene, 1989	13	19.2	19.2	12
1378	1860	Mangum, 1988	8	19.0	18.8	10
1351	1540	Waurika, 1988	8	20.1	20.4	11
1242	1550	Okeene, 1988	10	19.3	19.2	10
1213	1450	Okeene, 1988	11	17.4	17.5	11
1208	1400	Mangum, 1988	9	17.8	17.8	11

Fat constitutes, on an average, 10.1% of the body weight in female *Crotalus atrox* with yolked follicles; in males, 6.4% of the body weight is fat and 7.9% and 7.4% of the body weight is fat in nongravid females and the smallest gravid females (those less than 950 mm SVL), respectively. The relationship between mean follicle volume and snout-vent length is depicted in Figure 8. However, in each of these categories the extent of abdominal fat deposits was highly variable. Females having large follicles could usually be recognized by their plump appearance. Their follicles could be detected by abdominal palpation, but because the follicles were closely adherent, attempts to count them in live snakes were not successful. Abdominal fat deposits were prominent in females having large follicles. Presumably the large stores of fat in gravid females facilitate rapid growth, maturation, and ovulation of their follicles.

In the 138 ovigerous ovaries that we examined, the average number of relatively large yolked follicles is 13 ± 0.374 (range = 4–24; Fig. 6). Klauber (1956) reported an average brood of nine (4–23) from observations of litters born and dissections of snakes with ripe follicles. He noted the occurrence of exceptionally large litters of 22, 23, 24 and 46 (with 20 dead young and 26 alive). Armstrong and Murphy (1979) recorded viable litters of 6–25 in nine captive broods of *Crotalus atrox* from females captured in Mexico; they found that young matured in 30–36 mo in captivity. Tinkle (1962) examined a series of 62 ovigerous females from northern Texas and

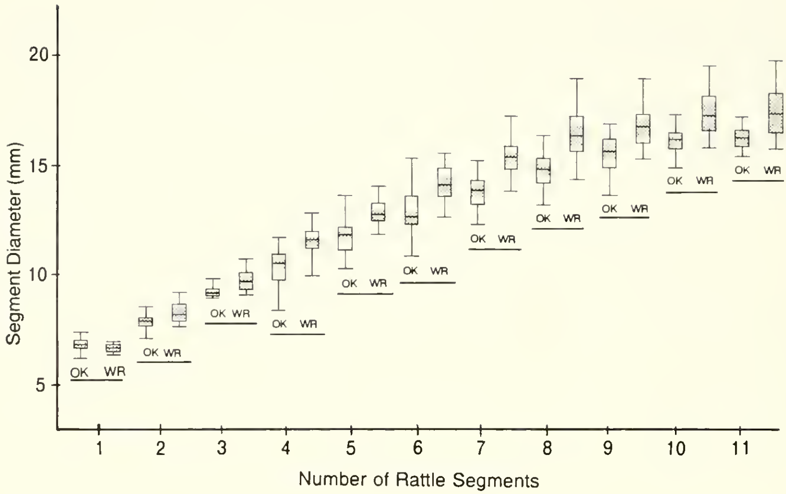


Fig. 9. Diameters of successive rattle segments in male *Crotalus atrox* from the Okeene (OK) and Waurika (WR) roundups. For each series, the mean, standard error, standard deviation, and range are shown.

estimated an average brood of 14.3 to be the maximum potential (if some undersized ova were included). He found egg complements to be proportional to female size; thus, excluding undersized ova, he noted females less than 900 mm SVL averaged 10 ova, those 901–1000 mm in length averaged 13 ova, and snakes 1001–1100 mm averaged 16 ova. Tinkle's criterion for female reproduction was presence of ovarian follicles greater than 8 mm in diameter; such a follicle should be about 12 mm long with a volume of about 603 mm^3. Our criterion was more restrictive (mean volume of yolked follicles exceeding 790 mm^3) and our smallest female possessing yolking follicles had a mean follicle volume of 2295 mm^3. Tinkle concluded that females of the *C. atrox* population that he studied reproduced biennially and it has been assumed generally that this pattern applies to the species throughout its range. However, our results indicate annual, rather than biennial reproduction in fully mature females in Oklahoma. Most of Tinkle's snakes were from elevations of 610–915 m, near the northern limits of the species' range, where climatic constraints may have affected their reproduction. There were infertile eggs and/or inviable young with most litters. Klauber (1956) estimated that these combined categories average about three per brood. Therefore, the means of 13 and 14.3 follicles found by us and by Tinkle, respectively, might translate to no more than 10 viable young per litter.

The observed correlation between numbers of follicles and snout-vent length suggests that litter size tends to increase with body size up to a

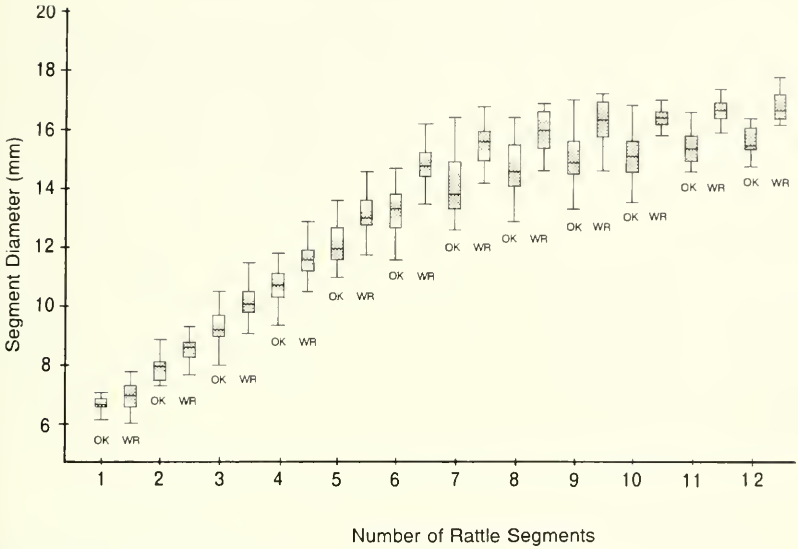


Fig. 10. Diameters of successive rattle segments in female *Crotalus atrox* from the Okeene (OK) and Waurika (WR) roundups. For each series the mean, standard error, standard deviation and range are shown.

maximum of about 16 young (Fig. 6). Correlation of follicle size with snout-vent length indicates that the largest females increase follicle volume rather than follicle number (Fig. 8). It is possible that neonates from the largest females are larger at birth or that they possess a greater store of postpartum yolk, either of which probably would increase juvenile fitness. However, the relatively large yolks of the largest females also may indicate that these individuals were more advanced in the yolking process than smaller females, because ova were still growing at the time of the roundups. Such accelerated development in large females might increase fitness in their young if they are born relatively early in the season.

Population Structure

The population structure of our sample of *Crotalus atrox* from Oklahoma is tabulated on the basis of sex, size, age, and rattle number in Table 2. Males were more numerous than females in each age class in our sample. The oldest group of snakes (judged either on the basis of unusually large size or of numbers of rattle segments present) were all males. Perhaps females are subject to somewhat higher mortality. A tentative age and total number of rattle segments was assigned to each individual snake based on the number of rattle segments present and the diameter of the terminal segment. For instance, a male snake with a string of seven rattle segments

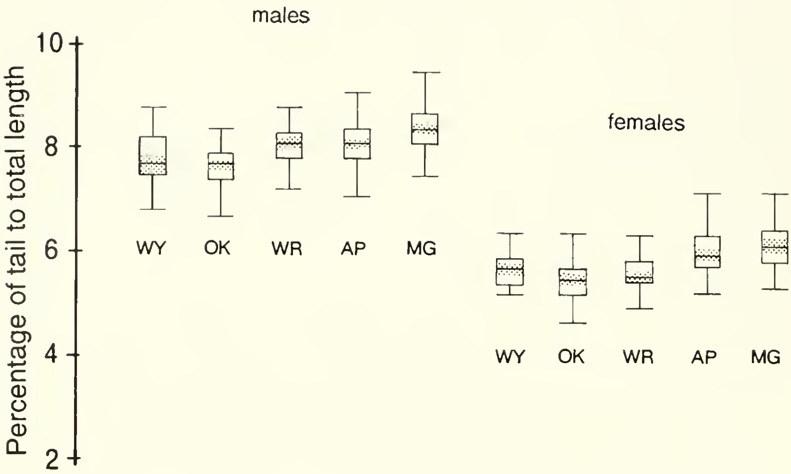


Fig. 11. Comparison of relative tail lengths in male and female *Crotalus atrox* from the five Oklahoma roundups. For each series the mean, standard error, standard deviation, and range are shown. AP = Apache; Mg = Mangum; OK = Okeene; WR = Waurika; WY = Waynoka.

and a terminal segment 15.7 mm in diameter is estimated to have already lost eight segments, including the natal button and to have been in the third-and-fourth-year cohort when he produced the 15.7-mm segment. The six rattle segments produced in the interval between his production of the 15.7-mm segment and his capture would raise his total to 13 and probably would span about 4 yr, allocating him to the seventh-and-eighth-year cohort. It is assumed that each snake produces one rattle segment in the fall after its birth and four segments in its first full growing season, and that adults produce segments at the rate of three every 2 yr. There is evidence for this schedule in a typical snake, but individuals vary. The accuracy of our estimates may be affected by the following factors: (1) *Crotalus atrox* in nature may not produce rattles at a rate comparable with that found by Klauber for zoo captives; (2) males may produce rattles at a faster rate than do females (Fitch, 1949); (3) young adults may produce rattles more rapidly than old adults; and (4) the amount of food consumed may drastically affect the number of sloughs.

The number of first-year young recorded in Table 2 is low. They probably make up as much as 40% of the spring population; this is supported by the statements of the snake hunters. A little more than half the snakes in our sample were second-year adolescents and young adults of the third-and-fourth-year age groups, indicating a rather rapid population turnover. It seems that annual adult mortality is about 20%. Five percent of our sample, a total of 46 snakes, was judged to be more than 10 yr old on the basis of

Table 4. Results of *t*–tests of tail-length ratios in southern (Apache-Waurika-Mangum) versus northern (Waynoka-Okeene) samples of male and female *Crotalus atrox*. SD = standard deviation; DF = degrees of freedom.

	Male populations		Female populations	
Statistic	Southern	Northern	Southern	Northern
Mean	8.2	7.7	6.0	5.5
SD	0.005	0.005	0.005	0.004
No. observ.	256	115	174	80
t–statistic	9.527	...	7.731	...
DF	369	...	252	...
Significance	0.001	...	0.001	...
Hypothesis	H_0: $\mu^1 = \mu^2$ H_a: $\mu^1 \neq \mu^2$		H_0: $\mu^1 = \mu^2$ H_a: $\mu^1 \neq \mu^2$	

large size and evidence that they had produced at least 20 rattle segments. Table 3 provides information concerning 11 of the largest and probably the oldest snakes examined, all of which are males. Their terminal rattle segments were of diameters usually not attained before an age of 10 yr, and the strings of 7–12 additional segments represent added spans of minimally 4–8 yr.

Although the segments of a typical rattle string progressively increase in diameter from the terminal button distally to the most proximal segment, occasionally, immature snakes bear two adjacent segments of exactly the same diameters. This probably indicates that no growth occurred from the time of one shedding to the next. In fact, growth rate is extremely variable among individuals and in the same individual at different times. Normal growth may be resumed after a temporary suspension indicated by uniform-sized rattle segments. When a rattle diameter of 17 mm (males) or 15 mm (females) had been attained usually about the fifth year (after 9 or 10 segments had been produced), growth became much slower. Several or many sloughs might be required to gain an additional millimeter in rattle diameter. A study of 1836 rattle measurements in adults showed increasing incidence of no-growth rattle segments in longer strings. In segments 13–19 of medium to large adults, there was actually a *decrease* in diameter from one segment to the next proximal segment in 3.4% of 1463 segments measured. An additional 22.3% showed no growth. Probably the observed decreases in rattle size occurred when snakes experienced exceptionally rigorous environmental conditions and severe undernourishment.

In contrast, occasional snakes demonstrated rapid and uninterrupted growth to near maximum size and rattle diameter. For example, a male from Mangum has a snout-vent length of 1260 mm and a string of eight rattle segments, with diameters of 20.5, 19.8, 19.6, 18.8, 17.7, 16.5, 14.8 and 13.1. If his early development was typical, he might have acquired his terminal segment of 13.1 mm in diameter as his sixth when he was about 1 yr old or a little less, and produced the seven additional segments in the next 4 yr. At this rate of growth, he would have been producing a rattle segment of near maximum size (20.5 mm) at an age of only about 5 yr.

Geographic Variation

Although *Crotalus atrox* has no recognized subspecies, it is subject to geographic change within its extensive range. Body size and pattern vary noticeably from one area to another; the variation may be genetic in part and also the result of environmental effects. Even within Oklahoma, there are minor differences among local populations. At the Apache roundup, snake-catchers pointed out well-defined differences between the lots of snakes from different habitats, respectively those from the sandy, rolling bluffs of the Red River area and those from the rugged granitic terrain of the Wichita Mountains. The snakes from this latter habitat have more sharply defined markings and are thought to have shorter rattle strings on the average, putatively because they are subject to more rapid wear on the rough rock surfaces.

There are significant differences in rattle growth (presumably reflecting SVL growth) between snakes from Okeene in the north and Waurika in the south (Figs. 9–10). In both groups, the average size of the natal buttons is approximately the same, but the segments added subsequently are consistently larger in the Waurika snakes than in their Okeene counterparts. The season of activity begins a little earlier and lasts a little longer for the more southern snakes, but it might be expected that this would result in earlier shedding rather than larger rattles. Perhaps the Waurika snakes have evolved to be genetically larger or perhaps they have a better food supply. The three largest snakes in our overall sample were from Waurika.

Subtle variation among local populations includes differences in relative tail length (Fig. 11). Subsamples from each of the five roundups have slightly different average relative tail length, with snakes from the more southern localities (and especially Mangum) having significantly longer tails (Table 4). Tail length, of course, is subject to allometric growth. In male neonates, relative tail length is already somewhat greater than in female neonates. In adults, the sexual difference is more than doubled, with females having a relative tail length slightly less than that of neonates, and males having a relative tail length that is markedly greater than that of neonates. Differences in the age structure of populations probably cannot account for variation among samples shown in Figure 11.

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