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A Comparison of Growth and Rattle Strings in Three Species of Rattlesnakes

By

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INTRODUCTION

The rattlesnake rattle was evolved in these highly venomous animals as a sematic organ to warn away potentially harmful animal associates, and perhaps particularly those that might unintentionally kill or injure a snake by trampling. The megafauna of North America included many large herbivores which might have posed a threat until the end of the Pleistocene more than 10,000 years ago. The evolution of the rattle involved a shortening of the tail, development of a complex musculature for its rapid vibration, and change in its shape, with transverse constrictions to hold the edge of the slough in place (Klauber, 1956). When the tail tip is shed, its dried slough continues to cling to the tail and eventually, after several or many sloughs, the loosely interlocking rattle segments, rapidly vibrated, have the potential to produce the characteristic buzzing sound of warning.

Klauber (1956) described the tapered rattle strings of juvenile and adolescent rattlesnakes and the untapered, parallel-sided strings that are found in many adults. In some snakes there is a reverse taper, that is a segment farther out on the string from the snake's body is larger than its nearest proximal segment. It is generally assumed that the undersized segments are produced because the snake is undernourished. Klauber (1956:274) had access to the many live snakes in the San Diego Zoo, and noted "...in captive specimens, segments acquired subsequent to captivity, particularly if the snake has failed to eat, may be smaller than those that had previously been acquired in the wild..."

MATERIALS AND METHODS

I attended seven rattlesnake roundups in Oklahoma; those at O'Keene and Apache were attended in 1988 and 1989, but those at Mangum, Waurika, and Waynoka were attended only in 1988. The snakes at these roundups were almost exclusively *Crotalus atrox* (Fitch and Pisani, 1993). I attended the roundup at Sharon Springs, Kansas, in 1992, 1993, 1994, and 1995; all snakes were *C. viridis*. When time allowed, each rattle segment was measured separately, but when large numbers of snakes were available for checking, only the length of the rattle string and the number of segments were recorded. The sample of *C. horridus* was based on snakes captured on or near the Fitch Natural History Reservation (FNHR), the Nelson Environmental

Study Area (NESA) and nearby areas in northeastern Kansas, one snake at a time. Rattle segments of timber rattlers were not individually measured until 1984. During routine checking of specimens at rattlesnake roundups in Kansas and Oklahoma I noticed that many adult snakes possessed untapered rattle strings with segments of uniform size, and in fewer individuals the more distal segments occasionally were slightly larger than those nearer the tail that had been shed earlier. In a rattlesnake the usual taper in more distal rattles reflects increased body size as the individual grew. Presumably undersized rattle segments are produced because of undernourishment and represent periods of stress in the lifetime of the snake. However, experimental evidence is largely lacking. The purpose of the present study was to compare the rattle strings in three species, *Crotalus atrox*, *C. horridus* and *C. viridis*.

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I thank the Oklahoma Department of Wildlife Conservation Nongame Program, and the Kansas Department of Wildlife and Parks for sponsoring my trips to the roundups in their respective states. Individuals who deserve special thanks for helping me at the roundups, even to the extent of handling the live snakes to control them while they were being examined by me include: Robert Clark, Deborah Cowman (Mrs. Donald A. Clark), Virginia Fitch, Hank Guarisco, David Reber, Randy Reiserer and Travis Taggart. My daughter, Alice Fitch Echelle, helped me with the manuscript in many ways.

Study Area (NESA) and nearby areas in northeastern Kansas, one snake at a time. Rattle segments of timber rattlers were not individually measured until 1984.

Nearly half the sample of *Crotalus horridus* was obtained in September and October, partly because neonate snakes were relatively abundant at that time of year, but also because field work was concentrated along the rocky, wooded hilltop edges that are favored timber rattlesnake habitat; 35 (43.3%) of the September-October sample were first-year young. In contrast, only 2.2% of the *C. atrox* sample and 2.6% of the *C. viridis* sample were first-year young (Fitch, 1999, 2000). Snout-vent length is abbreviated SVL.

RESULTS

Traits of rattle strings.—Although adult snakes may continue to grow slowly, the increment from one rattle to the next is so small as to make no noticeable difference in the size of the segments. Large and old rattlesnakes often have strings of several or many rattles with segments

appearing to be just the same size. Segments of the same size and segments with reverse taper occur frequently in all three species, but are most common in *Crotalus horridus* (Tables 1-3; Fig. 1). Reverse taper rarely occurs in more than one segment. Klauber (1956:279) stated "an

Table 1. Rattle number and body size in three species of rattlesnakes. Snout-vent length (SVL) includes mean \pm 1 standard deviation, followed by range in parentheses.

Intact rattle segments	<i>Crotalus atrox</i>				<i>Crotalus horridus</i>				<i>Crotalus viridis</i>			
	Males		Females		Males		Females		Males		Females	
	N	SVL	N	SVL	N	SVL	N	SVL	N	SVL	N	SVL
1	0	—	0	—	22	413.1 \pm 118.3 (298–495)	21	346.2 \pm 109.0 (305–422)	2	299.5 (297–302)	4	313.7 \pm 12.4 (284–328)
2	15	480.1 \pm 43.3 (436–530)	11	441.4 \pm 26.6 (408–492)	2	506.0 (482–530)	1	495.0	2	333.0 (318–348)	2	331.5 (308–355)
3	4	545.5 \pm 21.8 (509–582)	0	—	10	614.4 \pm 22.0 (593–678)	3	574.3 \pm 25.9 (548–610)	1	500	0	—
4	2	706.0 (702–710)	10	619.3 \pm 29.3 (588–660)	4	635.3 \pm 66.7 (577–712)	1	590.0	10	583.6 \pm 39.9 (504–660)	5	574.0 \pm 31.6 (510–610)
5	26	714.3 \pm 78.7 (615–830)	35	717.6 \pm 92.6 (592–1006)	6	735.7 \pm 56.1 (647–816)	5	715.6 \pm 128.7 (504–802)	13	659.1 \pm 30.1 (600–710)	2	683.0 (640–726)
6	56	804.1 \pm 70.2 (632–905)	35	793.9 \pm 59.7 (700–914)	5	803.2 \pm 95.0 (658–896)	3	858.0 \pm 43.0 (860–914)	17	740.2 \pm 68.4 (628–860)	14	753.6 \pm 69.4 (672–930)
7	44	895.4 \pm 67.4 (770–975)	32	885.0 \pm 90.1 (715–942)	5	851.2 \pm 112.2 (716–955)	6	849.0 \pm 48.5 (800–902)	39	800.7 \pm 60.2 (696–940)	29	792.0 \pm 48.2 (670–875)
8	48	1039.0 \pm 83.1 (755–1078)	32	930.0 \pm 70.9 (752–1023)	3	958.0 \pm 87.6 (880–999)	6	867.0 \pm 36.3 (812–900)	32	852.2 \pm 72.5 (681–965)	30	829.0 \pm 56.6 (700–930)
9	46	1039.0 \pm 12.8 (863–1230)	25	918.8 \pm 70.2 (780–1058)	5	881.2 \pm 65.4 (790–960)	3	919.3 \pm 35.1 (883–953)	32	882.2 \pm 57.5 (766–1025)	24	864.5 \pm 59.2 (760–970)
10	36	1077.9 \pm 88.3 (900–1270)	23	972.0 \pm 68.5 (810–1193)	1	980.0	3	905.3 \pm 41.3 (880–953)	24	864.5 \pm 59.2 (786–1050)	18	873.0 \pm 74.9 (796–1065)
11	15	1138.0 \pm 70.4 (963–1215)	21	963.6 \pm 54.1 (838–1040)	2	980.0 (970–990)	4	916.0 \pm 82.7 (802–977)	20	948.7 \pm 60.2 (830–1020)	12	904.4 \pm 55.1 (820–987)
12	17	1085.0 \pm 77.5 (902–1169)	13	971.6 \pm 60.4 (900–1110)	3	1060.0 \pm 79.4 (1000–1150)	1	977.0	15	971.4 \pm 66.3 (815–1080)	9	922.9 \pm 43.5 (860–965)
13	21	1121.0 \pm 80.9 (990–1265)	5	984.2 \pm 37.9 (926–1030)	3	1022.0 \pm 20.3 (1000–1040)	3	916.0 \pm 82.7 (802–977)	4	960.0 \pm 73.9 (870–1050)	2	852.0 (824–880)

investigation of long broken strings on wild rattlers shows clearly that the rattle-width increment eventually does fall to zero, and long before this happens the increment is completely masked by fluctuations in width up to 5 per cent on either side of the mean."

Correlation of age, size and rattle.—The sample of *Crotalus horridus* was accumulated over 53 years from the FNHR and vicinity. With the exception of seven snakes that were found as traffic casualties on county roads, the snakes of this sample were processed alive, individually marked, and released. Seasonal distribution of the 153 snakes (and percentages of young of the year) in this sample was: April 2.6% (40%), May 14.4% (24%), June 13.1% (9%), July 9.2% (23%), August 11.1% (0%), September 23.9% (23%), October 23.5% (58%), November 3.2% (50%). Two newly captured females gave birth to litters on 29 and 30 August, 1994. The mean SVL of young of two litters was 326.4 mm. Early growth in mean SVL is shown by 12 wild-caught young in September (344.9 mm), 19 in October (377.8 mm) and four in May (389.8 mm). One captured on 1 June 1958 still had only the natal button; three others captured in June (1) and July (2) each had two rattle

segments plus the button. Young with two segments plus a button were observed in May (1), June (1), August (1), September (2) and October (5). Young with three segments plus the button were found in June (3), September (1), and October (2), and those with four segments and a button were found in May (2), June (2) August (1), and October (6). The smallest gravid female (860 mm SVL) was captured in May. At an age of one year, most young have two rattle segments plus the original button, and two-year-olds typically have five rattle segments including the button, but they may have four or six segments. At an age of three years they are sexually mature and typically have six segments plus the button. Adult males that were recaptured usually conformed most closely to the pattern of two rattle segments gained per year. Only one adult female was captured long after marking and had gained three segments in approximately three years; thus an average (modal) gain of one rattle segment per year is tentatively accepted for adult female *C. horridus* (Fitch, 1985).

In a litter of 18 *C. viridis* born on 1 September to a freshly captured female from Sharon Springs the mean SVL in 11

Table 2. Extent of reverse taper in adults of three species of rattlesnakes.

Species	N	Mean percentage of next distal segment		
		Males	N	Females
<i>Crotalus atrox</i>	49	94.4	55	97.0
<i>Crotalus horridus</i>	14	95.8	15	96.7
<i>Crotalus viridis</i>	41	93.0	37	93.2

males was 268 mm, and seven females were the same. In the samples in the spring from Sharon Springs, there were 10 individuals that were obviously first-year young; four males had a mean SVL of 316 mm and six females 317 mm. These young are estimated to have had about 60 days of active life and had grown to be 48 mm longer than neonates, an average gain about 0.8 mm per day) in SVL if they were 268 mm at birth. At the time of the spring roundup, young with two rattle segments and a button were rare (only one found), but those with three segments plus button or four segments plus button were fairly common and obviously represent the second-year age class; 26 of them had a mean SVL of 618 mm. Thus, they had grown 302 mm on average (618 minus 316) in about 184 days of activity for the year. The early growth rate of 0.8 mm per day during the first two months had doubled to 1.6 mm per day (Fitch, 1998, 2000, Fitch and Pisani, 1993).

In an early study of *Crotalus viridis* in southeastern Wyoming, Rahn (1942) found that females in hibernation or emerging in spring had two types of oviducts: 1) active, filled with large ova, and 2) empty and shrunk; it seems that after giving birth females take a year out from breeding to rest, feed, and recuperate, and about half are productive in any one year. This was an influential paper. Subsequently it was assumed that the biennial cycle is the usual one in *C. viridis* and other Temperate Zone rattlesnakes. But *C. viridis* is known to be a plastic and variable species. The biennial breeding cycle occurs only in the northern Great Plains. At the latitude of Kansas, the majority of females (82% in my roundup sample) are reproductive. Farther south reproduction is annual, whereas at the northern edge of the range females may be triennial. Studies based on mark and recapture records are

needed. No data are available for Kansas but a study of *C. oregonus* in California (Fitch, 1949) supports the idea that emerging young in spring can be sorted into age classes on the basis of their rattles; first-year young may have only a button or may have one additional segment and second-year young have three or four additional segments plus the button. Other findings concerning *C. oregonus* in California might also apply to the Kansas population, e.g., an average of 1.5 rattle segments per year gained in adult males and 1.1 segments in adult females. *C. oregonus* and its subspecies were long considered conspecific with *C. viridis* until separation by Ashton (2001).

In *Crotalus atrox* from the Oklahoma roundups growth can be followed similarly. No neonate *C. atrox* were seen in the course of my study, but according to Klauber (1956) the average SVL is 330 mm. From the time of birth in the fall to the roundup the following spring, I estimate they may have an average of about 75 days of activity and, if so, the mean gains, 152 mm for males and 115 mm for females would amount to 2.02 mm per day for males and 1.53 mm for females. Second-year *C. atrox* are surely represented by snakes with three rattle segments and a button (1 male, 5 females) plus those with four segments and a button (20 males, 18 females), five segments and a button (30 males, 26 females), and perhaps most of those with six segments plus a button (22 males, 14 females). These groups include a total of 73 males (average SVL of 788.3 mm) and 63 females (average SVL of 718.8 mm), thus they had gained an average of 306 mm (males) and 275 mm (females) over the lengths of spring young that were one year younger. The relatively long growing season in the range of *C. atrox* extends to perhaps 200 days, thereby indicating length gain per day of 1.53 mm in males and 1.38 mm in females. Thirteen first-year snakes had SVLs of 408-530 mm, and 37 second-year snakes had SVLs of 588-750. Beyond the second year there is so much overlap in size between age-classes that the limits of age classes cannot be discerned.

Klauber (1956) emphasized the great amount of variation in rattle strings and stated that the number of segments lost from incomplete strings could not be estimated accurately from the size of those remaining. I

Table 3. Comparison of adult rattle segments in three species of rattlesnakes.

Species	Sex	Number of snakes	Adult rattle segments	Adjacent same-size segment pairs	Percent	More distant segment larger	Percent
<i>Crotalus atrox</i>	♂	259	2132	460	21.8	59	2.8
	♀	191	1400	399	28.5	38	2.7
<i>Crotalus horridus</i>	♂	27	134	72	53.7	15	11.2
	♀	18	96	45	46.9	12	12.5
<i>Crotalus viridis</i>	♂	175	690	2045	29.6	43	6.2
	♀	108	417	171	41.1	35	8.4

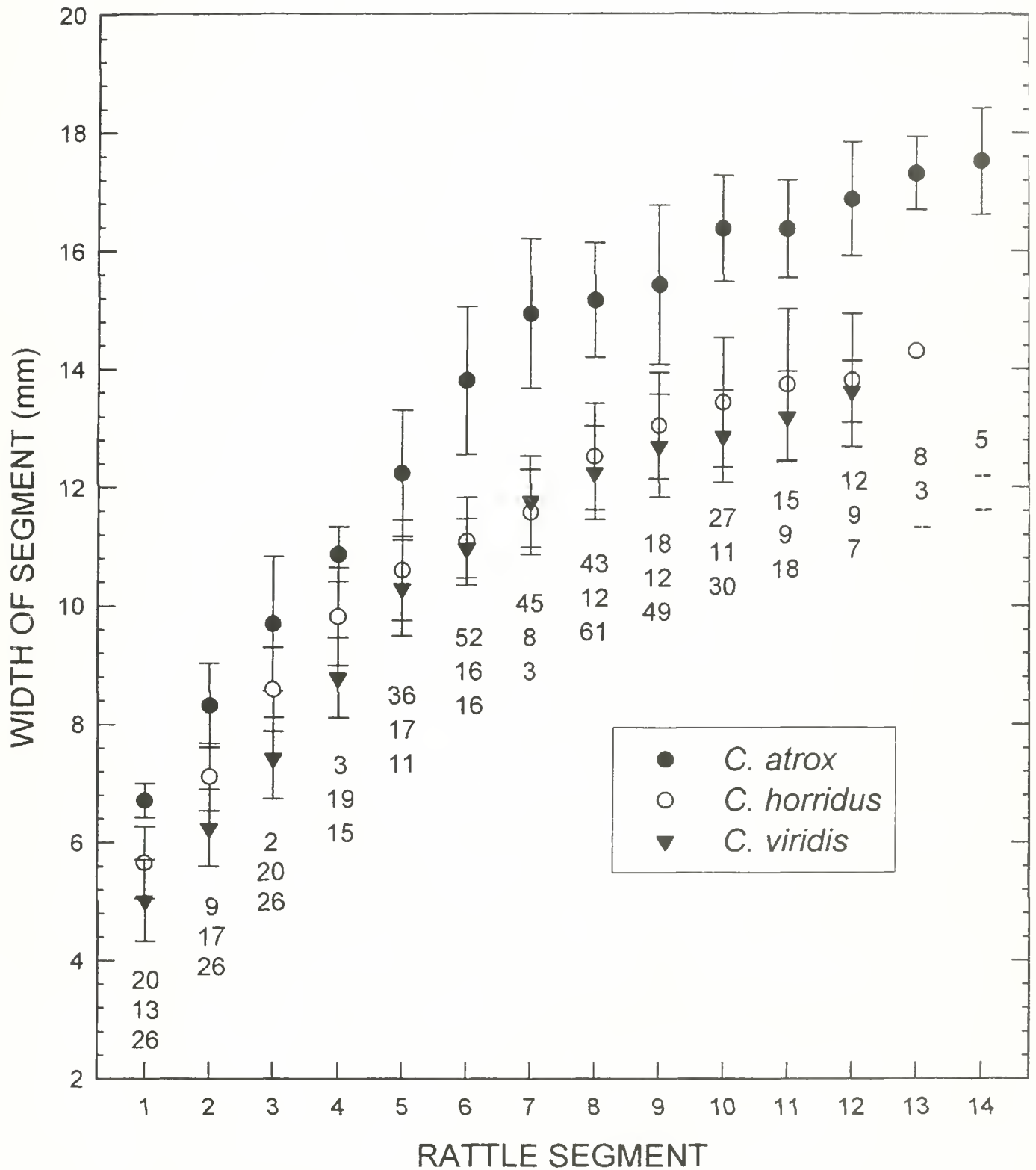


Fig. 1. Sizes of rattle segments are shown, according to sequential number in three species of rattlesnakes. All three species have strong sexual dimorphism in size of body and sizes of rattle segments. The sexes are combined in these samples. In each set of three figures, the upper one shows the numbers of *Crotalus atrox*, middle *C. horridus*, and lower *C. viridis*. The horizontal lines indicate one standard deviation from the mean, above and below for each series.

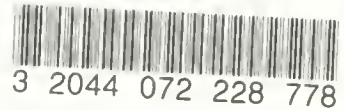
agree with Klauber that estimates are subject to error, but the terminal segments do reflect the size of the snake at the time they were formed and the taper of the string reflects the trend of growth. If only two or three segments plus the button are missing, the estimate will be correct more often than not. Although individual estimates are subject to error, they work well enough to divide a population into putative age groups, as Klauber did. Males are consistently larger than females that have the same number of rattle segments. For any rattle number there is a wide range of variance in length of snake with the shortest only 70 to 80 per cent of the longest, and with the variance in males somewhat greater than it is in females.

In the sample of 1011 *Crotalus atrox*, the largest and oldest snakes that had untapered rattle strings were only

4.2% of the sample, which consisted essentially of adults and adolescents, because first- and second-year young could not be collected legally at the roundups. The same constraints apply to samples of *C. viridis* from Sharon Springs, but in these samples the snakes were younger on average than in *C. atrox*. There were only four snakes (2 males, 2 females, 0.09% of sample) that were exceptionally large and had rattle strings consisting of several or many segments with no discernible taper. In the sample of *C. horridus* nearly one-third were first-year young; second-year young and adolescents also were well represented. However, there were eight large and old adults (5.3%) that lacked noticeable taper. It seems that *C. horridus* is longer-lived than *C. viridis* on average, and tends to resemble *C. atrox* in this respect.

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