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OBSERVATIONS ON RATTLE SIZE AND
DEMOGRAPHY OF PRAIRIE RATTLESNAKES
(*CROTALUS VIRIDIS*) AND TIMBER RATTLESNAKES
(*CROTALUS HORRIDUS*) IN KANSAS

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INTRODUCTION

Detailed life history studies have made possible interspecific comparisons of demographic parameters such as reproductive potential, age-specific mortality, and survivorship. These data are usually obtained from recaptures of marked individuals. However, these same parameters may be investigated from direct observation of population samples.

Here I provide demographic comparisons of two species of rattlesnakes, the prairie rattlesnake (*Crotalus viridis*) and the timber rattlesnake (*Crotalus horridus*). Few mark-recapture studies of rattlesnakes have been undertaken, but these snakes are unusual in carrying a record of individual growth and shedding, the rattle, consisting of accumulated successive sloughs from the tail tip. The correlation between size, age, and rattle number facilitates analysis of population composition through allocation of individuals to their annual cohorts.

As clarified by Klauber (1956) and other authors, each rattlesnake is born with the tail ending in an epidermal, keratinous tip, the "prebutton." Within a few days after birth the young snake sheds its skin, and the expanded knobby base of the corneous tail tip is then exposed, the whole structure being the snake's first rattle segment, the "button." At each subsequent shedding a new rattle segment appears, as each is actually shed skin from the terminal portion of the tail tip, designed by its shape to cling to the tail base. A typical rattle segment consists of three lobes, anterior, middle, and posterior, separated by deep transverse grooves. Except on the terminal rattle segment, only the anterior (proximal) lobe of each

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segment is exposed to view, as the second and third lobes fit inside the next posterior (more distal) segments and provide bases of attachment. As the snake ages and sheds, its rattle lengthens; the button and other terminal segments eventually are lost. Because each rattle segment has posteriorly tapering lobes, the rattle string may taper to the rear even if the snake is an older one that has lost its button and early rattles acquired during its first few years of active growth. There is widespread misunderstanding of this sequence and most lay observers do not distinguish between intact rattle strings ending with the original button and incomplete strings that lack the button and other early rattles lost through wear or accident. However, the button is of relatively small basal diameter, is rounded, and is loosely attached, whereas in a rattle lacking a button the terminal segment is a single rigid structure consisting of 2-4 (usually 3) successive lobes which are angular, relatively wide across the base of the anterior lobe, and have ridges and points on the posterior lobe.

METHODS AND MATERIALS

A sample of prairie rattlesnakes was obtained from the Cimarron National Grassland and adjacent private land in Morton County in the southwestern corner of Kansas; 25 snakes were captured, processed alive and released on 26 April and 1 and 2 May 1984; 45 others were collected by Steve Barnum of Straight, Oklahoma, and were similarly processed on 2 May 1984. Rattles, 84 in all, saved as trophies by Gary Norton of Hugoton, Kansas, and Ed Anderson of Elkhart, Kansas, were obtained as the snakes emerged from hibernation in the spring of 1983 and previous years, and were used to supplement the demographic data from the live snakes. Also, 38 preserved specimens of *C. viridis* in the Museum of the High Plains, Fort Hays State University, and 24 in the University of Kansas Museum of Natural History were examined. These museum specimens, shrunken to varying degrees in preservative, were used only for study of rattle strings and of reproduction.

The sample of timber rattlesnakes included 93 individuals captured from October 1948 to May 1984 on the University of Kansas Natural History Reservation and adjacent areas, 26 captured near DeSoto, Johnson County, in May 1983 and 1984, and five from near Clinton Reservoir, Douglas County, in May 1984. Most of these snakes (a total of 100, excluding 24 summer records), were captured in spring (April, May) or fall (late September, October) and hence represented the period between growing seasons and could be grouped in discrete annual cohorts. The youngest group consisted of those born in the preceding late summer and early fall, with no rattles other than the natal button.

The rattle of each snake was examined and the separate segments were counted and measured in order to correlate their size and number with the age, size and sex of the snake. Presence of the natal button was noted or, if the rattle string was incomplete, estimate of the number of missing segments was attempted. Three classes of rattle strings could be distinguished:

Type I: tapered terminally, and complete, including the postnatal button.

Type II: with noticeable taper, but incomplete, lacking the terminal button and perhaps other segments.

Type III: incomplete, non-tapered, having only segments of large and relatively uniform size.

Incomplete rattles that are tapered indicate that few segments are missing, whereas those that are non-tapered show that all segments acquired while the snake was growing, and perhaps others produced subsequently, have been lost. "First-year" snakes in this account are those less than one year old; "second-year" are those between one and two years, and "third-year" are those between two and three. Diameter of each rattle segment was measured with calipers to the nearest tenth of a millimeter, the greater (dorso-ventral) diameter or height (termed "width" by Klauber, 1956) of the proximal (anterior) lobe of each segment.

The samples of *C. viridis* (Table 2) and *C. horridus* (Table 3) were divided into tentative age groups on the basis of rattle number. Neonates comprised a discrete and easily recognizable class in the fall-spring samples, and second- and third-year young also were fairly separable both from the neonates and from adults. The adults were assigned arbitrarily to most probable age classes on the basis of rattle number. Those of *C. viridis* were assumed to add rattles at an average rate of approximately 1.5 per year. This figure seems plausible in view of the findings that one shedding per year is normal for *C. v. oregonus* in the relatively short growing season of northern Idaho (Diller and Wallace, 1984) and between one and two sheddings in California (Fitch, 1949). Two sheddings per year have been found in *C. horridus* in Shenandoah National Park (W. H. Martin III, pers. comm.) and that is supported in my study by the recapture of an adult male marked 2 June 1953, which had added 4 rattles by 16 October 1954.

RESULTS

Prairie rattlesnake. Evidence from the relative size of successive rattle segments indicated that in *C. viridis* (and also in *C. horridus*) most growth takes place between the first four sheddings, and that increase in diameter of successive segments is relatively slight (less than 5%) after the seventh ecdysis (Table 1). Type II rattles usually have one to four segments missing (including the button), and are from relatively young snakes. The oldest individuals in the population have a Type III rattle of several or many segments, all of about the same diameter, because they were acquired after the snake had completed its growth or had slowed to a negligible rate of gain.

The population from Morton County, Kansas, bore out Klauber's (1956) statement that immature *Crotalus v. viridis* in den collections were concentrated in the one-rattle and five-rattle classes, representing first- and second-year age classes (Table 2). When only the button or two or three terminal segments were missing and the rattle string had a distinct taper

Table 1. Diameters (in mm) of rattles in Kansas rattlesnakes.

Sequential number of rattle segment	<i>Crotalus viridis</i>				<i>Crotalus horridus</i>			
	\bar{x}	range	N	\bar{x} (♂ and ♀ combined)	\bar{x}	range	N	\bar{x} (♂ and ♀ combined)
First ("button")	♂ 5.36	4.7-6.0	29	5.25	♂ 5.39	5.2-6.1	15	5.71
	♀ 5.15	4.5-6.0	30		♀ 6.06	5.4-6.7	14	
Second	♂ 6.32	5.4-7.2	27	6.20	♂ 6.99	6.0-7.9	9	7.21
	♀ 6.11	4.9-7.0	33		♀ 7.31	6.7-7.7	17	
Third	♂ 7.59	6.5-8.7	25	7.50	♂ 8.18	7.1-9.3	13	8.51
	♀ 7.39	6.3-9.0	25		♀ 8.82	7.5-10.2	16	
Fourth	♂ 8.88	7.5-10.0	26	8.7	♂ 9.46	8.4-10.2	17	9.56
	♀ 8.82	6.6-10.8	25		♀ 9.68	8.8-10.5	17	
Fifth	♂ 10.27	8.6-11.7	27	9.60	♂ 10.41	9.6-11.6	16	10.41
	♀ 8.82	7.5-11.7	25		♀ 10.47	9.2-11.4	18	
Sixth	♂ 11.24	8.9-13.0	25	11.24	♂ 11.05	9.5-12.3	12	11.21
	♀ 11.22	9.9-12.5	18		♀ 10.08	9.3-12.5	16	
Seventh	♂ 12.39	11-14	21	12.09	♂ 11.11	10.5-12.3	9	11.71
	♀ 11.71	9.8-13.1	17		♀ 11.78	11.4-12.2	8	
Eighth	♂ 12.79	12.2-14.0	14	12.43	♂ 12.2	11.9-12.4	4	10.5-12.3
	♀ 12.0	10.7-13.1	12					
Ninth	♂ 14.05	12.3-14.7	8	13.34				
	♀ 12.53	11.8-13.8	7					
Tenth	♂ 14.12	13-15	12	12.75				
	♀ 12.75	12-14	7					
Eleventh	♂ 14.2	13-15	8					
Twelfth	♂ 14.3		4					

(Type II), it was possible to account for the missing segments easily with little margin of error. In a few of the largest snakes having almost uniformly wide rattle segments (Type III) the allocations are speculative. In such instances, the *minimum* possible ages and segment counts were used, and I assumed the snake must have lived at least four years and produced at least eight rattle segments before it began to produce those of maximum size. Thirty of the 70 snakes (43%) and 36 of the 84 rattle strings (43%) had one or more distal segments missing, and so were Type II or Type III rattles.

Klauber's (1956) discussion of the frequency of shedding and rattle gain in *C. v. viridis* was based upon abundant material from dens near Platteville, north-central Colorado. He stated that in these hibernating aggregations there were many young of the year (with only the button) but there were few young with two or four rattles, almost none with three, and many with five. The latter group thus represented the mode for one-year-olds. Klauber (1956) and Heyrend and Call (1951) noted that first- and second-year young were not well represented in denning aggregations in Colorado and Utah. In my Morton County sample also, such young are relatively few. However, in a normal population, there must be more one-year-olds than two-year-olds, and more first-year young than one-year-olds.

Klauber (1956) also noted geographic variation in rate of rattle gain; one-year-old *C. v. helleri* in San Diego County, southern California, and *C. v. oreganus* in Madera County, central California (Fitch, 1949), typically have four rattles but *C. v. lutosus* in northwestern Utah most often has three (sometimes four) according to Heyrend and Call (1951). *C. v. viridis* of southwestern Kansas is similar to those of Platteville, Colorado, but different from more western populations of the species having a more rapid rate of rattle gain. The modes for first-year and second-year cohorts are, respectively, 1 rattle and 5 rattles, and for the third-year cohort, 8 rattles (but with 7 almost as often).

Births of *Crotalus viridis* are concentrated in August and September, hence the youngest, or "first-year" snakes in the spring sample (late April and early May) from Morton County, Kansas, were about eight months old, but they had been in hibernation most of the time since birth the previous autumn, and therefore probably had grown little. The next cohort consisted of those about 20 months old with successive annual groups about 32, 44, 56 and 68 months old (Table 2).

Snakes with seven-, eight-, nine-, and ten-segmented rattles comprised the majority of adults and 45% of the total sample (Table 2). Those having seven- and eight-segmented strings must be predominantly in their third year and newly matured. Evidently at adolescence there is an abrupt slowing in both growth rate and shedding frequency, so that snakes of the third-, fourth-, and fifth-year age classes overlap widely in both snout-vent length and number of rattle segments.

The incidence of mortality in adults is suggested by the rapidly decreasing numbers of older snakes as indicated in Table 2; third-year, fourth- and fifth-year, and sixth- and seventh-year classes had respec-

Table 2. Prairie rattlesnakes (*Crotalus viridis*) of a spring sample (70 live snakes, 84 detached rattles) from Morton County, Kansas, divided into tentative age cohorts on the basis of size (SVL) and rattle segments.

Tentative age cohort	Number of rattle segments ¹	N	Percentage of sample	$f - \bar{x}$ ratio ²	Snout-vent length in mm
First-year immatures	1 (button only)	23	14.9	6-7	334 (291-360) in 13
	2 (1 + B)	3	2.0	—	
Second-year adolescents	3 (2 + B)	1	0.6	—	
	4 (3 + B)	8	5.2	1-2	557 (520-620) in 3
	5 (4 + B)	11	7.1	7-2	670 (636-710) in 9
Third-year adults	6 (5 + B)	9	5.8	2-2	733 (708-820) in 4
	7 (6 + B)	14	9.1	3-4	863 (760-890) in 7
Fourth-year adults	8 (7 + B)	24	15.6	6-7	846 (723-905) in 13
	9 (8 + B)	15	9.8	3-3	890 (830-930) in 6
Fourth- and fifth-year adults	10 (9 + B)	15	9.8	2-2	932 (646-1020) in 4
Fifth-year adults	11 (10 + B)	14	9.1	3-3	934 (880-1038) in 6
Sixth-year adults	12 (11 + B)	9	5.2	3-0	947 (900-1000) in 3
Sixth- and seventh-year adults	13 (12 + B)	5	3.3	0-1	950
Seventh-year adult	14 (13 + B)	1	0.6	1-0	978
Eighth-year adults	15 (14 + B)	1	0.6	—	
	16 (15 + B)	1	0.6	—	

¹ Many of longer rattles reconstructed from incomplete strings; figures somewhat speculative for certain strings of more than 10 segments.

² Live snakes only (exclusive of detached rattle strings).

tively, 38, 44, and 6 individuals, with only 2 that were judged to be older than seven years. However, the allocations in age classes are somewhat speculative, as beyond the third year age cohorts overlap in both size and number of rattle segments.

Among the 20 sexually mature female prairie rattlesnakes that were palpated, 14 (70%) had enlarged ova that could be counted, whereas six had no detectable ova and presumably were not going to produce young during the 1984 season. Similarly, in New Mexico, Aldridge (1979) found 73% of 44 females of *C. v. viridis* to be fecund. In the northern Great Plains there is a well-defined biennial cycle (Rahn, 1942). One Kansas female dissected on 26 April had enlarged follicles (18×9mm), and follicles in those palpated seemed to be about this size or larger. Egg complements counted by palpating were 5, 6, 7, 8, 8, 9, 10, 10, 11, 11, 12

and 18 follicles, mean 9.7. In museum specimens females had egg complements of 6, 7, 9 and 16. Marr (1944) mentioned two Kansas litters of 14 each. For the combined sample of 19 Kansas litters, mean clutch size was 10.11 ± 0.79 , which is within the known range for the species and for the subspecies *C. v. viridis*.

Stillborn young and abortive infertile eggs are common in rattlesnake litters. Klauber (1956) stated that in 28 broods (of various species) at the San Diego Zoo, there were 274 eggs or young, with 70% live young, 12% dead young, and 18% infertile eggs. For *C. v. viridis* under more natural conditions, in northern Idaho, Diller and Wallace (1984) found that 24 of 197 ova failed to develop because of infertility or fetal death, a loss of 12.2%. If this figure applies in *C. v. viridis* populations of Kansas, the mean of 10.1 eggs ovulated would produce a litter of 8.9 live young. In the combined sample (rattles and live snakes) 104 of 154 were considered adults (third year or older) with an estimated 52 females. If 70% of them were fecund, with an average litter of 8.9, the annual crop would total 324 young.

The mortality rate in first-year young would be expected to exceed that in older age groups. However, the relatively rapid and progressive decline in older snakes (recognizable by large size and numerous rattle segments) suggests that adults of all ages also are subject to high rates of mortality. Various mortality rates were empirically tested against the figures at hand for estimated ages of the snakes in the actual sample. The most plausible mortality rates are 60% in the first-year young and 50% in each subsequent year. These rates would give the following numbers (each rounded to the nearest whole number) of survivors from an initial cohort of 324: 130, 65, 32, 16, 8, 4, 2, and a single individual living into the ninth year. Probably few *C. v. viridis* live to be older than eight years in the wild, although prairie rattlesnakes have been known to survive considerably longer in captivity.

In the sample of 154 *C. v. viridis* there were four tapered Type II incomplete rattles that were each estimated to have had at least 12 segments if the rattles had been intact; probably they were at least five years old. Eight others with missing segments but no taper (Type III rattles) were those of relatively old snakes that probably had lost six or more segments previously. Their rattles had 3 segments (in 3), 5 (in 2), 6 (in 2) and 8 (in 1). On the basis of size and number of rattle segments any of them could have been as young as six or seven years, but might have been much older, perhaps as old as 12 to 15 years.

Timber rattlesnake. Table 3 shows the numbers of timber rattlesnakes of each sex and of various sizes and rattle numbers in a fall-spring sample. It shows that first-year young with only the postnatal button were far more numerous than snakes of any other rattle number, comprising 37% of the total. My age correlation is based upon the fact that first-year and second-year snakes constitute recognizable cohorts, the former with one rattle, the button, and the latter with usually three rattles, sometimes four. The divisions among older snakes with longer rattle strings are made partly on

the basis of deduction from the known rate of development in the first year, and partly on the basis that free-living timber rattlesnakes, including adults, have gained two rattle segments per season in known instances.

The sample of 100 timber rattlesnakes in Table 3 is subject to biases of various sorts. On the University of Kansas Natural History Reservation where most of the records were obtained, no full-grown adults (exceeding 90 cm snout-vent length) were captured in traps because the traps' funnel entrances were too small, averaging only 2.5 to 3.0 cm in diameter. Most captures of immature snakes (53 of 70) were made in these traps. The sex ratio was close to parity in the overall sample, 52 males to 48 females, but with ratios changing as follows: in first-year young, 16 males to 21 females; second- and third-year young, 17 males to 10 females; adults, 19 males to 17 females.

Of 16 large snakes (100 cm or more SVL) only two had intact rattles, of 10 and 16 segments. Nine of the 16 had untapered, Type III rattles, suggesting that since attainment of full size, each had lost part of its string including the natal button and at least six terminal segments acquired during its first three years while rapid growth was occurring. Thus, for a snake with ten rattles of uniform width, a *minimum* age of eight years could be estimated—five years to produce the ten adult rattles, plus three more years to produce earlier smaller segments that were subsequently lost.

The ratio of first-year to second-year young changed seasonally, 32 to 12 in fall, 9 to 5 in spring. The fact that the youngest cohort was 2.7 times as numerous as the next oldest cohort in fall but only 1.8 times as numerous in spring suggests that approximately one-third of them did not survive their first winter. Presumably they were subject to a comparable mortality rate during their months of activity.

Records of young per litter in Kansas *C. horridus* include one of 6 young (Collins, 1982), another of 8 (KU) and counts of follicles palpated in the live snakes or in dissected specimens as follows: 5, 5, 6, 9, 10, 11, 11, 14. For the combined total of 10 litters the mean is 8.5 ± 0.91 . Evidently the female cycle is most often triennial, judging from the findings of W. S. Brown and W. H. Martin III, but a biennial cycle may occur in some Kansas females. Those that were gravid had rattles of at least 7 segments and were longer than 800 mm, SVL. On the basis of size and rattle number they were believed to be in their fourth year or older. Hence, the first three annual cohorts, including first-year with only a button or 2 rattles (SVL 298–495 in 37), second-year, 3 or 4 rattles (SVL 548–670 in 14), and third-year, 5 or 6 rattles (SVL 504–855 in 13), are considered immatures. Like other rattlesnakes, *Crotalus horridus* is known to produce stillborn young and abort infertile eggs frequently. William S. Brown (pers. comm.) found that in Warren County, New York, 186 eggs ovulated by 20 females produced 149 living young, 12 stillborn, and the remaining 25 were infertile. Thus only 80% produced viable young. If a similar ratio applies in the Kansas population studied, litters would average 6.8 living young. In the fall-spring sample of 100 snakes, 36 are adults and 17 of these are females, about one-third of which may be fecund each year if

Table 3. Timber rattlesnakes (*Crotalus horridus*) of a spring-and-fall sample of 100 from northeastern Kansas, divided into age cohorts on the basis of size (SVL) and rattle segments. B = button.

Tentative age cohort	Number of rattle segments	SVL in mm		N ♂ ♀
		\bar{x}	range	
First-year	Button	371	(298-413)	37(15-22)
First-year	2 (1 + B)	495		1 (0- 1)
Second-year	3 (2 + B)	603	(548-665)	10 (7- 3)
Second-year	4 (3 + B)	605	(577-670)	4 (2- 2)
Third-year	5 (4 + B)	720	(504-802)	9 (6- 3)
Third-year	6 (5 + B)	840	(814-855)	4 (2- 2)
Fourth-year	7 (6 + B)	842	(800-870)	7 (2- 5)
Fourth-year	8 (7 + B)	906	(812-995)	8 (3- 5)
Fifth-year	9 (8 + B)	932	(898-991)	5 (3- 2)
Fifth-year	10 (9 + B)	1001	(966-1031)	2 (0- 2)
Sixth-year	11 and 12	1013	(922-1082)	4 (3- 1)
	(10 and 11 + B)			
Seventh-year	13 and 14 (est.)		(1142-1230)	2 (2- 0)
Eighth-year	14, 16, 16, 16 (est.)		(1010-1175)	4 (4- 0)
Ninth-year	17 (♀ est.), 18 (♂ est.)		(1038-1196)	2 (1- 1)
Tenth-year	19 (est.)		(1000)	1 (0- 1)

Table 4. Comparison of demographic traits in Kansas prairie rattlesnakes (*Crotalus viridis*) and timber rattlesnakes (*Crotalus horridus*). Means are shown with standard errors.

	<i>Crotalus viridis</i>	<i>Crotalus horridus</i>
Female age at maturity	third year	fourth year
Incidence of fecundity in adult females	70%	33%
Litter size	10.1 ± 0.8 (5-18)	8.5 ± 0.9 (5-14)
Estimated live births per litter	8.8	6.8
Percentage survival through fifth year	2.5	17.3
Adult snout-vent length, mm		
Male	\bar{x} = 932 ± 14.5 811-1038 (n = 20)	\bar{x} = 1092 ± 22.7 980-1270 (n = 14)
Female	\bar{x} = 873 ± 10.6 783-950 (n = 16)	\bar{x} = 987 ± 21.2 895-1038 (n = 7)
Adult weight, gms		
Male	\bar{x} = 487 ± 33.8 295-655 (n = 11)	\bar{x} = 891 ± 72.5 580-1874 (n = 10)
Female	\bar{x} = 339 ± 14.2 265-435 (n = 11)	\bar{x} = 557 ± 47.3 388-883 (n = 11)
First-year young (fall-spring)		
Snout-vent length, mm	\bar{x} = 335 ± 6.7 291-360 (n = 13)	\bar{x} = 364 ± 7.2 298-423 (n = 31)
Weight, gms	\bar{x} = 13.7 ± 1.2 9-18 (n = 11)	\bar{x} = 33.94 ± 1.5 23-55 (n = 31)

they are on a triennial schedule. These 17 females each reproducing triennially would total an average of about 39 young annually. The small and inconspicuous first-year young were not caught in their true numbers in relation to adults, even though many of them were caught in live-traps that were not effective for catching the adults. As in the case of *C. viridis*, various mortality rates were empirically tested against the figures at hand for estimated ages of the snakes in the actual sample. A mortality of 45% in first-year young and 25% annually, thereafter, seems most plausible and would result in the following numbers of survivors in successive years, from the original cohort of 39 newborn young: 21, 16, 12, 9, 7, 5, 4, 3, 2, 2 and a single survivor living into the 11th year.

Table 3 shows concentrations of young timber rattlesnakes with rattles having 1, 3, 5 and 7 segments, the modal numbers for first-year, second-year, third-year and fourth-year categories, whereas relatively few in the fall-and-spring sample had the intermediate numbers of 2, 4, and 6 segments.

DISCUSSION

In both the timber rattlesnake (*Crotalus horridus*) and the prairie rattlesnake (*C. viridis*) population, turnover in Kansas is fairly rapid, with newly matured adults making up a high proportion of the populations. However, in all respects the prairie rattlesnake shows more life history traits that emphasize high reproductive potential and an accelerated life cycle, whereas the timber rattlesnake has, instead, much lower reproductive potential and greater longevity. Judging from information available in the literature, the same contrast applies, in varying degrees, between the prairie rattlesnake in Kansas, and various other species and subspecies elsewhere, including the more western subspecies of *C. viridis*. The climatic extremes and the open terrain in the area occupied by *C. v. viridis* perhaps result in a higher incidence of mortality from both predation and weather, compared with *C. horridus*.

One of the most impressive characteristics in each sample was its variability. Snakes of any given rattle number spanned a wide size range, and those of any size category were variable in number of rattles. Growth, much accelerated in some and retarded in others, is seemingly controlled by a combination of innate genetic traits and the effects of fluctuating environmental factors. In northern Idaho, Diller and Wallace (1984) found that females of *C. v. oregonus*, at the onset of sexual maturity, varied from 550 to 630 mm SVL, and had four to nine rattles. Probably those of the present study were equally variable, although minimum size and minimum rattle number at sexual maturity were both markedly higher.

For both *C. viridis* and *C. horridus* there was notable constancy in size of the natal button, but gain in the size of each new rattle was highly variable. Gain in diameter from the button to the second rattle, from the second to the third, or from the third to the fourth, was negligible in some individuals, and as high as 40% in others (Table 1).

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