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## Population Structure and Biomass of Some Common Snakes in Central North America

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**ABSTRACT** Samples of 113 to 1762 individuals were obtained from local populations of 11 common species of snakes in Kansas and one in Oklahoma. An age-size correlation was established for each species from the records of marked individuals that were recaptured. Each snake in the samples was tentatively allocated on the basis of its snout-vent length (or alternatively on its rattle string in *Crotalus*). Local populations were interpreted to consist of from eight (*Thamnophis sirtalis*) to 18 (*Crotalus atrox*) annual age cohorts. In samples of *Coluber constrictor*, *Nerodia sipedon*, and *Thamnophis sirtalis*, females outnumbered males and attained larger mean size. In *Nerodia* and *Thamnophis*, females survived longer than males; in *Coluber* the sexes were similar in longevity. In *Agkistrodon contortrix*, *Crotalus atrox*, *C. horridus*, *C. viridis*, *Elaphe obsoleta*, *Lampropeltis calligaster*, *L. triangulum*, and *Pituophis catenifer*, males outnumbered females, grew larger, and survived longer on average. In *Diadophis punctatus*, males were more numerous than females and survived longer, but females had average larger size. In each species sample, first-year young were poorly represented, with only 4 to 46% of expected numbers, and it seemed that their cryptic behavior and markings caused them to be overlooked much more often than adults, regardless of the method of sampling. Biomass calculations indicated that *Diadophis punctatus* constituted nearly half of the total, with *Coluber constrictor*, *Elaphe obsoleta*,

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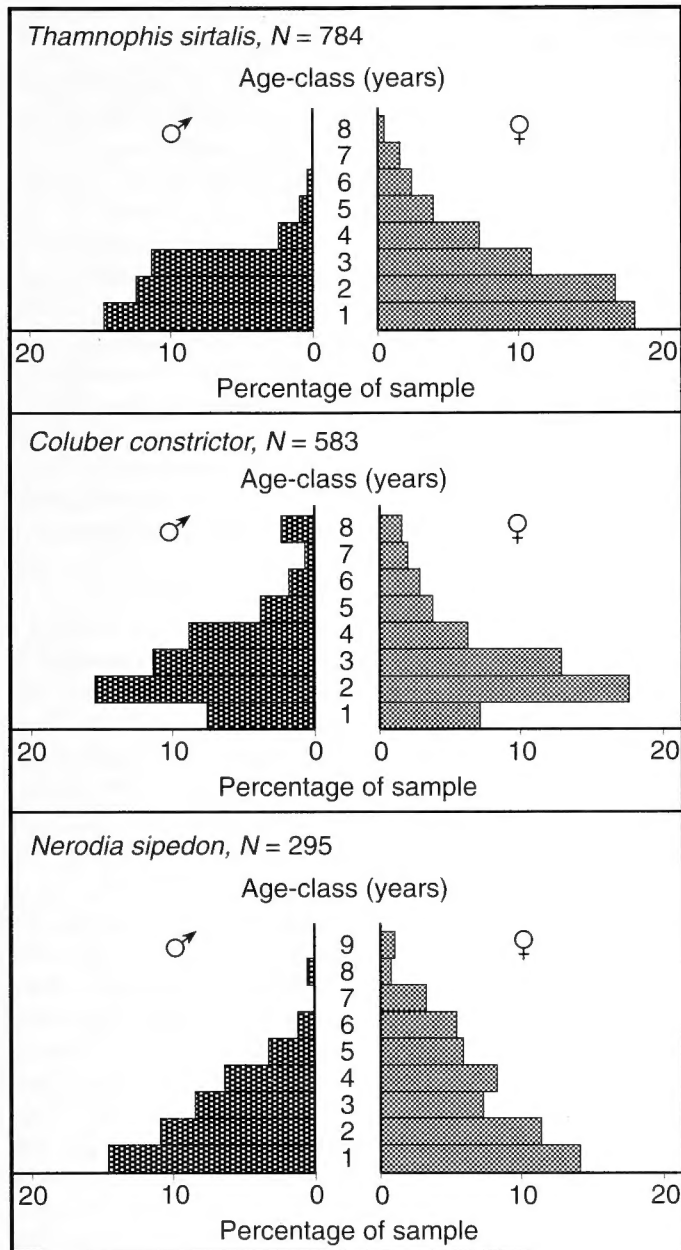


Fig. 1. Age-pyramids of three short-lived species of snakes based on putative age-size cohorts; females outnumber males and survive longer.

only minor irregularities. First-year young make up 27.7% of the *Nerodia* sample (vs. 22.1% for second-year young) but presumably are not represented in their true ratio. *Nerodia sipedon* is the most prolific of the 12 species studied (mean litter size 19.9 in a sample of the local population); thus more first-year young are to be expected in the year-round sample. The Fall sample of 784 *Thamnophis sirtalis* seem to represent eight annual cohorts of females and six for males. Females outnumber males in each age-

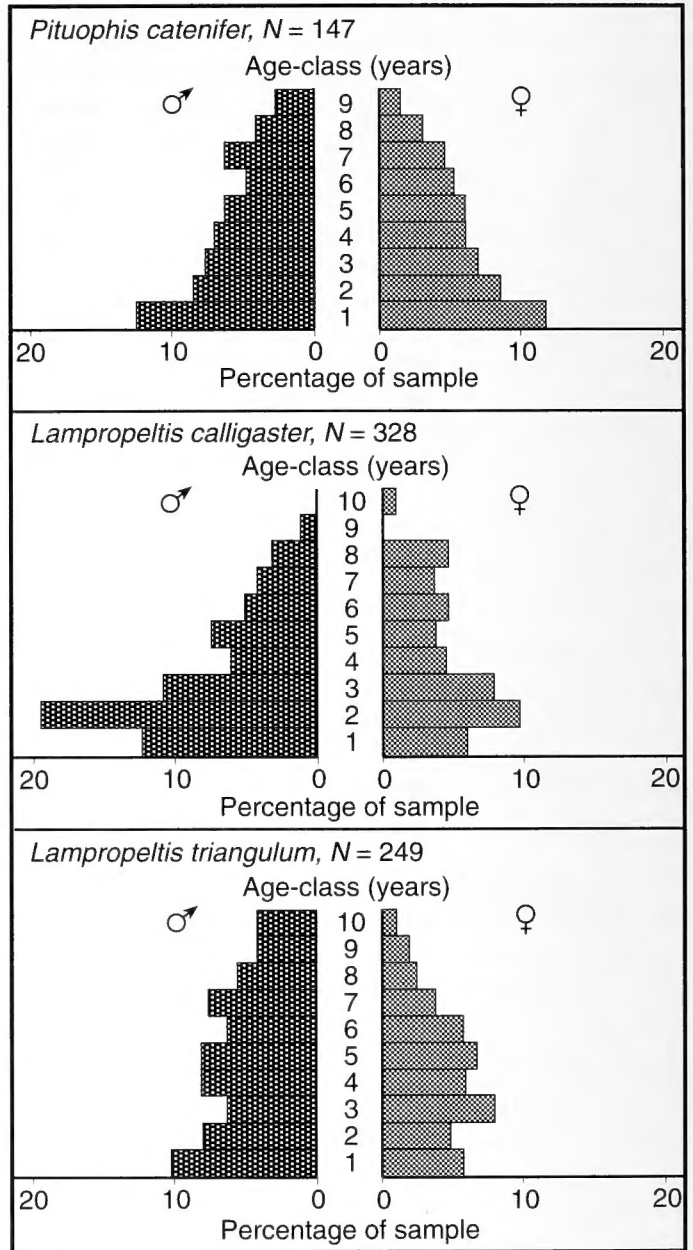


Fig. 2. Age-pyramids of three colubrine species of snakes based on putative age-size cohorts; males outnumber females, tend to grow larger, and survive longer.

class, and the disparity increases with age. First-year young are obviously under-represented in the sample, as they are only slightly more numerous than second-year individuals.

The 147 *Pituophis catenifer* apparently represent nine annual age classes forming a well-shaped pyramid with only one irregularity (more seventh-year than sixth-year males). First-year young are well represented (32), as compared with 22 second-year young. The samples of *Lampropeltis* (328 for *L. calligaster* and 249 for *L. triangulum*)

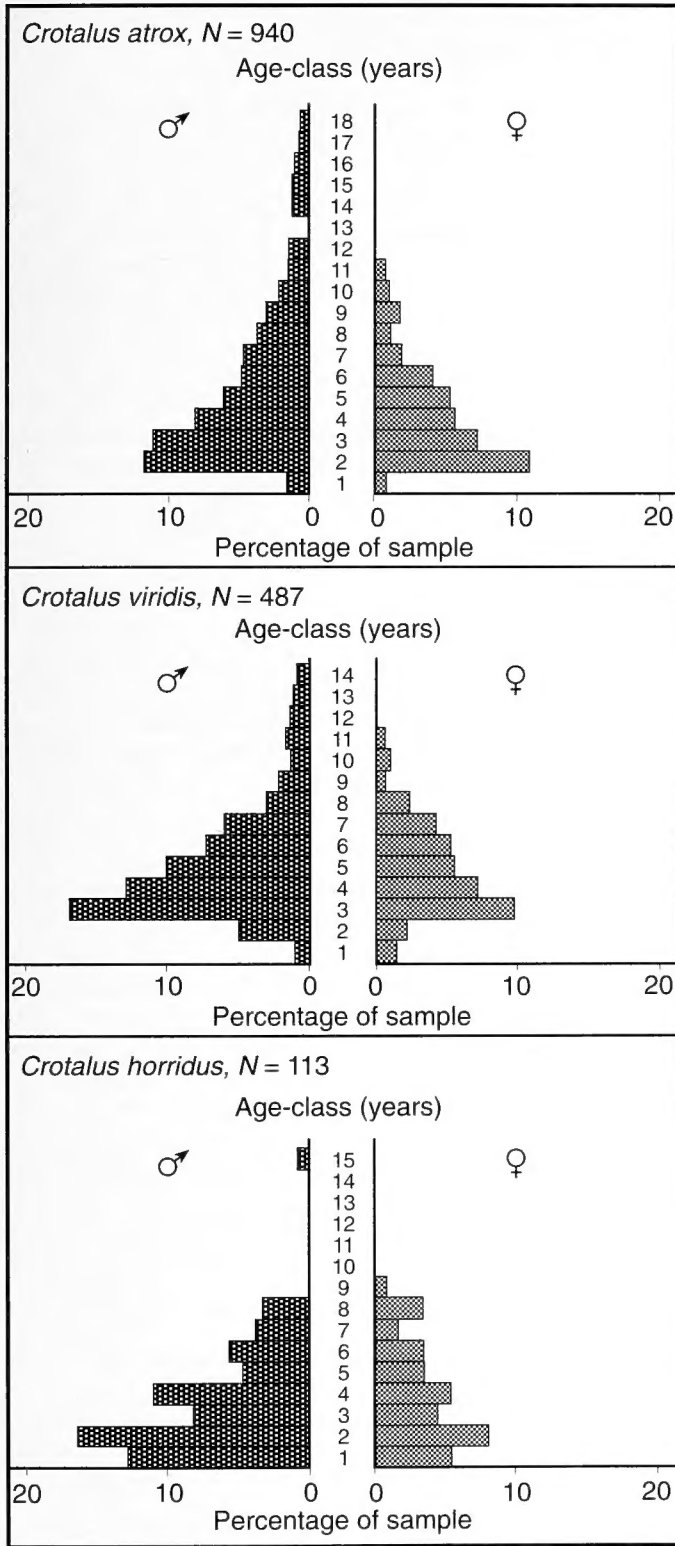


Fig. 3. Age-pyramids of three species of rattlesnakes based on number and taper of rattle segments; males outnumber females, tend to grow larger, and survive longer. The samples of *Crotalus atrox* and *C. viridis* were obtained at "rattlesnake round-ups" and included few young because it was illegal for hunters to collect them.

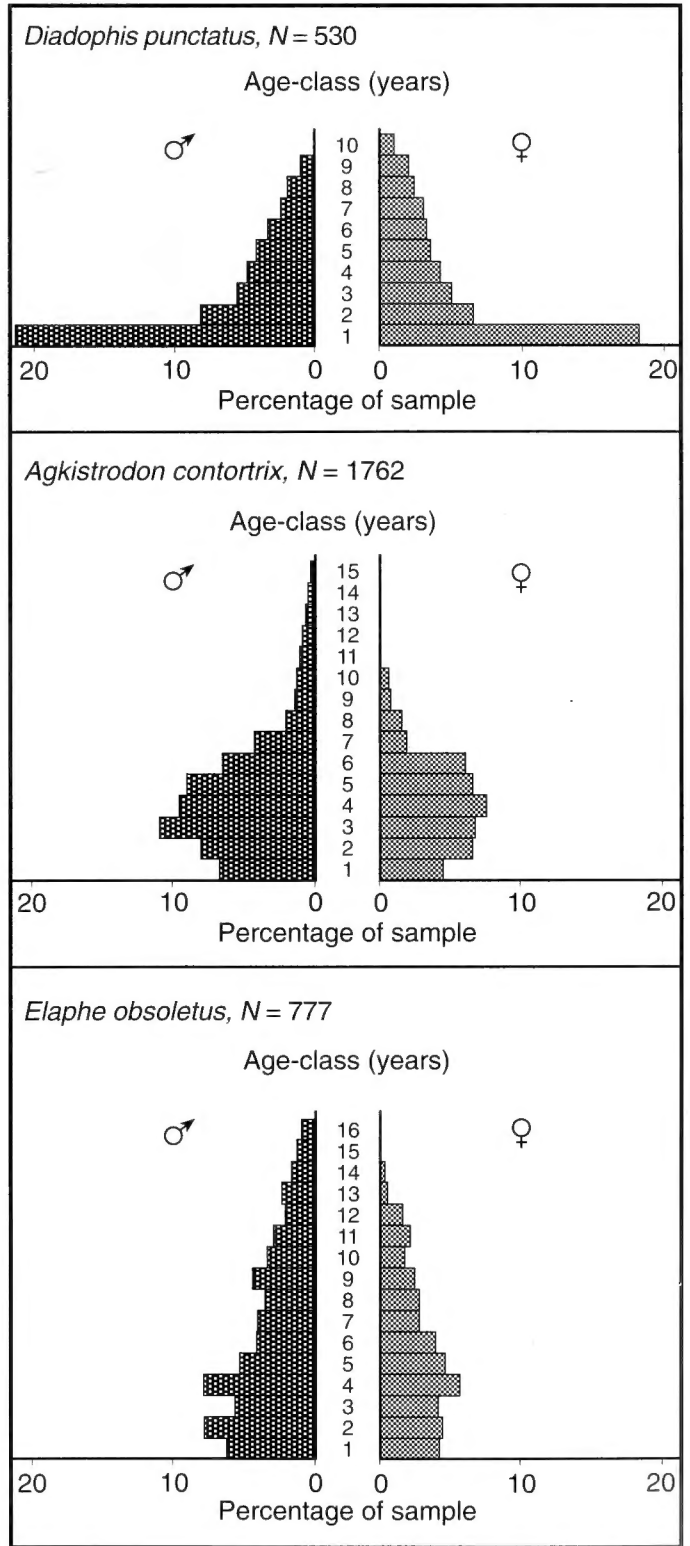


Fig. 4. Age-pyramids of three species of relatively long-lived snakes based on putative age-size cohorts. In *Diadophis punctatus*, males are smaller than females; the average size of males of *Agkistrodon contortrix* and *Elaphe obsoleta* is larger than females. In all three species, males are more numerous than females and tend to survive longer.

Table 1. Maximum biomass of snakes from the Fitch Natural History Reservation.

Species	Maximum density per hectare	Mean weight of snakes in sample	Biomass (grams per hectare)	Percent of snake biomass
<i>Agkistrodon contortrix</i>	4.90	103.6	504.7	5.6
<i>Coluber constrictor</i>	14.80	109.2	1616.6	18.0
<i>Crotalus horridus</i>	0.30	397.5	119.2	1.3
<i>Diadophis punctatus</i>	1603.00	2.57	4119.0	45.9
<i>Elaphe obsoleta</i>	3.60	300.1	1080.4	12.0
<i>Lampropeltis calligaster</i>	4.00	149.2	596.8	6.6
<i>Lampropeltis triangulum</i>	0.70	45.8	32.1	0.4
<i>Nerodia sipedon</i>	0.30	104.9	31.8	0.4
<i>Pituophis catenifer</i>	0.13	497.5	149.3	1.7
<i>Thamnophis sirtalis</i>	14.70	49.2	723.2	8.1
Combined species	1646.03	9470.1	8973.1	100.0

each seem to represent ten annual age classes. Both are pyramids and have several irregularities, and each has an under-representation of first-year young.

The tall, steeple-shaped pyramid for the 530 *Diadophis punctatus* in the late Fall apparently represents 12 annual age-classes, with first-year young forming a broad base. The pyramid benefits from the large sample and its restriction to a season when age and sex differences in behavior are believed to be minimal. Males constitute 52.5 % and females 47.5 % of the sample, whereas samples from other seasons are much biased with males more numerous in spring but females more numerous in the early summer up to the time of egg-laying (Table 2). The composition by sex- and age-classes in a year-round sample of *Diadophis punctatus* demonstrates the drastic effect of season on these ratios; adult males and females and young all undergo different behavioral changes that affect their ratios during the course of a year. Undoubtedly, there are somewhat parallel changes in other species.

The sample of 1762 *Agkistrodon contortrix* represent fall sampling of snakes returning to hibernacula and are less

biased than other samples of the species that are influenced by seasonal differences in behavior and habitat. The records are interpreted as including 15 annual age-classes, but with no males in the 14th age class and no females in the 13th, 14th and 15th year-classes. Except for the under-representation of young, the male half of the pyramid has a typical shape, but the female half does not show well the progressive reduction in numbers that occurs in successively older age groups. Adult growth is much less in females than in males, so it is less feasible to allocate females in their age-cohort on the basis of size.

The 777 records of *Elaphe obsoleta*, interpreted as representing 16 annual age-classes, form a tall, spire-like pyramid with the first-, second-, and third-year classes poorly represented. Females are consistently less numerous than males and are lacking for the 15th and 16th year classes. The few minor irregularities in the pyramidal form probably can be ascribed to the heterogeneity of the sample assembled over 50-year time span. Amount of growth in adults was found to differ according to the food supply (Fitch, 1999). With an abundance of food in some years and scarcity in others, individuals of the same age-cohort might cover a wide size range. Probably incorrectly aged individuals result in irregularities in the age-pyramid derived from them. The biased sex ratio (64.3% males in a sample of 846) may be real. In 87 hatchlings of 10 clutches, 63% were males (Fitch, 1999).

The relative scarcity of first-year young in each sample (from 4.2% in *Coluber constrictor* to 47.0% in *Diadophis punctatus*; Table 3) needs to be explained, and it seems that all of these small snakes have a well-developed capacity to avoid detection and capture. For example, experimental evidence for *Crotalus viridis* supports the idea that crypsis is relatively prominent in juvenile behavior in contrast to sematic display in adults. Kissner et al. (1997) found that young prairie rattlesnakes approached by a human remain motionless without rattling longer and allow closer approach than would adults, especially males.

Table 2. Changing percentage of age-sex categories in samples of a population of *Diadophis punctatus* in 1966.

Age and sex	Month							Year
	March	April	May	June	July-August	September	October	
N	216	438	498	145	54	146	111	1606
Adult male	33.8	33.2	50.1	26.9	15.6	23.3	30.6	36.1
Adult female	15.3	22.8	31.3	42.6	25.0	17.1	34.2	27.4
Second year male	4.6	4.1	4.4	4.1	3.1	11.0	9.9	5.3
Second year female	2.8	0.9	2.0	3.5	18.8	7.6	13.6	3.5
First year male	22.2	22.8	7.8	9.7	28.1	17.0	8.1	14.9
First year female	21.3	16.2	5.2	13.7	9.4	24.0	3.6	12.8

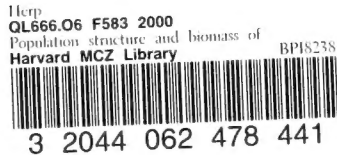
Table 3. Productivity in ten species of snakes (actual versus estimated numbers of young).

Species	Snakes in sample (N)	Adult females	Estimated breeding females	Mean clutch or litter	Estimated annual production	First-year young in sample	Percent actual vs. estimated 1st-year young
<i>Agkistrodon contortrix</i> *	1762	432	216.0	5.1	1110	249	22.4
<i>Coluber constrictor</i> *	583	179	166.0	11.8	1960	82	4.2
<i>Crotalus horridus</i>	113	26	14.5	7.2	104	20	19.2
<i>Diadophis punctatus</i> *	530	130	128.0	3.4	436	205	47.0
<i>Elaphe obsoleta</i>	777	176	59.0	9.7	525	78	13.6
<i>Lampropeltis calligaster</i>	328	89	59.4	9.2	545	53	9.7
<i>Lampropeltis triangulum</i>	249	65	64.2	6.9	443	35	7.8
<i>Neorida sipedon</i>	295	92	92.0	19.9	1830	83	4.5
<i>Pituophis catenifer</i>	147	35	33.0	11.2	392	32	8.2
<i>Thamnophis sirtalis</i>	784	196	139.0	16.2	2260	254	11.2

\*Samples from collecting in the Fall; other samples are from year-round.

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