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

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CONTENTS

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. Biomasss calculations indicated that *Diadophis punctatus* constituted nearly half of the total, with *Coluber constrictor, Elaphe obsoleta,*

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Thamnophis sirtalis, Lampropeltis calligaster, and *Agkistrodon contortrix* making up from 18% to 5%, whereas *Crotalus horriidus, Lampropeltis triangulum, Nerodia sipedon,* and *Pituophis catenifer* made up only very small percentages

Key words: Biomass; population structure; rattle strings; snakes.

INTRODUCTION

Information is sparse concerning sex ratios and age classes in natural populations of snakes. Samples are rarely large enough to yield reliable statistics, and behavioral differences may distort the ratios between the sexes and between young and adults. My 50-year study of snakes in northeastern Kansas on the Fitch Natural History Reservation (FNHR) and my records from "rattlesnake roundups" in Oklahoma and Kansas (Fitch, 1998; Fitch and Pisani, 1993) have provided the opportunity to study sizable samples of several species. My objectives herein are to compare sex and age ratios in natural populations of 12 species of snakes common in the central United States, and to identify and evaluate the factors that might affect the ratios in such samples.

In general reptiles are relatively long-lived. All 12 species in the present study often have been kept in captivity in zoos and private collections, and these have yielded many records of individual longevity. Occasional individuals exceeding 30 years in some (*Crotalus horridus, Pituophis catenifer*), and exceeding 20 years in most others (*Agkistrodon contortrix, Crotalus viridis, Lampropeltis calligaster, L. triangulum, Elaphe obsoleta;* Snider and Bowler, 1992). My field data suggest that such ages are seldom if ever attained in natural populations that have to cope with diverse mortality factors and especially anthropogenic losses. Motor traffic, farm machines, domestic animals, and herpetophobic humans take their toll and may be somewhat selective in eliminating the largest and oldest individuals. Herpetophilic humans may endanger certain species such as the milk snake.

Remarkably little has been published concerning population structure in snakes. A noteworthy contribution was that of Voris and Jayne (1972), who studied growth, reproduction, and population structure in the beaked sea snake (*Enhydrina schistosa*) at Muar, Malaysia. In this very common snake there is a distinct annual breeding season, first-year young comprise a well-defined cohort, recognizable by size, and second-year females are sexually mature. Only 10–20% of neonates survive their first year and about 6% of females survive to reproduce. Most reproduction is by second and third-year females; only a tiny fraction of females were estimated to represent the fourth- and fifth-year classes. Although there are behavioral differences between young and adults that affect their ratios in samples, these differences seem to be less disruptive than those in terrestrial snakes. *Enhydrina schistosa* has a relatively short life span and few age classes, with a relatively simple population composition in contrast to most species of the present study.

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MATERIALS AND METHODS

In my long-term study on the FNHR, hundreds of snakes of approximately known ages when they were marked were recaptured and remeasured, and an age-size correlation was established for both sexes of each species (Fitch, 1999). The correlation was based on the records of snakes marked as first- or second-year young and recaptured as well-grown young or adults. The majority of recaptured snakes had been marked when already adult; hence their ages were not definitely known, either at the time of original capture or recapture, but the age of each was estimated by projecting from the records of individuals of known age. Although many individuals are markedly larger or smaller than the mean for their age-cohort, the means consistently show a pattern of sexual size difference and slowing growth with increasing age.

Sizable series were accumulated even for the less common species: 113 *Crotalus horridus*, 249 *Lampropeltis triangulum*, 147 *Pituophis catenifer*, 295 *Nerodia sipedon*, 328 *Lampropeltis calligaster*. For each of these, the sample consisted of year-round collections, with pooled data for many years. *Crotalus horridus* and *Pituophis catenifer* dwindled and finally disappeared from the FNHR as ecological succession resulted in habitat deterioration. The four most abundant species, *Agkistrodon contortrix, Coluber constrictor, Diadophis punctatus and Thamnophis sirtalis* produced such a surfeit of records that only subsets were used; *e. g.* for *Diadophis punctatus* only records from dates later than 12 October were included, thereby avoiding the strong bias to adult males that occurs at other times, especially in spring. The late Fall sample of 530 *Diadophis* records was less unwieldy than the total sample for all *Diadophis* records would have been. The sample of 784 *Thamnophis* records includes only those found under artificial shelters; all records of trapped garter snakes were excluded because most first-year young can pass through the quarter-inch wire mesh of the traps that were used. The sample of 1762 *Agkistrodon contortrix* and that of 583 *Coluber constrictor* were snakes trapped in the Fall at hilltop limestone outcrops where the snakes had come to hibernate. These Fall samples, taken at a time when all members of the population are active in search of hibernacula, may be subject to minimum bias compared with samples collected at other times of year, especially spring, when the drive to find mates causes adult males to be more active than females or immatures. In the Fall samples of *Agkistrodon*, *Coluber*, and *Diadophis*, young of the year were only a few weeks old, and obviously had undergone less reduction than the first-year young in the year-round samples of some other species, which had already passed one hibernation.

Data on *Crotalus atrox and* C. *viridis* were obtained from the "rattlesnake roundups" in Oklahoma and Kansas, respectively. The 940 *C. atrox* included some from each of the Oklahoma round-ups (Apache, Mangum, Okeene, Waurika, Waynoka) in 1988 and from Apache and Okeene in 1989. The 487 records of *C. viridis* were obtained from the Sharon Springs, Kansas, round-up in 1992, 1993, and 1994. The data set for each species consists of pooled records of many snakes from diverse localities, some of them remote from the sponsoring town. The round-up records were from early spring, soon after the snakes emerged from hibernation. First-year young could not be collected legally at the round-ups, and therefore they were meagerly represented. The few that were brought in served to show their approximate size and rattle development at the time of their emergence in early spring.

RESULTS

Conventional age pyramids (Figs. 1–4) show population structure in samples of each of the 12 species. Nearly all the diagrams deviate from the typical pyramidal shape, notably in having the basal bar, which represents first-year young shorter than bars that represent older cohorts – evidence that some of the young were missing from the sample.

The records for *Crotalus atrox* and C. *viridis* produced the most satisfactory age pyramids (except for the lack of immature snakes), and it seems that rattle strings provide a better basis than body size for estimating age. The diagram for C. *horridus* (Fig. 3), also based on rattle strings but with a relatively small sample of snakes (113) , was distorted by many irregularities. Second-year young comprised the most numerous cohort, and they were found in approximately the ratio expected to the other age cohorts. One male, (much larger, and presumably much older than any of the others), was estimated tentatively to be in its 15th year at the minimum, whereas the next oldest was judged to be in its ninth year. The rationale for estimating an age of about 15 years is that this snake was first captured on 2 June 1953, again on 16 October 1954, and lastly on 13 October 1959; it added 10 uniform-sized rattles between first and last captures. At the time of its first capture, it was already much larger (1270 mm snout-vent length) than any of the other 112 snakes in the sample; at that time it had five large rattle segments of uniform size, which presumably represented a time span of about three years. Previously, during the time required to grow to maximum size, as much as seven years must have elapsed and the snake must have produced a tapered string of perhaps 11 rattle segments including the button, all of which had been lost by the time of his initial capture in 1953.

Many census figures were presented in an earlier report for the 10 species occurring on the FNHR (Fitch, 1999). These were derived from Petersen Index calculations, each on a small acreage where intensive live-trapping or other sampling procedures were used. Table 1 shows biomass estimates, each based on the maximum population density obtained for the species The total biomass for all 10 species combined would have been much smaller for any specific area or any specific time period. It is noteworthy that *Diadophis punctatus* makes up nearly half of the total snake biomass, although it is by far the smallest species. *Coluber constrictor*, *Elaphe obsoleta*, *Thamnophis sirtalis*, *Lampropeltis calligaster* and *Agkistrodon contortrix* made up 18.0, 12.0, 8.1, 6.6, and 5.6% of the biomass, respectively, whereas *Lampropeltis triangulum*, *Nerodia sipedon*, and *Pituophis catenifer* make up only small percentages of the total biomass.

DISCUSSION

In three of the species studied (*Coluber constrictor*, *Nerodia sipedon*, and *Thamnophis sirtalis*) age pyramids were relatively low and flat, reflecting relatively rapid population turnover. In all three, females were larger and more numerous than males, and in *Nerodia* and *Thamnophis* they survived longer on the average than males. In a series of 583 *Coluber constrictor*, all from Fall trapping at hilltop limestone outcrops, first-year young were meagerly represented. Snakes interpreted as representing the second to seventh annual age cohorts form a well-shaped pyramid. The 295 records of *Nerodia sipedon* apparently represent nine annual age cohorts in a well-formed pyramid having

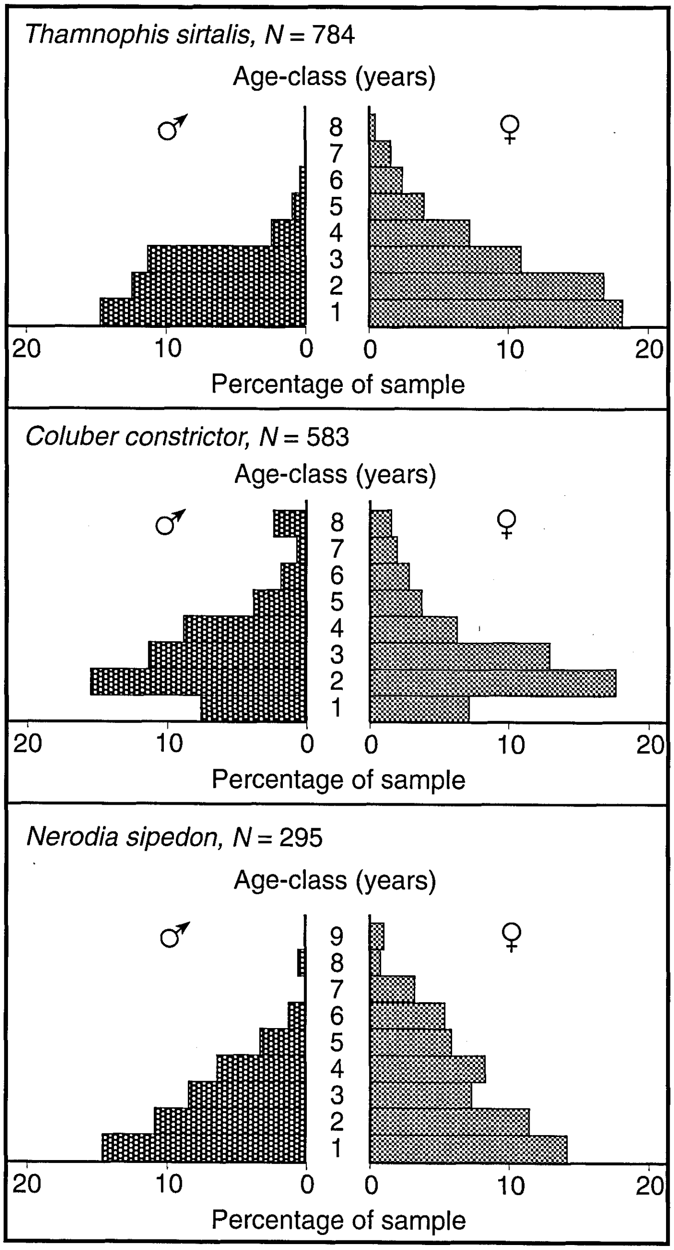

Fig. 1. Age-pyramids of three short-lived species of snakes based on putative age-size cohorts; females outnumber males and survive longer.

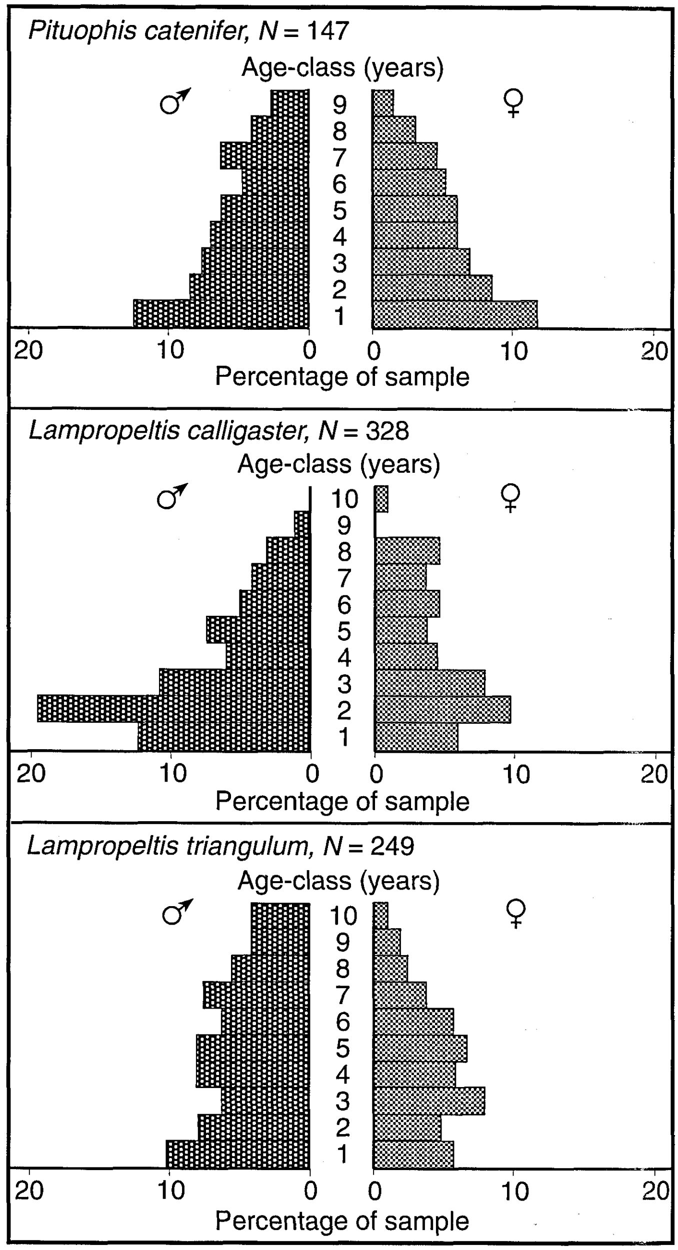

Fig. 2. Age-pyramids of three colubrine species of snakes based on putative age-size cohorts; males outnumber females, tend to grow larger, and survive longer.

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-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*)

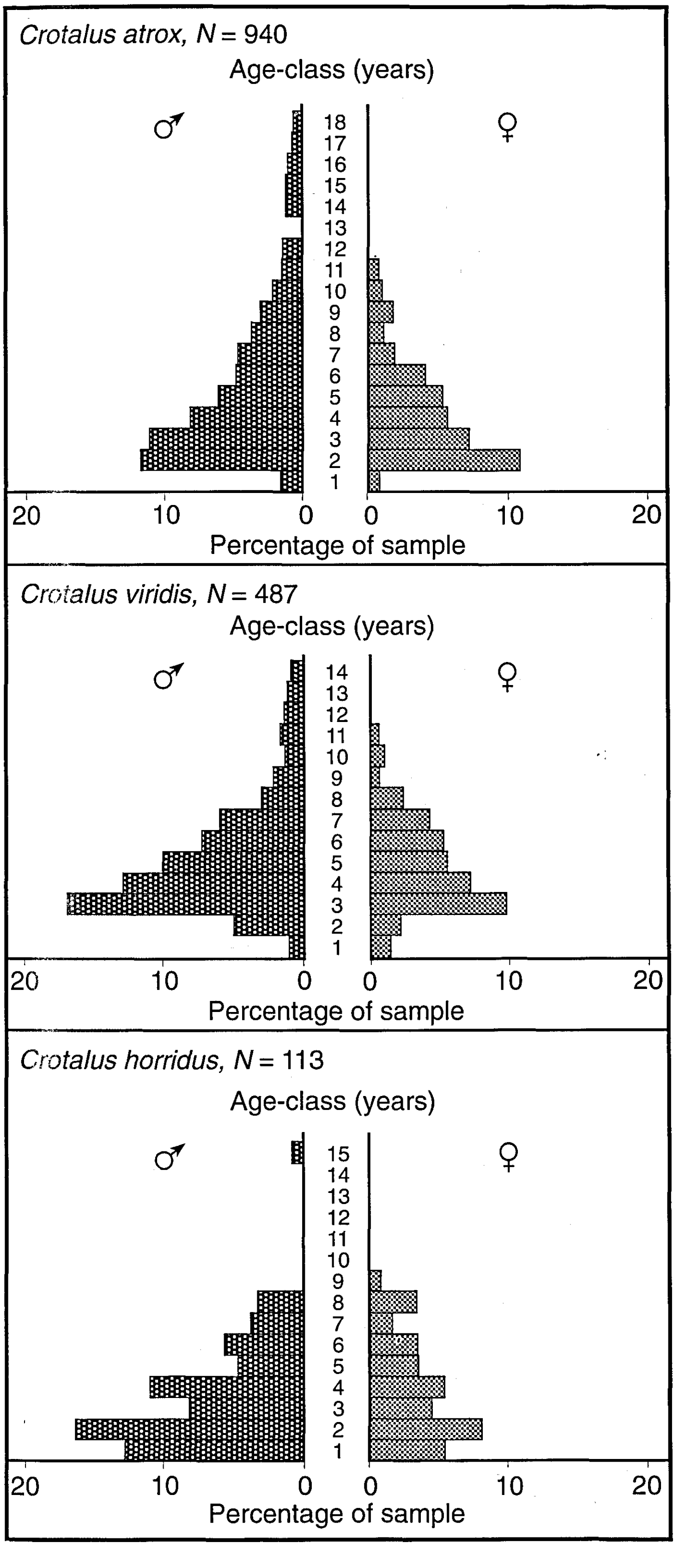

Fig. 3. Age-pyramids of three species of rattlesnakes based on number and taper of rattle segments; males outnumber females, tend to grow larger, and survive longer. The samples of *Crotalus atrox* and *C. viridis* were obtained at "rattlesnake round-ups" and included few young because it was illegal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

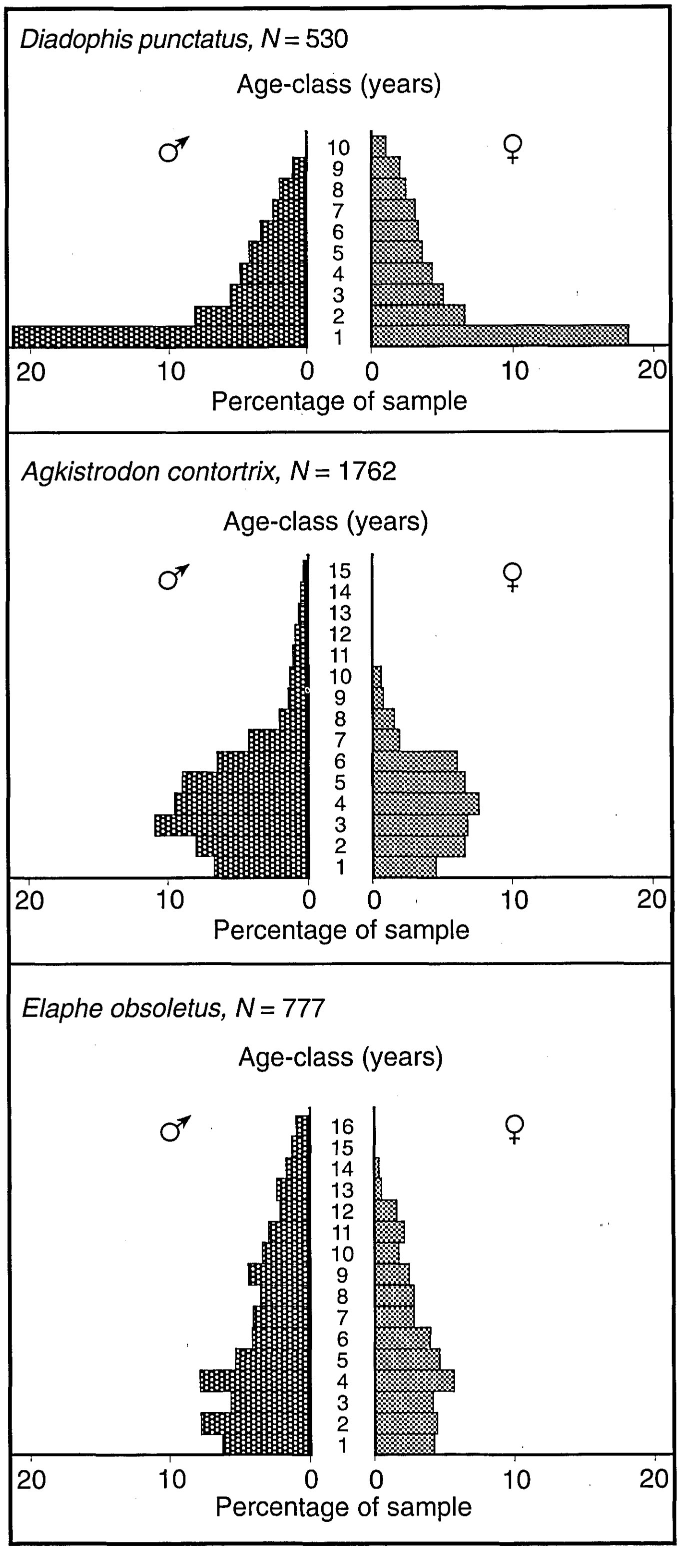

Fig. 4. Age-pyramids of three species of relatively long-lived snakes based on putative age-size cohorts. In *Diadophis punctatus*, males are smaller than females; the average size of males of *Agkistrodon contortrix* and *Elaphe obsoleta* is larger than females. In all three species, males are more 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
Agkistrodon contortrix	4.90	103.6	504.7	5.6
Coluber constrictor	14.80	109.2	1616.6	18.0
Crotalus horridus	0.30	397.5	119.2	1.3
Diadophis punctatus	1603.00	2.57	4119.0	45.9
Elaphe obsoleta	3.60	300.1	1080.4	12.0
Lampropeltis calligaster	4.00	149.2	596.8	6.6
Lampropeltis triangulum	0.70	45.8	32.1	0.4
Nerodia sipedon	0.30	104.9	31.8	0.4
Pituophis catenifer	0.13	497.5	149.3	1.7
Thamnophis sirtalis	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
*Agkistrodon contortrix**	1762	432	216.0	5.1	1110	249	22.4
*Coluber constrictor**	583	179	166.0	11.8	1960	82	4.2
Crotalus horridus	113	26	14.5	7.2	104	20	19.2
*Diadophis punctatus**	530	130	128.0	3.4	436	205	47.0
Elaphe obsoleta	777	176	59.0	9.7	525	78	13.6
Lampropeltis calligaster	328	89	59.4	9.2	545	53	9.7
Lampropeltis triangulum	249	65	64.2	6.9	443	35	7.8
Neorida sipedon	295	92	92.0	19.9	1830	83	4.5
Pituophis catenifer	147	35	33.0	11.2	392	32	8.2
Thamnophis sirtalis	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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