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DEMOGRAPHY OF GREEN SNAKES (*OPHEODRYS AESTIVUS*)

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ABSTRACT: Sex ratio, population size, age structure, and survivorship of an *Opheodrys aestivus* population were studied by mark-recapture in Arkansas. Sex ratio varied monthly, favoring males in early season (60–80%) and females in midseason (60–80%). Females predominated in one year but the sex ratio was 1:1 in two other years. Population density (approximately 430/ha) was statistically constant over two years. Age structure of females varied little between years, but age structure of younger males changed from one year to the next. Age-specific survivorship, assumed to be constant in adults, was greater in females (49%) than in males (39%). Survivorship during the first year was low (21%). A life table yielded a net reproductive rate ($R_0 = 0.84$) insufficient to sustain the population. The calculated survival rate of first-year snakes, and possibly of adults, apparently underestimated actual survival.

Key words: Reptilia; Colubridae; Demography; Mark-recapture; Survivorship; Life history

REPTILIAN demographic studies have been concerned primarily with lizards. The fact that demographic and other ecological studies have provided much insight into ecological processes led Huey et al. (1983) to state: "Clearly, for many types of ecological studies lizards are model organisms—moreover, they now challenge birds as the paradigmatic organism of ecology." Demographic studies of their close relatives, the snakes, have not been as instructive. Several attributes of snakes generally contrast those of lizards and contribute to snakes being less tractable study subjects. These attributes include inconspicuousness, nocturnality, unpredictable and potentially extensive movements, long periods of inactivity, and apparent low population densities. Recent evaluations of the suitability of snakes for demographic studies (Lillywhite, 1982; Turner, 1977) have not been favorable.

The rough green snake, *Opheodrys aes-*

tivus, is an arboreal species which prefers the brushy vegetation of fence rows and forest edges. In contrast to many snake species, it has attributes that would appear to enhance demographic analysis. Although diurnally cryptic, green snakes are abundant, have low vagility, and have a conspicuous sleeping posture at night (on the distal ends of branches) which renders them easily and predictably collected (Plummer, 1981). Some demographic attributes, such as reproduction and growth, have been reported (Plummer, 1984, 1985). The purpose of this paper is to analyze sex ratio, population size, age structure, and survivorship. Field observations from August 1977 to September 1984 indicated that my study population was remarkably stable. If these observations were correct, the analysis of the interaction of reproduction and mortality should yield a net reproductive rate that would sustain the population over the long term.

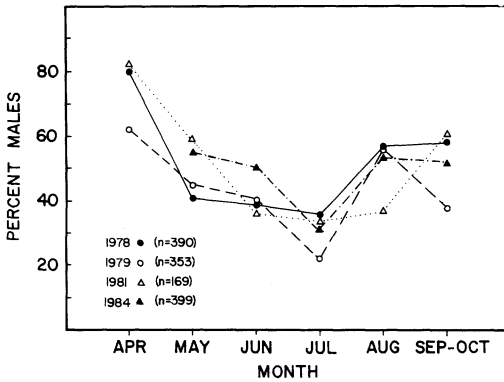


FIG. 1.—Sex ratio variation in monthly samples of *Opheodrys aestivus*.

METHODS

The study area was the forest bordering a narrow (approximately 50 m) 700 m long channel where Overflow Creek entered Bald Knob Lake in White County, Arkansas. The habitat has been described previously (Plummer, 1981). Green snakes inhabited the dense forest edge vegetation near the shoreline and were collected by hand after searching the vegetation at night with a spotlight while slowly cruising the shoreline in a boat. Collecting occurred 2–3 times per week from late April through early October in 1978 and 1979 and irregularly in 1977 and after 1979. In 1984, snakes were sampled biweekly from Bald Knob Lake and nearby localities for related studies. These data were included in the sex ratio analysis. On initial capture in 1977–1979, snakes were given a unique mark by clipping ventral scutes (Brown and Parker, 1976). Date, snake number, sex, and snout–vent length (SVL) were recorded at each capture. Snakes were processed in the field and were released within 10 min at the point of capture. Statistical procedures follow SPSS Inc. (1983).

At this locality, green snakes grow primarily from May through September. Oviposition occurs in June–July and hatching in August–early September. Snakes enter into hibernation by October and emerge in late April–early May

TABLE 1.—Observed frequencies of single and multiple captures of *Opheodrys aestivus* compared to a zero-truncated Poisson distribution of expected frequencies assuming catchability was constant.

No. of monthly samples in which an individual was captured	1978		1979	
	Observed no. of snakes	Expected no. of snakes	Observed no. of snakes	Expected no. of snakes
1	126	131.88	114	114.89
2	65	57.24	44	51.53
≥3	19	20.88*	28	19.58*
	$\chi^2 = 1.48$ $P > 0.10$		$\chi^2 = 4.73$ $P < 0.05$	

* Cells with expected frequencies ≤ 5 were pooled.

(Plummer, 1981, 1984, 1985). I assigned snakes to age classes according to the size-age criteria of Plummer (1985). Age classes were: age class E = egg (from oviposition to hatching), H = hatchling (from hatching to first hibernation), 0 = first-year snake (from May following the first hibernation through September of the same year), age class 1 = 1-yr-old (from May following the second hibernation through September of the same year), age class 2 = 2-yr-old (from May following the third hibernation through September of the same year), and so forth.

RESULTS

Sex Ratio

From April 1978–October 1979, 743 captures were made on 333 snakes in the study area. In 1978, the overall sex ratio of 0.94 male:1 female (210 snakes) was not significantly different from 1:1 ($\chi^2 = 0.30$; $P > 0.50$). In 1979, the overall sex ratio of 0.72 male:1 female (186 snakes) was significantly different from 1:1 ($\chi^2 = 4.83$; $P < 0.05$). Removal collecting of 169 snakes in 1981 at the opposite end of the lake yielded a sex ratio of 1.01 male:1 female which was not significantly different from 1:1 ($\chi^2 = 0.01$; $P > 0.90$). Sex ratio varied monthly in all years (Fig. 1). Males tended to predominate in early season samples and again, but to a lesser extent, in late season samples. Females predominated in mid-season (late June–July)

TABLE 2.—Statistics of population estimates of *Ophiodrys aestivus* by the Schumacher-Eschmeyer method. Confidence limits were calculated according to Caughley (1977). Correlation coefficients and significance levels of regression equations are indicated. See text for an explanation of the meaning of the last four columns.

Year	Estimated population size (N)	95% confidence limits of N	No. snakes captured	Regression of m_i/n_i on M_i	1/N	r	P
1978	303	275–337	210	$y = 0.001 + 0.0033x$	0.0033	0.99	<0.001
1979	256	219–307	186	$y = 0.007 + 0.0038x$	0.0039	0.98	<0.001

samples when oviposition occurred (Plummer, 1984).

Population Size

An assumption of population estimation methods by mark-recapture is the equal probability of capture of all individuals. To test this assumption on *Ophiodrys*, I fitted the observed number of snakes captured 1, 2, and 3 or more times in monthly (May–September) samples to a zero-truncated Poisson distribution of frequencies to be expected if catchability was constant (Caughley, 1977). The null hypothesis of equal catchability can be rejected for samples in 1979 but not in 1978 (Table 1).

Population sizes in each year were estimated by the method of Schumacher and Eschmeyer (1943) from monthly (May–September) samples. The equation is

$$N = \frac{\sum M_i^2 n_i}{\sum M_i m_i}$$

where N is the estimated population size, M_i is the number of individuals marked prior to the i th sampling period, and n_i is the number of individuals captured in the i th sample of which m_i had been marked previously (Caughley, 1977). The method assumes no birth, mortality, emigration, or immigration during the census. Young of the year were not included in the census. No estimate of emigration or immigration was available; the mean distance between recaptures was only 26 m (Plummer, 1981). Two advantages of the Schumacher-Eschmeyer method are allowing a standard error of N to be calculated and providing an additional check on the as-

sumption of equal catchability. Unless the assumption of equal catchability is violated, regression of m_i/n_i on M_i is linear through the origin with slope $1/N$ (Caughley, 1977). Correlation coefficients for both regressions were highly significant and, corroborating the checks of equal catchability (Table 1), the intercept was closer to the origin and there was closer agreement between $1/N$ and slope in 1978 than in 1979 (Table 2). For these reasons, I consider the population estimate for 1978 to be closer to the actual number of that year. Since the population estimate for 1978 is contained within the confidence limits for 1979, it is likely that the estimates for the 2 yr are not significantly different.

Based on a population size of 300 (Table 2), there were approximately 0.21 *O. aestivus* per linear meter of shoreline. This density is similar to those reported (no./m) for other shoreline snakes (*Regina septemvittata* 0.18–0.26, Branson and Baker, 1974; three spp. *Nerodia* 0.03–0.18, Hebrard and Mushinsky, 1978). Plummer (1981) found that *O. aestivus* activity was concentrated near the shoreline with 86–88% of all captures made within 3 m of the shoreline and 96–97% made within 5 m. Using the habitat boundaries of 3 m and 5 m, respectively, I calculated population densities of 714 snakes/ha and 429/ha. While the exact extent of habitat utilization away from the shoreline may be argued, at a conservative estimate of 429 snakes/ha, this population of *O. aestivus* was, with few exceptions, among the most dense of reported snake populations (Andren and Nilsen, 1983; Blaesing, 1979;

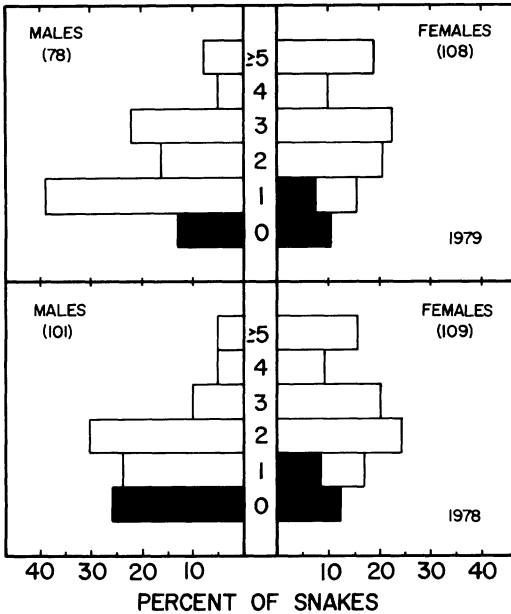


FIG. 2.—Age structure of an *Ophedrys aestivus* population in 2 yr. Data include only those snakes actually captured. Open bars indicate mature individuals, closed bars represent immatures. Numbers in parentheses are sample sizes.

Brown, 1970; Clark, 1974; Clark and Fleet, 1976; Fitch, 1982; Freedman and Catling, 1978; Godley, 1980; Madsen and Osterkamp, 1982; Spellerberg and Phelps, 1977; Stickel et al., 1980; Turner, 1977). Perhaps the greater extent of the vertical component of the habitat of this arboreal snake permitted greater density than in non-arboreal species.

Population Structure and Survivorship

The resulting age structure (Fig. 2) showed a year-to-year constancy in females which suggested that a stable age distribution had been achieved. The age distribution of males was more variable especially in the 0–2-yr-olds.

Reproduction in this population was of the birth-pulse type. Because of the small size of hatchlings and, consequently, the difficulty of sampling them, and the restricted period in which to sample them before winter mortality occurred, I estimated reproductive output indirectly from

fecundity of the 1978 population (Fig. 2). Using the function, number of eggs = $-4.1 + 0.023 \text{ SVL}$ (Plummer, 1984), the estimated 1978 egg production was 482 eggs of which 241 were males and 241 females since the sex ratio at hatching, like most snakes (Shine and Bull, 1977), was 1:1 (Plummer, 1984).

Only 10 male and 11 female first-year snakes were captured in 1979. Based on egg production in 1978, these capture data provide survivorship estimates of 4.1% and 4.6%, respectively.

For age classes ≥ 0 , I determined sex-specific survivorship by the proportion of individuals in each 1978 age class n present in the 1979 age class $n + 1$. Survivorship from age class 0 to age class 1 was 38.5% for males and 30.8% for females. For age classes ≥ 1 , I regressed the natural logarithm of the number of survivors ($\ln S$) in an initial cohort of 100 on age x (in years). The regression equations were, for males, $\ln S = 5.43 - 0.947x$ ($r = -0.995$, $P < 0.001$) and, for females, $\ln S = 5.48 - 0.722x$ ($r = -0.995$, $P < 0.001$). As with snakes in general (Brown and Parker, 1982; Parker and Brown, 1980; Turner, 1977), the correlation coefficients indicated only slight deviations from the hypothesis of linearity (age-constant mortality) (Turner, 1977).

The slopes for males and females were significantly different (ANCOVA, $P < 0.01$). Annual adult (≥ 1 yr of age) survival ($S = e^b$, where b is the slope from the above regressions and e is 2.718) for males was 38.8% and for females 48.6%. The greater adult survivorship of females apparently influenced the sex ratio from younger to older snakes (Fig. 2). The χ^2 values for the 0, 1, and 2-yr-olds were not significantly different from a 1:1 sex ratio in 1978 ($\chi^2 = 3.46$, $P > 0.05$) or in 1979 ($\chi^2 = 0.01$, $P > 0.90$). In contrast, the χ^2 values for the 3, 4, and ≥ 5 -yr-olds significantly departed from 1:1 in favor of females in both 1978 ($\chi^2 = 12.86$, $P < 0.001$) and 1979 ($\chi^2 = 11.58$, $P < 0.001$).

A life table for *O. aestivus* (Table 3) was based on these assumptions: (1) age E

began at oviposition; (2) fecundity was determined from median-sized snakes in each age class by the previous function and adjusted by assuming 50% of females reproduced at age 1 and 100% thereafter (Plummer, 1985); (3) sex ratio at birth was 1:1; (4) survivorship in age classes ≥ 1 was 0.486; (5) survivorship from the egg to age 1 (= "first-year") was calculated indirectly by dividing the mean number of 2-yr-old females in 1978-1979 (25) by survivorship in age class 1 (0.486) to determine the mean number of snakes in age class 1 that should have been present in 1978-1979 (number of 1-yr-olds = mean no. 2-yr-olds/survivorship in age class 1 = 25/0.486 = 51). Survivorship in the first year (0.212) was calculated as the number in age class 1/number in age class E = 51/241 = 0.212).

DISCUSSION

Male preponderance in early spring samples has been found in other snakes (Clark and Fleet, 1976; Fitch, 1949, 1975; Gregory, 1977; Turner, 1977; Voris and Jayne, 1979), and probably is related to greater male activity when searching for mates. Whether the same explanation holds true for the much less pronounced preponderance of male *O. aestivus* in the fall is uncertain. Richmond (1956) observed fall mating of *O. aestivus* in Virginia, but Plummer (1984) found no evidence of fall mating in the Bald Knob Lake population. The preponderance of females in midseason may be related to the greater conspicuousness of the already larger females being swollen with eggs. An alternative explanation is that males decrease feeding and become relatively inactive as occurs in *Nerodia sipedon* (Feaver, 1977). Was the skewed sex ratio in 1979 favoring females the result of greater collecting effort in June-July? It was not likely because 164 June-July captures of 390 total captures (42.1%) in 1978 compared favorably to the 151 June-July captures of 353 total captures (42.8%) in 1979.

Parker and Brown (1980) and Brown

TABLE 3.—Life table for *Opheodrys aestivus*: x = age (years); l_x = age-specific survival rate; m_x = age-specific fecundity rate; R_0 = net reproductive rate. See text for assumptions.

x	l_x	m_x	$l_x m_x$
E	1.000	0	0
1	0.212	1.03	0.218
2	0.103	2.81	0.289
3	0.050	3.25	0.163
4	0.024	3.52	0.084
5	0.012	3.67	0.044
6	0.006	3.75	0.023
7	0.003	3.81	0.011
8	0.001	3.84	0.004
			$R_0 = 0.836$

and Parker (1984) found greater adult survival rates in snakes than reported in other studies. They attributed their results to techniques of enclosing virtually entire populations by fencing around communal dens which resulted in capturing most individuals each year. In most studies, such as the present, where such enclosure techniques were not feasible, any estimate of survivorship probably is lower than the true rate because of less reliable recapture proportions (Parker and Brown, 1980). In *O. aestivus*, several lines of evidence suggested that actual survivorship, especially in the first year, was much greater than that estimated. Foremost was an unbelievably low net reproductive rate ($R_0 = 0.058$) which could be calculated using an estimated first-year survivorship of 0.014 (survivorship from egg to age 0 \times survivorship from age 0 to age 1 = 0.046 \times 0.308 = 0.014), and assuming a constant adult survivorship of 0.486 and the above fecundity schedule. This calculation indicated that the population was rapidly decreasing in 1978-1979. If continued, this would quickly lead to local extinction, a conclusion inconsistent with field observations from August 1977-September 1984 which indicated that the population was remarkably stable. As demographic attributes in snakes are known to vary considerably from year to year (Brown and Parker, 1984; Feaver, 1977; Parker and Brown, 1980), 1978 may have been an un-

usually low year for survival. However, the constancy of the female age structure in 1978–1979 (Fig. 2) points toward the attainment of a stable age distribution which can result only from a relatively long-term constant mortality schedule and rate of increase or decrease (Caughley, 1977).

Because of the discrepancy between field observations and estimated survivorship, I estimated first-year survivorship of females by another independent method. Age class 2 is the first class to contain more individuals than the next older age class (Fig. 2), at least in 1978. In a population with a stable age distribution, this pattern probably exists because proportionally more 2-yr-old females were caught relative to the actual number in the class than in any younger age class. Therefore, I assumed that population size, mortality, and fecundity had been constant for several years, and I calculated a first-year survivorship (0.212, above) based on the observed number of 2-yr-olds. The life table constructed from these assumptions resulted in an R_0 of 0.836 (Table 3), a value still less than the $R_0 = 1.0$ needed for each female to replace herself each generation, but probably much closer to reality than the estimate based on actual recapture of survivors in classes 0 and 1.

My best estimate of first-year survivorship in *O. aestivus* (0.212) is similar to those found for other colubrids such as *Coluber constrictor* 0.156 (Fitch, 1963b); *Rhabdophis tigrinus* 0.199 and *Elaphe quadrivirgata* 0.177 (Fukada, 1969); *Coluber constrictor* 0.170, *Masticophis taniatus* 0.145, and *Pituophis melanoleucus* 0.200 (Brown and Parker, 1982); and *Nerodia sipedon* 0.235 (Feaver, 1977). If in fact actual adult survivorship was underestimated (cf. Brown and Parker, 1984; Parker and Brown, 1980), any increase in this value also would increase R_0 . Further, annual adult (snakes ≥ 1 -yr-old) survival estimates in *O. aestivus* (males 0.388, females 0.486) are toward the low end of published values of approximately 0.30–0.86 ($\bar{x} = 0.57$) for 12 species of colubrids

(Brown and Parker, 1982; Feaver, 1977; Turner, 1977).

Implicit in demographic analysis by mark-recapture is the assumption of equal probability of capture of all individuals. This assumption held true because no *Opheodrys* ever escaped capture once sighted. However, if the behavior of any snake had decreased the probability of its being seen, the assumption would be violated. Unequal catchability could not be statistically demonstrated in 1978 but was likely in 1979 (Table 1). Possible sources of unequal catchability included the tendency of males for greater movement (Plummer, 1981), and seasonal differences in activity between the sexes (Fig. 1). Another possible source, with probably greater impact, concerned juvenile snakes. Numerous authors have commented on the difficulty in sampling juveniles (Brown and Parker, 1984; Clark, 1970; Clark and Fleet, 1976; Fitch, 1960, 1963a,b, 1965; Gregory, 1977; Hirth and King, 1968; Jackson and Franz, 1981; Lillywhite, 1982; Parker and Brown, 1973, 1980; Platt, 1969; Semlitsch et al., 1981; Stickel et al., 1980). The possibility of juveniles having behavior patterns different from adults such as relative inactivity or different microhabitat preferences (Fitch, 1960, 1963a; Gibbons et al., 1977; Jackson and Franz, 1981; Lillywhite, 1982; Semlitsch et al., 1981; Voris and Jayne, 1979) would contribute to bias if the behavioral differences caused visible access of juveniles to be lower than that of adults. Despite the lack of correlation between perch height and SVL in *O. aestivus* (Plummer, 1981), the possibility existed that juveniles spent relatively more time on the ground or in the lowermost vegetation stratum where visible access was minimal. Combined with their small size, this behavior would render them less susceptible to capture and would result in an unrealistically high mortality estimate and an underrepresentation of the group in the age structure (cf. Fig. 2).

Maximum longevity also suggested that survivorship was greater than measured. Two 3-yr-old females first captured in

September 1977 were recaptured in July–August 1981, and thus survived to their seventh year. Another female (505 mm SVL) was first captured in April 1978 and was recaptured in April 1981. Although estimating age at this size was not reliable (Plummer, 1985), conservatively (if it were a fast grower), an estimate of 5 yr would be realistic and would indicate that this snake survived to at least its eighth year. If my inferred survivorship in the population was correct, the chances of surviving to an age of 7 and 8 yr, would be three in 1000 and one in 1000, respectively (Table 3). In fact, these three snakes represented an approximately one in 100 chance (three survivors in a population of approximately 300). An even greater number of snakes actually survived to at least their fifth or sixth year despite the calculated probability being less than 12 in 1000.

Feaver (1977) identified two general life history tactics among 17 species of colubrid and viperid snakes. One, in which *O. aestivus* better fits, is characterized by early maturity, small female size at maturity, large clutches, steep increase of clutch size with female size, annual clutches, females the larger sex, and low adult survivorship. Various measures of reproductive output were relatively invariable both within (Plummer, 1983; Seigel and Fitch, 1984) and between *Ophedrys* populations (summary in Plummer, 1984). In contrast, lipid storage in the Arkansas population was highly variable annually and presumably was affected by food availability (Plummer, 1983). A reproductive tactic of a relatively invariant reproductive output compared to stored lipids has been predicted to develop in relatively long-lived species in environments where juvenile survivorship is highly variable and unpredictable (Congdon and Tinkle, 1982).

Demographic studies of snakes in which the interaction of mortality and reproduction has been evaluated have yielded net reproductive rates below that necessary for long-term stability (*Nerodia sipedon*,

Feaver, 1977; *Xenochrophis vittata*, *Coluber constrictor*, and *Carpophis vermis*, Turner, 1977 (from data of Bergman, 1950; Clark, 1970; Fitch, 1963b); *O. aestivus*, present study). Exceptions include only the viperid *Agkistrodon contortrix* (Vial et al., 1977) and those few colubrid populations which could be completely enclosed by fencing around communal dens (*Pituophis melanoleucus*, *Coluber constrictor*, *Masticophis taeniatus*, Brown and Parker, 1984; Parker and Brown, 1980). Despite the attributes of *O. aestivus* (above), I was unable accurately to assess survivorship, especially in juveniles. This lack of success resulted in an R_0 insufficient to sustain the population over the long term and was in direct contrast to field observations. Because of these results, I agree with Turner (1977) and Lillywhite (1982) that snakes probably are poor candidates for studies of pure demography. Why they are poor candidates, however, is an interesting question in itself. While population studies in snakes are proliferating, the life history stages that we know least about, the egg, hatchling, and first-year stages, are receiving little attention. Few authors have ever found snake eggs in the field, and the literature is replete with statements regarding the unavailability of juveniles (above). Although juvenile snakes may be “miniature adults” morphologically, the chances seem quite good that their ecology is fundamentally different from adults. Many behavioral and ecological characteristics of reptiles have underlying physiological bases, some of which change profoundly through ontogeny (Pough, 1983). For example, juveniles of several species of snakes have limited endurance capacities compared to adults (Pough, 1983). Such differences could fundamentally affect foraging and other activity patterns.

Assessment of juvenile survivorship appears to be the single greatest problem in snake demography. Approaches to the study of such stages perhaps could include marking large numbers of hatchlings or neonates obtained from laboratory fe-

males and releasing them in the field (Blanchard and Finster, 1933; Fukada, 1969) or by constructing artificial nesting sites in the field. Whatever the approach, innovative work needs to be focused on these little known and apparently vulnerable stages in the life histories of snakes.

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