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POPULATION ECOLOGY OF GREEN SNAKES (*OPHEODRYS AESTIVUS*) REVISITED

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ABSTRACT: A population of rough green snakes (*Opheodrys aestivus*) was studied by mark-recapture at Ransom Lake (RL) in north-central Arkansas over 7 yr (1986–1992). Results are compared to those obtained previously from a population in similar habitat located 12 km distant (Bald Knob Lake, BKL). Over 2700 captures made along the RL shoreline were nonrandomly distributed within areas of dense vegetation. Green snakes lived within home ranges averaging 67 m in shoreline length and differing in location between years by about 50 m. Individuals were recaptured on average every 19 days, in which time they had moved linearly along the shoreline about 28 m. About 3% of all movements were over water. Each of these spatial parameters at RL was very similar to those obtained at BKL.

Growth rates of individual snakes decreased linearly with snout-vent length (SVL) and were similar to those characterizing snakes at BKL. However, greater variance in growth rates at RL resulted in a weaker relationship between body size and age. Females grew to be larger than males. Body size of females was slightly larger at RL than at BKL. Younger age groups were proportionally larger at RL than at BKL. Sex ratio was 1:1 both in adults and in all snakes combined. In 1987 and 1988 when about 60% of the population consisted of adult snakes, sex and age structure of the population were similar between years.

Maximum population density was about 800 snakes/ha. Catchability of individual snakes in monthly samples was equal in 1987 but equivocal in 1988. Survivorship was measured directly by age-specific recapture proportions. Adult survivorship (males 28%, females 41%) was less at RL than at BKL. Calculated overall first-year survivorship (21.5%) was similar to that at BKL and was slightly greater than hatchling survivorship measured directly by recapture (15–19%). Survivorship for ages ≥ 0 in both sexes showed a linear logarithmic decline with age (type II survivorship curve). As at BKL, overall clutch size at RL averaged 6 eggs. Unlike at BKL, clutch size at RL differed among years concordant with body condition (weight-length ratio) of snakes. As at BKL, the net reproductive rate at RL ($R_0 = 0.60$) was insufficient for sustaining the population over the long term. Estimated population size varied fivefold over 7 yr and decreased from approximately 350–500 snakes in the first 3 yr (1986–1988) to 100–200 in the last 4 yr (1989–1992). The rapid population decline apparently was due to unusually high mortality among adults, and the increased mortality, in turn, was correlated with unusually hot and dry weather leading to a decrease in the body condition of snakes. Predation by snakes and birds may have contributed to the decline.

Although snake populations are often regarded as being relatively stable, this study demonstrates that populations of a small insectivorous species are not immune to environmental vagaries and may respond by decreasing density as do other vertebrates.

Key words: Mark-recapture; Demography; Survivorship; Population density; Spatial distribution; Movements; Drought; Arboreal snake; *Opheodrys*

IN AN EARLY TRIP to southern Florida, the botanist J. K. Small (in Safford, 1917) wrote, "There is everywhere present a beautiful green snake. It inhabits the hammocks and is especially abundant in those of the Everglades. . . . One has usually to be careful to look before laying hold of the limb of a tree for support, or he may grasp something of quite different consistency from that of wood." Small's early observations suggest that the rough green snake, *Opheodrys aestivus*, was widespread and locally abundant, and in fact, rough green

snakes can occur in some of the highest densities reported for any snake species (Parker and Plummer, 1987). In addition, *O. aestivus* is strongly arboreal with limited vagility and a preference for vegetational edges, characteristics that promote their occurrence in discrete populations inhabiting dense shoreline vegetation surrounding certain bodies of water (Goldsmith, 1984; Plummer, 1981a). These habitat and dispersion characteristics render green snakes good candidates for comparative population studies. I had conducted earlier

studies on the population ecology of green snakes in such habitat (Plummer, 1981a, 1983, 1984, 1985a,b). In 1985, an initial survey of a population at Ransom Lake (RL) located approximately 12 km N of the site of the earlier study (Bald Knob Lake, BKL) resulted in a greater capture rate of juveniles compared to that of the BKL population. Because the direct measurement of first-year survivorship is a major problem in snake demography (Parker and Plummer, 1987), and one in which green snakes are not exempted (Plummer, 1985b), a relatively large initial capture rate of juveniles at RL prompted the current investigation. This paper reports on the RL study and compares various quantitative ecological characteristics between the RL and BKL populations. To facilitate making such comparisons directly (Dunham et al., 1988a,b), I used the same field techniques and methods of data analysis for each population.

Over the years, many investigators (e.g., Cagle, 1953; Dunham et al., 1988a,b; Gibbons, 1990; Seigel et al., 1995; Tinkle, 1979) have stressed the need for detailed, long-term demographic and life history studies of reptile populations, including (especially) those on snakes. However, demographic processes of snake populations are notably difficult to assess because individual snakes are frequently unavailable for sampling. The resulting biases are due in part to the general secretive nature of snakes but also are strongly influenced by snakes' accentuation of the general ability of ectotherms to be inactive and reclusive for extended periods (Pough, 1980). Specifically, activity may be reduced after snakes feed, albeit infrequently, on large prey (Gans, 1961; Pough and Groves, 1983) and when they seek extended refuge when shedding (Madsen, 1984; Plummer and Congdon, 1994; Weatherhead and Charland, 1985). Comparative studies on the population ecology of snakes have focused on interspecific comparisons of syntopic populations (e.g., Brown and Parker, 1982; Diller and Wallace, 1996; Kephart, 1981; Parker and Brown, 1980) and intraspecific comparisons of populations differing in macrogeographic (e.g., Brown and

Parker, 1984; Gregory and Larsen, 1993, 1996) or in microgeographic location (e.g., Brown and Parker, 1984; Kephart, 1981). If intraspecific studies with similar techniques repeated in similar habitats across microgeographic space and time yield similar results, confidence in our ability to portray snake populations in more robust ecological models should increase.

Arboreal snakes from various evolutionary lineages display a remarkable suite of convergent adaptations involving body size and shape, coloration, and specializations in locomotor, visual, and cardiovascular structure and function (Lillywhite and Henderson, 1993). In a recent review of the behavioral and functional ecology of arboreal snakes, Lillywhite and Henderson (1993) stressed the need for additional studies on these animals to promote our understanding of more general questions related to the adaptive radiation of arboreal vertebrates (e.g., Pounds, 1991).

MATERIALS AND METHODS

The study area was the shoreline vegetation of Ransom Lake, a 21 ha lake impounded in 1972 and located 2 km W of Denmark, White County, Arkansas. Ransom Lake is located in the foothills of the Ouachita Mountain Region of the Interior Highlands of Arkansas (Foti, 1974). Fieldwork was conducted usually three times per week from June–October 1986, throughout the active season (mid-April to mid-October) in 1986–1988, and from mid-April to July in 1989–1992. Resulting sample sizes varied according to sampling frequency. For each year, the number of captures and number of individual snakes were: 1986, 249 (195); 1987, 989 (387); 1988, 821 (372); 1989, 336 (167); 1990, 179 (106); 1991, 53 (45); and 1992, 68 (50).

The shoreline at the upper end of the narrow (approximately 75 m) L-shaped lake was cleared for farmland. The remaining shoreline was thickly vegetated especially with alder (*Alnus rugosa*) in a thick, continuous stratum up to approximately 3–4 m high, providing optimal structural habitat for the arboreal green snakes (Fig. 1; Plummer, 1981a). Imme-



FIG. 1.—Habitat of green snakes at Ransom Lake showing three distinct vegetation strata: (A) a lower stratum of emergent water willow (*Justicia*), (B) a middle stratum of alder (*Alnus*), and (C) an upper stratum of oak–hickory forest. This photograph was taken at location 1750 m where alder height and density were relatively high and where the largest number of green snakes within 50 m segments of shoreline was captured (see Fig. 2).

diately behind the narrow (1–4 m) band of alder was an oak–hickory (*Quercus–Carya*) forest typical of the area and which provided nesting habitat for green snakes (Plummer, 1990a). Emergent water willow (*Justicia*) was found in shallow water along most of the shoreline. The ground was rocky with loose, sandy loam soils. To facilitate precise location of snakes, I marked the vegetated portion of the shoreline at 20-m intervals from 0 to 2100 m with plastic flagging.

Field procedure basically followed that of the previous study at BKL. Green snakes are strictly diurnal and spend the night coiled on the distal end of branches in shoreline vegetation. This position, together with their reflective white ventral surface, rendered them easily detectable and collectable when approached from below with a strong spotlight (Plummer, 1981a). Effort expended on each collect-

ing trip was roughly equal. A single night's sampling effort consisted of slowly cruising the flagged portion of the shoreline (from 0 to 2100 m) one time in a boat while searching the vegetation with a 12 volt spotlight. Several assistants were used during the course of the fieldwork, and, as in most studies, adjustment of capture numbers for possible interobserver differences in ability to visually detect snakes was not feasible (Rodda, 1993). Upon capture, each snake's location was recorded to the nearest 5 m. I individually bagged captured snakes and took them to the laboratory where they were identified if previously marked, sexed, measured (snout-vent length, SVL, in mm; weight in g), gently palpated to determine reproductive condition and count oviductal eggs. Upon its initial capture, each snake was marked by clipping a unique combination of ventral scales (Brown and Parker, 1976). To

obtain an unbiased "empty" body weight and to obtain fecal material for analysis (Plummer, 1991), I gently removed fecal material from the posterior gut by palpation before weighing. Snakes were released at their capture sites the following day. Some late gravid females were retained briefly in the laboratory for the purpose of obtaining their eggs. Following established procedures of incubation (Plummer, 1984), hatchlings obtained from lab-incubated eggs were measured, carefully marked using micro-ophthalmic surgical scissors under magnification, and released in the field. Hatchlings did not appear to be adversely affected by marking. All procedures conformed to stipulated guidelines for using live reptiles in field research (Anon., 1987).

I computed growth rates of individual snakes as the difference between SVL measurements on successive captures divided by the recapture interval in days. The rate data were fitted to the Von Bertalanffy growth model using a finite difference approximation form of the differential equation (Andrews, 1982). This model predicts that growth rate in length is a decreasing linear function of length:

$$GR = a - b \cdot SVL, \quad (1)$$

where GR is growth rate, a is initial growth rate, b is growth constant, and SVL is snout-vent length (Andrews, 1982). Because growth was measured over finite periods, I regressed growth rate on mean SVL (MSVL) to avoid underestimating or overestimating instantaneous growth rates if initial or final SVLs, respectively, were used. For adult snakes, in which measurement error was large relative to growth for small increments of growth, I used growth data with a minimum of 60 d between captures. For fast-growing first-year snakes, I used growth data with a minimum of 30 d between captures.

Following Van Devender (1978), the growth rate equation (Equation 1) was expressed as a differential equation:

$$dSVL/dt = a - b \cdot SVL, \quad (2)$$

which was integrated to yield an equation that related age and SVL:

$$Age(t) = (1/b) \ln(a + b \cdot SVL) + c. \quad (3)$$

The constant of integration, c , can be calculated if age at any body size is known. To calculate c , I used mean SVL at hatching (151 mm; Plummer, unpubl.) for both sexes.

At this locality, the growth season lasts 5 mo from May through September (Plummer, 1985a), oviposition occurs in late June to mid-July and hatching occurs in August to early September (Plummer, 1984, 1990a). Date of birth (= hatching) was assumed to be 1 September for all snakes. Snakes enter into hibernation by October and emerge in late April to early May (Plummer, 1981a, 1984, 1985b).

Based on time of year and size-age criteria obtained from growth analyses, I assigned an age to each snake. Ages were: H = hatchling (from hatching through the first hibernation), 0 = first-year snake (from May following the first hibernation through September of the same year), 1 = 1-yr-old (from May following the second hibernation through September of the same year), 2 = 2-yr-old (from May following the third hibernation through September of the same year), and so forth.

To estimate the abundance of green snakes, I used either Bailey's modification of the single-census Petersen method or the multiple-census Schumacher-Eschmeyer method (Caughley, 1977) depending on the data available for each year. In 1987 and 1988, the large samples obtained in each month of the activity season were more amenable to a multiple-sampling design. In estimating population size, an important assumption of equal catchability for individual snakes was tested. Standard errors for each population estimate were calculated following Caughley (1977).

Statistical analyses were conducted either with SYSTAT (Wilkinson et al., 1992) or with SigmaStat (Fox et al., 1994) and closely follow those of Plummer (1981a, 1985a,b) to facilitate direct comparisons with the dynamics of the Bald Knob Lake population. Before using parametric tests, data were determined to have met the assumptions of normality and homogeneity

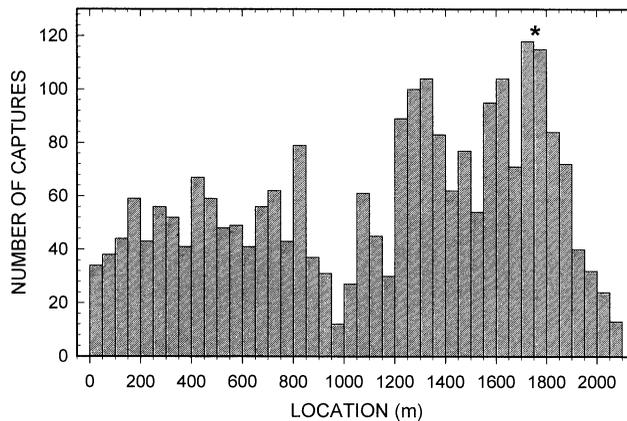


FIG. 2.—Distribution of 2450 captures of green snakes along the shoreline at Ransom Lake. Asterisk indicates location of photograph shown in Figure 1.

of variances. Before testing for differences between intercepts in analysis of covariance (ANCOVA), slopes were tested for homogeneity. To test for possible annual differences in body condition, I used an ANOVA on residuals from the regression of body weight on SVL. The variance/mean ratio was used as an index of dispersion (Krebs, 1989). Unless stated otherwise, sample means are presented with their standard deviations and sample sizes.

RESULTS

Spatial Distribution

The distribution of 2450 captures of green snakes strongly reflected the density of shoreline alder vegetation (Fig. 2). An earthen dam at the lower end of RL (from 900 to 1050 m) was sparsely vegetated and produced few captures (Fig. 2). From 0 to 900 m, the shoreline had lower (range 2–3 m high), less dense alder than the shoreline from 1050 to 2100 m, which had higher (range 3–4.5 m high), more dense alder. Fewer captures were produced in the former sector of shoreline, whereas the latter yielded a greater number of captures (Fig. 2). This pattern of capture distribution was observed in each year of the study as well as separately for both males and females. There was no evidence of sexual or age differences in habitat selection. No green snakes were obtained along the upper end of RL (>2100 m), an unvegetated zone except for low grass. Local pockets of sparse

vegetation resulting from various natural and human factors also produced few captures. For example, on 27 April 1987 a fire burned all the vegetation in the zone between approximately 1000 and 1500 m. Much of the vegetation quickly recovered except for that at 1150–1200 m; thereafter, this sector produced relatively few captures (Fig. 2). Likewise, a low number of captures at 1500–1550 m (Fig. 2) reflected recent clearing of vegetation for a lake access. With man-made clearings excluded, the mean number of captures per 50 m of shoreline for 0–900 m (50.4 ± 11.8 , $n = 18$) was significantly less than the capture rate for 1200–1900 m (90.3 ± 17.4 , $n = 13$; Mann–Whitney $U = 319.5$, $P < 0.001$). In each of these respective shoreline sectors, the spatial distribution of individual snakes was significantly different from random (0–900 m, $s^2/\bar{x} = 2.8$, $t = 5.25$, $P < 0.001$; 1200–1900 m, $s^2/\bar{x} = 3.4$, $t = 5.88$, $P < 0.001$), and, because the variance was greater than the mean, judged to be clumped.

Movements

For calculation of distance moved within years, I assumed that snakes moved along the shoreline in their normal habitat, and that overwater movements usually did not occur. However, occasionally snakes were observed in the water with their tails anchored to *Justicia* stems. Overwater crossings were judged to have occurred

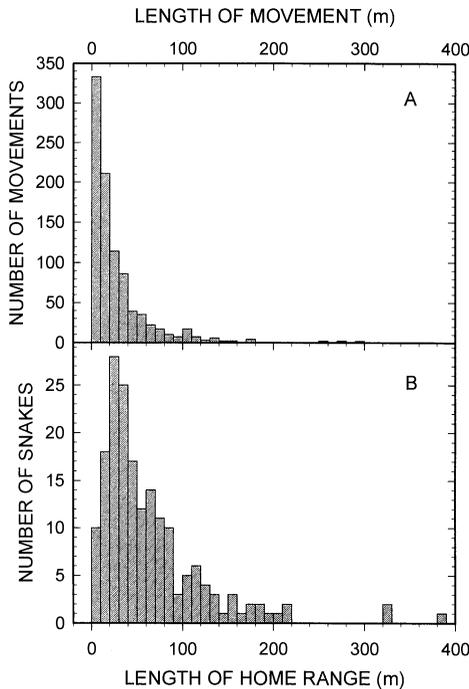


FIG. 3.—(A) Number of movements of green snakes according to length of movement. (B) Number of individual green snakes according to home range length.

when a snake was found on the opposite side of the lake directly across from its previous location. If a snake had reached this point by moving around the lake along the shoreline, such a peripheral movement would have required traveling 800–1900

m. Such extremely long sojourns were judged unlikely as the actual straight-line distance across water was <100 m. Based on these comparisons of habitat and known behavior, water crossings occurred in 39 of 1650 (2.4%) individual movements.

Mean distance and time between 1297 consecutive captures of individual snakes were 28 ± 42 m and 19 ± 20 d. Movements ($n = 933$) within years for snakes in which captures were separated by at least 7 d clustered around short (<20 m) distances (Fig. 3A). Distance of movement did not differ according to sex ($t = -1.35$, $P > 0.15$, $df = 931$) but was only weakly related to the time between captures (Spearman's $r_s = 0.08$; $P < 0.05$, $n = 925$). Because green snakes normally confined their activities to the narrow strip of alder vegetation along the shoreline, their movements were largely parallel to the shoreline. Movements perpendicular to the shoreline were limited. Therefore, I expressed home range size as a shoreline distance. Within a single year, home range lengths calculated for 181 snakes captured four or more times within a single year averaged 67 ± 67 m and did not differ according to sex ($t = -0.016$, $P > 0.90$, $df = 179$) (Fig. 3B). Between consecutive years, for 20 snakes recaptured ≥ 4 times, mean distance between midpoints of their two sequential home ranges was 51 ± 111

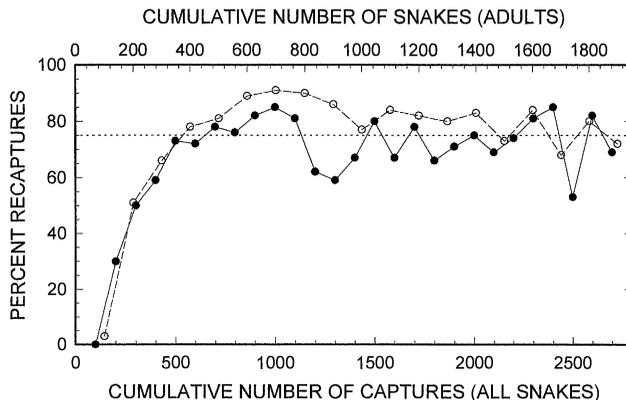


FIG. 4.—Percentage of recaptures of green snakes in successive 100-snake samples as a function of cumulative number of captures in adults (open circles, dashed line) and in all age classes (closed circles, solid line). Dotted line is a 75% reference line.

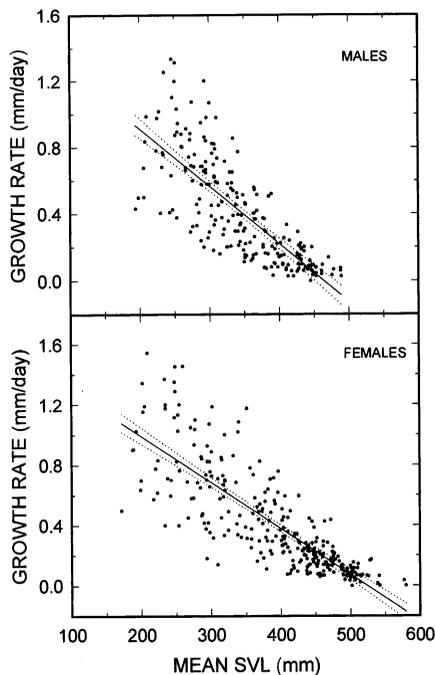


FIG. 5.—Growth rate (GR) as a function of mean snout-vent length (MSVL) in male and female green snakes. For males, $GR = 1.605 - 0.00346 \text{ SVL}$ ($r = 0.78$, $P < 0.001$, $n = 223$) and for females $GR = 1.606 - 0.00306 \text{ SVL}$ ($r = 0.82$, $P < 0.001$, $n = 286$). Dotted lines represent 95% confidence limits of slopes of the regression lines. Data were determined from records of growth within the growing season (May–September).

m. By comparing the location of the last capture in September–October to that of the first capture the next April–May, specific overwintering locations for individual snakes were inferred. The mean distance between these locations was only 27 ± 31 m ($n = 68$ snakes).

Rate of Recapture

In the 7 yr of this study, 885 snakes were captured a total of 2701 times. After approximately 500–600 captures, the percentage of recaptures approached 75% and remained around that value throughout the study (Fig. 4). Samples of adults varied over time narrowly around 80% whereas the percentage of recaptures in samples of all ages was somewhat less (about 70%). Data for the various ages were also more variable (Fig. 4), likely reflecting higher rates of mortality among

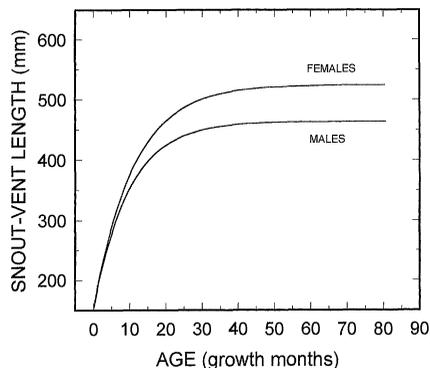


FIG. 6.—Predicted relationship of body size (snout-vent length) and age (posthatching growth months) in male and female green snakes. The curves are plots of Equation 3 (see text) for males ($\text{age} = [-289 \ln(1.605 - 0.00346 \text{ SVL}) + 23]/30$) and for females ($\text{age} = [-327 \ln(1.606 - 0.00306 \text{ SVL}) + 44]/30$). A growth period of 1 mo after hatching was assumed before the first hibernation. To convert growth age to chronological age (total months since hatching), add 7 mo (inactive) to growth ages 2–6, 14 mo to ages 7–11, 21 mo to ages 12–16, 28 mo to 17–21, etc. (e.g., growth age 4 mo = chronological age 11 mo; growth age 14 mo = chronological age 35 mo).

younger animals and annual recruitment of hatchlings.

Growth and Aging

Growth rate was a decreasing linear function of MSVL (Fig. 5). Analysis of covariance, using MSVL as a covariate, revealed a significant difference ($F_{1,506} = 62.0$, $P < 0.001$) between the regression lines of males and females, with females having a more slowly declining growth rate. The regression of GR on MSVL explained 61% of the variance in growth rate in males and 69% in females. Figure 6 shows the size-age curve generated from Equation 3 for each sex.

I attempted to validate the size-age curves in each of three ways. First, a few snakes provided relatively complete individual growth data because of recaptures extending over several years. For snakes that were marked in their first year (<300 mm SVL), nine males grew to over 400 mm SVL and seven females grew to over 450 mm SVL. The growth histories of these 16 snakes (Fig. 7) were similar to the predicted sex-specific growth trajectories

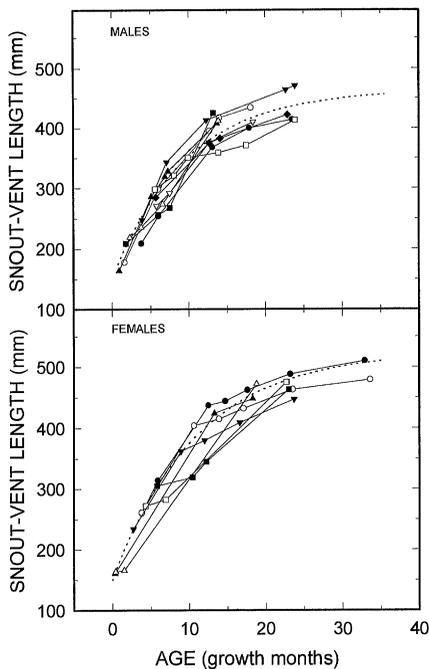


FIG. 7.—Growth histories of 16 individual green snakes compared to their predicted sex-specific growth trajectories. Criteria for inclusion were initial capture during the first year of life (<300 mm SVL), growth to at least 400 mm SVL for males ($n = 9$), and growth to at least 450 mm SVL for females ($n = 7$). For clarity, only the first and last captures and evenly spaced intermediate data points for each individual snake are plotted.

(Fig. 6). Second, I plotted SVLs of known-age snakes on each size-age curve (Fig. 8). There generally was close agreement between the predicted growth trajectories and sizes of known-age snakes. The greatest disparity occurred in snakes in their first year at ages <5 growth months and SVLs <300 mm in males, and at ages of 5–10 growth months and SVLs of 300–400 mm in females (Fig. 8). Size-age curves were used to estimate the age of snakes of unknown age at the time of their initial capture. Because aging of snakes by body size involved only those individuals >300 mm in SVL, the disparity between actual and predicted ages in first-year snakes did not have important demographic consequences. Third, the mean SVL of the 25 largest males in the population (466 ± 14.9 mm, range 450–494) was remarkably close to 464 mm, the asymptotic SVL for

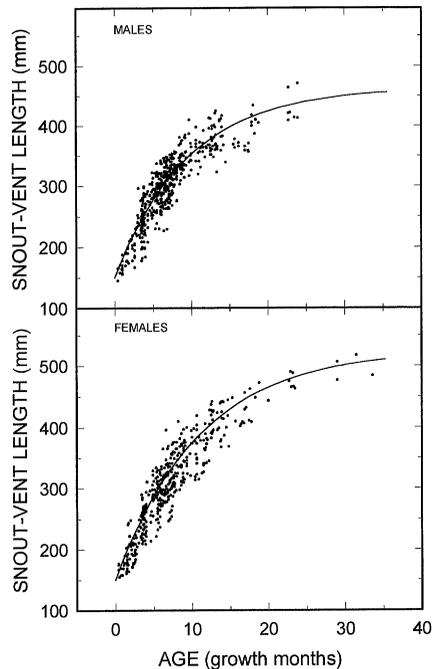


FIG. 8.—Size-age trajectories generated from Equation 3 (see text) for male and female green snakes compared to sizes of known-age snakes marked in their first year. Data represent 562 captures of 144 individual males and 455 captures of 101 individual females.

males predicted from Equation 3. The upper portion of the male growth curve was thus validated. Mean SVL of the 25 largest females in the population (536 ± 24.3 mm, range 514–618), although 11 mm larger than the 525 mm asymptotic SVL for females predicted from Equation 3, was still sufficiently concordant for validation.

The mean SVLs of 11 males (480 ± 10.5 mm, range 465–494) and 13 females (551 ± 25.5 mm, range 532–618) exceeded predicted asymptotic sizes (by 3% and 5%, respectively). Instead of predicted growth rates near zero, calculated growth rates for 20 of these snakes were similar to those exhibited by much smaller snakes, averaging 0.110 mm/day for males ($SD = 0.077$, $n = 11$) and 0.064 mm/d for females ($SD = 0.065$, $n = 9$). No males and only two females did not grow during the study period.

The mean ($\pm SE$) SVL of the 25 largest males was similar at the two sites (RL, 466

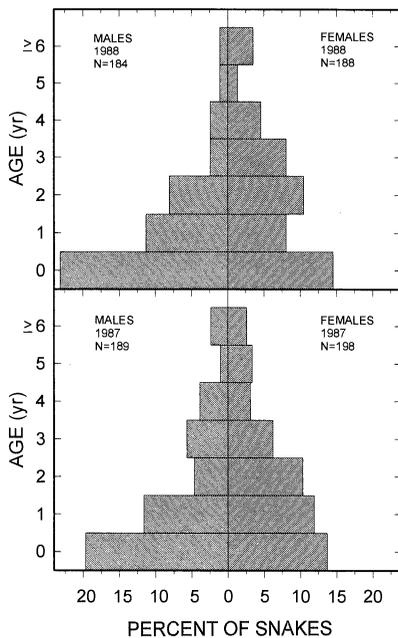


FIG. 9.—Age structure in the Ransom Lake green snake population in two successive years. Data include only those snakes actually captured, including hatchlings.

± 3.0 mm; BKL, 468 ± 3.4 mm). However, the 25 largest females were slightly larger at RL (RL, 536 ± 4.9 mm; BKL, 522 ± 4.3 mm; $t = 2.15$, $P < 0.05$). A sexual size dimorphism ratio (mean adult female SVL/mean adult male SVL) calculated for all adults averaged 1.17. For the 25 largest snakes of each sex, the dimorphism ratio was 1.15, and based on the predicted asymptotic SVLs, the dimorphism ratio was 1.13.

Population Structure

Population age structure was similar in both years (1987, 1988) in which intensive sampling was conducted throughout the entire activity season (Fig. 9). Males constituted 48.8% of the snakes captured in 1987 ($n = 387$) and 49.5% in 1988 ($n = 372$) (Fig. 9). Sex ratio did not differ from 1:1 in either year (1987, $\chi^2 = 0.21$, $P > 0.50$; 1988, $\chi^2 = 0.04$, $P > 0.50$). At BKL, all males and 50% of the females mature at age 1 yr and all snakes aged ≥ 2 yr are mature (Plummer, 1985a). Assuming that the ages at maturity for RL snakes were

TABLE 1.—Observed frequencies of monthly captures of green snakes (*Opheodrys aestivus*) compared with a zero-truncated Poisson distribution of expected frequencies assuming constant catchability.

No. monthly samples in which an individual was captured	1987		1988	
	Observed no. snakes	Expected no. snakes	Observed no. snakes	Expected no. snakes
1	149	149.5	228	219.3
2	107	112.1	85	104.2
3	63	56.1	41	33.0
4	24	21.0	12	7.8
5	4	8.3	0	1.7
		$\chi^2 = 3.74$ $P > 0.05$		$\chi^2 = 9.79$ $P < 0.05$

similar, adult males constituted 48.1% of the RL snakes captured in 1987 ($n = 235$) and 45.2% in 1988 ($n = 217$). In both years (1987, $\chi^2 = 0.34$, $P > 0.50$; 1988, $\chi^2 = 2.03$, $P > 0.05$), sex ratio of adults did not differ from 1:1. Mature snakes constituted 60.7% of the population sampled in 1987 and 58.3% of the population sampled in 1988.

Population Size

An important assumption of population estimation methods by mark-recapture is the equal probability of capture of all individuals (Caughley, 1977). To test this assumption, the observed number of snakes captured in monthly (May–September) samples was fitted to a zero-truncated Poisson distribution of frequencies to be expected if catchability were constant (Caughley, 1977). In 1988, the null hypothesis of equal catchability could be rejected whereas it could not be rejected in 1987 (Table 1). An additional check on equal catchability is provided by the Schumacher–Eschmeyer procedure. If an assumption of equal catchability is not violated, a ratio of the number of marked individuals (m_i) to the total number of individuals (n_i) in the i th recapture sample regressed on the number of individuals marked previous to the i th sample (M_i) should be linear through the origin with a slope equal to $1/N$ (Caughley, 1977). The close correspondence between regression ($r^2 > 99\%$) and population characteristics

TABLE 2.—Statistics for annual population estimates of green snakes (*Ophedrys aestivus*) by the Schumacher–Eschmeyer method (cf. Caughley, 1977); see text for explanation. Estimates do not include hatchlings.

Year	Estimated population size (N)	95% confidence limits	No. snakes captured	Regression of m/n , on M_t	1/N	r^2	P
1987	393	370–435	349	$y = 0.0214 + 0.0024x$	0.0025	>99%	<0.001
1988	504	494–515	365	$y = 0.0028 + 0.0020x$	0.0020	>99%	<0.001

in both years suggests that catchability was constant in both 1987 and 1988 (Table 2).

Population size of green snakes varied as much as fivefold over the 7 yr of this study. After gradual increases in population size from 1986 to 1988, an abrupt and lasting decrease in observed population size is indicated from 1989 to 1992 (Fig. 10C).

Annual variation in estimated population sizes yielded calculated densities of 0.05–0.24 snakes per linear meter of shoreline. Because non-nesting green snakes normally limit their daily activities to a narrow (3–5 m) strip of shoreline vegetation (Plummer, 1981a, 1990a), areal densities during the course of the study ranged from approximately 100–800 snakes per hectare (respective values correspond to calculations based on use of either a 5-m or 3-m strip).

Population Dynamics

Survivorship.—Of 163 hatchlings obtained from eggs incubated in the laboratory, marked, and released in the field in August, 31 were recaptured the following calendar year. Of 82 field-hatched hatchlings captured and marked in August and September, 12 were recaptured the following calendar year. Therefore, survivorship of hatchlings was 14.6% in field-hatched and 19.0% in laboratory-hatched snakes. Subsequently, no snake marked as a laboratory hatchling was recaptured after its first year; one snake marked as a field hatchling was recaptured three times at ages of 0, 1, and 2. Overall first-year survivorship, estimated by comparing the number of eggs likely produced by females in 1987 ($n = 335$) with the number of 1-yr-olds in the population in 1988 ($n = 72$; Fig. 9), was 21.5%.

For ages ≥ 0 yr, I calculated sex-specific

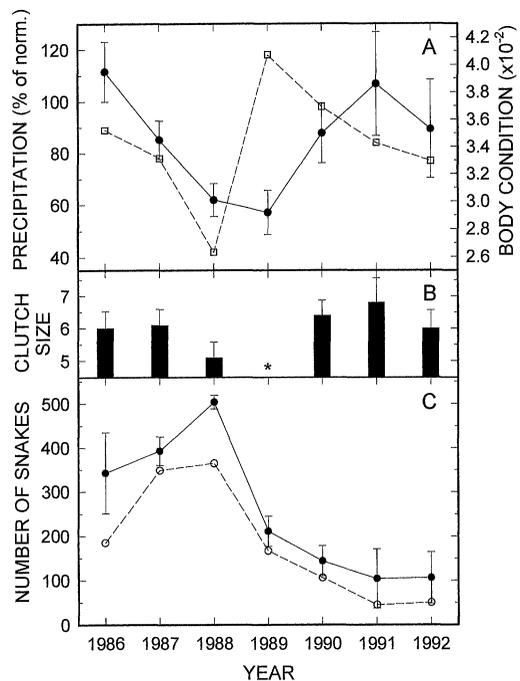


FIG. 10.—(A) Body condition of adult males (closed circles, solid line) and total precipitation from May through August (open squares, dashed line) over 7 yr. Body condition was calculated as a ratio of mass to length based on the SVL and body mass values measured on the first capture in each year for a given snake. Sample sizes for body condition were: 1986, $n = 55$; 1987, $n = 126$; 1988, $n = 103$; 1989, $n = 67$; 1990, $n = 44$; 1991, $n = 18$; 1992, $n = 18$. Vertical lines indicate ± 2 SE. (B) Mean annual clutch size adjusted for SVL. Vertical lines indicate ± 2 SE. *Clutch size data for 1989 were not available. (C) Number of green snakes estimated by mark–recapture methods (closed circles, solid line) and number of snakes actually captured (open circles, dashed line) over 7 yr. Vertical lines indicate ± 2 SE of the population estimate. Population estimates were made by the Petersen method in 1986 and 1989–1992, and by the Schumacher–Eschmeyer method in 1987 and 1988. Population estimates do not include hatchlings.

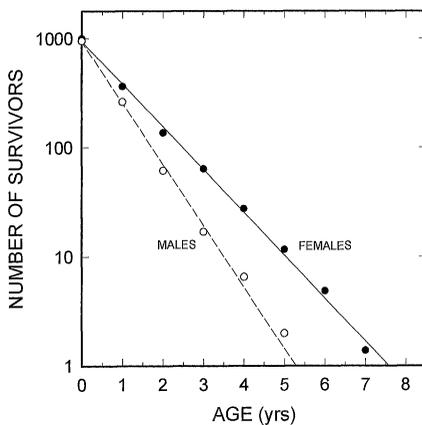


FIG. 11.—The relationship of the number of survivors, calculated over all years, to age for male and female green snakes. Age 0 begins following the first hibernation after birth. The regression equations are $\ln S = 6.84 - 1.30 \cdot \text{age}$ (males, $r^2 = 99.4\%$, $P < 0.001$, $n = 7$) and $\ln S = 6.84 - 0.900 \cdot \text{age}$ (females, $r^2 = 99.6\%$, $P < 0.001$, $n = 8$).

survivorship by first determining the proportion of individuals in each age x that were present in age $x + 1$ over all years. I then regressed the natural logarithm of the number of survivors ($\ln S$) in an initial hypothetical cohort of 1000 snakes on age x (in years) (Fig. 11). The slopes for male and female survivorship curves were significantly different (Fig. 11; ANCOVA, $F_{1,11} = 73.49$, $P < 0.001$). Average annual survivorship ($S = e^b$, where b is the slope from the above regressions) was 27.4% for males and 40.7% for females. To facilitate direct comparisons of adult survivorship with the BKL population, I also analyzed sex-specific survivorship for adults only (age ≥ 1 yr). The resulting regression equations were $\ln S = 8.19 - 1.28 \cdot \text{age}$ (males, $r^2 = 99.0\%$, $P < 0.001$, $n = 6$) and $\ln S = 7.85 - 0.890 \cdot \text{age}$ (females, $r^2 = 99.6\%$, $P < 0.001$, $n = 7$). The slopes for adult male and female survivorship curves were significantly different (ANCOVA, $F_{1,9} = 39.53$, $P < 0.001$). Average annual adult survivorship was 27.8% for males and 41.1% for females.

Variation in mortality.—Mortality varied among years in both sexes, and was highest in 1988–1989 (Table 3). Within-season variation in mortality was examined by dividing the activity season into five ap-

TABLE 3.—Annual variation in mortality in green snakes (*Opheodrys aestivus*) at Ransom Lake.

	Rate of mortality					
	1986	1987	1988	1989	1990	1991
Males	0.60	0.73	0.80	0.79	0.79	0.78
Females	0.35	0.60	0.74	0.67	0.62	0.47

proximate 1-mo periods relative to the period of oviposition (20 June–20 July; Plummer, 1990a). The time of the last capture (“death”) for each snake was determined for those years in which sampling was approximately equal throughout the activity season (1986–1988). A null hypothesis of equal mortality (chance of “death”) in each period was tested by chi-square analysis of the observed and expected number of deaths. There appeared to be considerable variation in mortality with more males than females dying in the spring and more females than males dying in the summer (Fig. 12). However, the null hypothesis of equal mortality within the activity season could not be rejected for either sex (periods 1–4; Table 4). As determined by last capture analysis, approximately 26% (females) and 31% (males) of the annual mortality occurred during the overwintering period (Fig. 12). Overwintering survi-

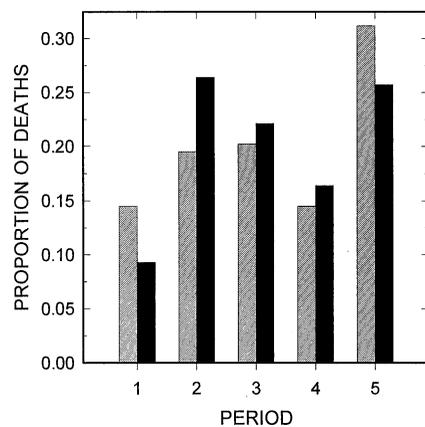


FIG. 12.—Time of the last capture (“death”) for 282 male and 280 female green snakes over 3 yr (1986–1988). Crosshatched bars represent males, solid bars represent females. Period 1, 1 April–19 May; period 2, 20 May–19 June; period 3, 20 June–19 July; period 4, 20 July–19 August; period 5, 20 August–30 September.

TABLE 4.—Observed number of last captures (“deaths”) of green snakes (*Opheodrys aestivus*) in the activity season compared with expected number of deaths, assuming an equal chance of dying (i.e., mortality). Data compiled for years in which sampling effort was approximately equal throughout the activity season (1986–1988). Period 5 is not included (cf. Fig. 12) because snakes could not be sampled immediately after period 5 during hibernation.

Period	Females			Males		
	Total no. captures	Obs. no. deaths	Exp. no. deaths	Total no. captures	Obs. no. deaths	Exp. no. deaths
1. 1 Apr–19 May	133	26	30.8	111	41	32.6
2. 20 May–19 Jun	306	74	70.9	180	55	52.8
3. 20 Jun–19 Jul	286	62	66.4	228	57	66.7
4. 20 Jul–19 Aug	172	46	39.9	143	41	41.9
Total	897	208	208.0	662	194	194.0
			$\chi^2 = 2.11$			$\chi^2 = 3.68$
			df = 2			df = 2
			$P > 0.10$			$P > 0.10$

vorship, a function of the proportion of the annual mortality of snakes dying over winter and annual survivorship (Table 5) was 19% for males ($[1 - 0.31] \times 0.28$) and 30% for females ($[1 - 0.26] \times 0.41$).

Body condition.—As an index of general body condition, annual variation in length-specific body mass of adult males was examined. Females were excluded because of their large within-year variation in mass due to variation in reproductive condition. An ANOVA on the residuals from the regression of body weight on SVL revealed significant differences among years ($F_{6,424} = 8.63, P < 0.001$) resulting primarily from low body condition values in 1988–1989 (Fig. 10A).

Fecundity.—Over all years, clutch size averaged 6.0 ± 1.69 eggs (range 2–11, $n = 113$) and was dependent on maternal SVL ($r = 0.70, P < 0.001, n = 113$). Clutch size, using SVL as a covariate, differed among years (ANCOVA, $F_{5,106} = 4.16, P < 0.01$) and was concordant with male body condition (Fig. 10A, B). Eight adult female snakes were captured in a gravid condition in two different years and three others were captured in three different years. The mean difference in clutch size among years in these individuals was 1.1 ± 1.56 eggs (range 0–3). In 9 of these 11 snakes, clutch size increased with time and growth as predicted by the clutch size–SVL relationship (Fig. 13); however, clutch size decreased by two eggs in each of two large females (511 and 533

mm SVL) in successive years (1990–1991 and 1991–1992, respectively).

Group variances of clutch size did not differ among years ($F_{max} = 2.11, P > 0.05$). Following the analytical methods of Shine and Seigel (1996), coefficients of variation in clutch size (CV = 16.7 to 31.0) also did not differ among years (ANOVA, $F_{5,107} = 0.98, P > 0.40$). The percentage of adult females gravid in June of each year was 1986, 95% ($n = 22$); 1987, 100% ($n = 50$); 1988, 90% ($n = 29$); 1989, 90% ($n = 10$); 1990, 94% ($n = 35$); 1991, 93% ($n = 15$); 1992, 95% ($n = 19$).

DISCUSSION

Spatial Distribution

For completely asocial snakes living in environments homogeneous with respect to critical resources, random spatial pattern would be expected (Gregory et al., 1987). However, because snakes are not completely asocial (Gillingham, 1987; Gregory et al., 1987), and because few environments are homogeneous over even small areas, one might predict that snakes should be nonrandomly dispersed except on a temporary seasonal basis or at very low population densities (Gregory et al., 1987). There apparently, however, has not been a quantitative study of the actual dispersion of individual snakes that could test this hypothesis (Gregory et al., 1987). In the present study, green snakes occurred at high densities, were almost completely

TABLE 5.—Population attributes of green snake (*Ophedryx aestivus*) populations at Ransom Lake (present study) and Bald Knob Lake (Plummer, 1985*b*). It is assumed that both populations were at maximum density.

Characteristic	Population	
	RL	BKL
Years of study	1986–1992	1978–1979
Maximum linear density (snakes/m)	0.24	0.21
Maximum areal density (snakes/ha)	800	714
Annual adult survivorship (age \geq 1; %, M/F)	28/41	39/49
Overall first-year survivorship (egg to age 1; %)	22	21
Fecundity (eggs/clutch)	6.0	6.0
Net reproductive rate	0.60	0.84

limited in distribution to a narrow strip of shoreline alder vegetation, and, within this strip, were nonrandomly distributed. I found no evidence of behaviors that would result in overdispersion (even spacing) of individual green snakes (e.g., territoriality) and the only known behavior that would result in underdispersion (clumping) of individuals was the communal nesting of gravid females, a short-term behavior reported both in the laboratory (Plummer, 1981*b*) and in the field (Palmer and Braswell, 1976). Thus, there were no obvious social interactions producing the demonstrated clumped dispersion outside of the nesting season. In addition, other than minor variations in population density and obvious sites of shoreline clearing by human activities, the shoreline alder vegetation at RL appeared to be relatively continuous and uniform in terms of physical structure (Fig. 1), availability of food (Plummer, 1991) and nesting habitat (Plummer, 1989, 1990*a*). In the higher and denser zone of alder vegetation (1200–1900 m) compared to that of lesser height and density (0–900 m), almost twice as many green snakes were caught suggesting that vegetation structure affected snake abundance and that the clumped distributions within both vegetation zones resulted from minor variations in plant density within each zone.

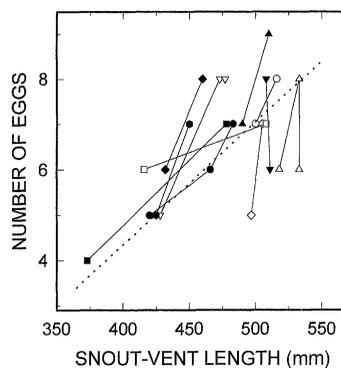


FIG. 13.—Relationship of the number of eggs in a clutch and the snout-vent length of the mother in eight individuals captured in each of two years and in three individuals captured in each of three years. Each female and her clutch size are indicated by a unique symbol. The dotted line indicates the predicted clutch size-SVL relationship (number of eggs = $-6.46 + 0.027 \cdot \text{SVL}$, $r = 0.70$, $P < 0.001$, $n = 113$).

As in many arboreal vertebrates (Pounds, 1991), arboreal snakes often possess a suite of morphological, physiological, and behavioral traits that are related to living in vegetation above ground. Such snakes in various lineages often are slender, cryptically colored (often green), and behaviorally adapted to enhance these traits, e.g., slow swaying locomotion, frequent feeding and defecation (Lillywhite and Henderson, 1993). Furthermore, these traits may be related to rather specific structural components of their microhabitats (Lillywhite and Henderson, 1993). Although not measured, the microhabitats used at RL by *Ophedryx* appeared to be strongly related to the structure of the vegetation, as they were at BKL, where snakes chose perch sites not according to taxonomic composition of the vegetation, but according to various structural variables such as vegetation density, and the height, diameter, and angle of perches (Plummer, 1981*a*). Size and spacing of perches often are key structural variables for various arboreal vertebrates (Henderson and Winstel, 1995; Moermond, 1979; Pounds, 1991; Tolson, 1988) as well as for semi-aquatic snakes basking in above-water vegetation (e.g., Mills et al., 1995). In contrast to some snakes (e.g., *Corallus*, Henderson and Winstel, 1995; *Crotalus*, Macartney,

TABLE 6.—Movement statistics for green snakes (*Opheodrys aestivus*) at Ransom Lake (present study) and Bald Knob Lake (Plummer, 1981a). All distances are in meters.

	Ransom Lake	Bald Knob Lake
Distance between captures	28 ± 42	26 ± 30
Days between captures	19 ± 20	27 ± 28
Percent overwater moves	2.6	3.5
Home range length	67 ± 67	62 ± 44
Shift in HR location between years	51 ± 111	45 ± 62

1985; *Acrochordus*, Shine, 1986; *Vipera*, Viitanen, 1967), green snakes did not segregate into habitats by sex or age.

Movements

Various statistics of movement were remarkably similar between the BKL and RL sites. The limited vagility of green snakes as determined both by mark-recapture at BKL and RL and by radiotelemetry of gravid females at RL (Plummer, 1981a, 1990a) is further supported by this study in terms of distance between successive captures, frequency of overwater movements, size of home range, and differences between home range locations in successive years (Table 6). In general, arboreal snakes have smaller home ranges than terrestrial species (Macartney et al., 1988) but such comparisons may be misleading because home ranges of arboreal snakes obviously have a strong third dimensional vertical component that to date has not been measured by any investigator (Lillywhite and Henderson, 1993). Contributing to the stability of home range location of *Opheodrys* from year to year, perhaps was a high availability of overwintering sites nearby. Most of the area immediately behind the flagged portion of the shoreline probably would have provided suitable overwintering sites because of its loose rocky substrate with numerous deep crevices. A notable proximity of locations of the last fall capture and the first spring capture for individual snakes suggests that green snakes probably overwintered individually at sites within their individual home ranges. This strategy is the normal pattern for other snakes at this latitude,

approximately 35°N (Sexton et al., 1992). It should be noted, however, that specific overwintering refuges of this widespread and common snake have not yet been reported. Neill (1948), who summarized local overwintering data for 101 species of amphibians and reptiles (including 34 species of snakes), stated that overwintering sites for rough green snakes were unknown and "... somewhat of a mystery."

The skewed right tail of both movement and home range (Fig. 3) represented snakes that made relatively long treks or had unusually large home ranges. Some of these outliers could have resulted from the nesting behavior of gravid females, as they are known to migrate out of their home ranges to nest, returning to the same or nearby home range (Plummer, 1990a). Based on the timing of consecutive captures of individual females during long movements, the large home range sizes of at least 12 of 16 females who had extreme outlying home range sizes (i.e., those >3 SE of the mean, or >110 m) could have resulted from postnesting females not returning to the exact home range that each occupied before nesting.

Rate of Recapture

Recapture percentages obtained at RL were unusually high relative to those reported in most mark-recapture studies of snakes (mean = approximately 20% for 44 studies of 35 species; Parker and Plummer, 1987). The lower percentage and greater variability in recapture rate for snakes of all sizes compared to recaptures among solely adult snakes (Fig. 4) likely resulted from the higher mortality of immature snakes and the annual recruitment pulse of hatchlings.

Growth and Aging

Examination of Figures 6–8 shows that the probability of error in aging increases with body size because of a decrease in growth rate with size of snake and a high observed variance in growth rates among individuals. For BKL snakes, Plummer (1985b) reasoned that errors in aging larger adults might be compensated by relatively large sample sizes. Assuming that in-

dividual and temporal variation in growth rates at RL were similar to those at BKL, the calculated variances at RL should have been reduced because of a much larger sample size (almost fourfold). However, the proportion of variance in growth rates explained by regression on body size at RL was notably less than at BKL (r^2 values for males 61–81%, for females 69–77%) despite a much larger sample size. These results suggest that growth rates at RL were more variable than those were at BKL. Among 52 species of reptiles, including 15 snake species, growth data suggest that body size and age typically are only weakly correlated and that there is usually a large variance in body size within a given age class, primarily because of large variances in the growth of juveniles (Halliday and Verrell, 1988). High variability in growth probably reflects the general energy-conservative nature of reptilian life (Pough, 1983). As in many reptile species (Halliday and Verrell, 1988), it is likely that unusually large green snakes (those exceeding asymptotic SVL) represent rapidly growing individuals rather than unusually old snakes.

The various calculations of sexual size dimorphism at RL were similar to those determined for most populations of *O. aestivus* throughout its geographic range (Plummer, 1987). As is the usual case for snakes (Shine, 1990), the sexual size dimorphism exhibited by adult *O. aestivus* reflects the direction and degree of dimorphism present when sexual maturity was attained (Plummer, 1985a).

Population Size

Estimates of population densities of green snakes at RL ranged from 100 to 800 snakes/ha and were similar to estimated densities at BKL (Table 5). Densities of green snakes are among the highest reported for snakes (Parker and Plummer, 1987), consistent with a hypothesis that arboreal snakes may be relatively more abundant than terrestrial species (Lillywhite and Henderson, 1993). Green snake densities apparently are subject to rapid declines, as observed in the present study. That the changes in density were real is

supported by the equal catchability of individual snakes (although equivocal in 1988). Mark-recapture models are not particularly robust to violations of their assumptions, and small deviations from the assumptions can produce large errors in the results (Caughley, 1977). However, the magnitude of the changes in annual population estimates relative to their standard errors leads to confidence in the results. Such changes in abundance are in agreement with subjective field observations on the relative number of green snakes sampled throughout the study and also with the actual number of snakes collected each year.

What caused the decreased abundance in 1989–1992 at RL? Short-term variation in absolute density of snakes is known to result from migratory movements between habitats (e.g., *Regina alleni*; Godley, 1980). Short-term changes in apparent density of snakes often result from varying activity levels in general (Gibbons and Semlitsch, 1987; Parker and Plummer, 1987), and *O. aestivus* in particular (Dalrymple et al., 1991). Neither of these phenomena probably had significant influence on densities of green snakes at RL. Changes in density as seen at RL most likely indicated changes in basic demographic characteristics such as fecundity, clutch frequency, and survivorship, traits known to exhibit considerable nongenetic phenotypic plasticity (Dunham et al., 1988a; Seigel and Ford, 1991). Over all years, fecundity of green snakes at RL did not differ from two separate estimates of fecundity in different years at BKL (Table 5; Plummer, 1983). However, fecundity at RL varied annually unlike estimates between two climatically different years at BKL (Plummer, 1983). At RL, the population decline after 1987 occurred too rapidly to be accounted for by reduced fecundity or clutch frequency alone, thus it is likely that increased mortality was responsible for the reduction in population size. Overall rates of annual adult mortality at RL, calculated over 7 yr, were higher than those at BKL (Table 5). Among years mortality was highest in 1988 and was reflected in a markedly decreased abundance of snakes the next year. A cor-

relate of the population's decline was a significant decrease in the body condition of adult male snakes in 1988–1989. Also in 1988, I observed unusually high predation on gravid females implanted with radio-transmitters (Plummer, 1990*b*). Crawling performance, known to be reduced in gravid *O. aestivus* (Plummer, 1997), would likely be exacerbated in a snake in poor body condition. Luisella et al. (1996) reported high mortality rates for smooth snakes (*Coronella austriaca*) that were emaciated after parturition.

Mortality

The environmental correlates of variation in mortality rates in snakes are often difficult to identify. In one of the better examples, Brown and Parker (1984) showed distinct variation in annual survivorship in *Coluber constrictor* associated with variation in annual precipitation. In the present study, accompanying the population decline in *Opheodryx* was unusually hot and dry weather in 1988. In the central USA, 1988 featured a drought severe enough to be considered one of the worst national weather-related disasters on record (Anon., 1996). Locally from May to August 1988, total precipitation averaged only 42% of normal (Fig. 10A) and maximum temperatures averaged 2.5 C higher than normal. Drought likely exerts its influence on green snake survivorship by limiting foraging success. Strong relationships between precipitation and insect biomass have been reported for both temperate (Ballinger, 1977) and tropical (Janzen and Schoener, 1968) regions. In insectivorous lizards, Dunham (1978) found that an individual's foraging success was linked to prey abundance, which itself was dependent on annual precipitation. In 1981 at BKL, a climatically similar year resulted in a 70% decrease in stored body fat in *O. aestivus* presumably reflecting decreased foraging success (Plummer, 1983). Possibly the same environmental conditions affecting population size also resulted in the high variability in growth rates noted earlier. Dalrymple et al. (1991) reported that the number of *O. aestivus* captured in Florida was significantly correlated with

rainfall. Prolonged drought has been implicated in the population declines of both aquatic (e.g., Dodd, 1993; Seigel et al., 1995) and terrestrial (e.g., Brown and Parker, 1982, 1984) snake species.

In snakes, both seasonal and annual variation in mortality rates have been reported (Brown and Parker, 1982, 1984; Feaver, 1977; Parker and Brown, 1974, 1980). Costs of reproduction associated with reproductive activities, such as increased movement of males when searching for mates (Aldridge and Brown, 1995) and, for females, bearing a clutch, birthing, or moving associated with oviposition or birthing would likely increase the risk of death (but see Baron et al., 1996). Consistent with this expectation, Feaver (1977) noted that among male *Nerodia sipedon* about half of the annual mortality occurred in the spring whereas in females about half occurred in the summer. As expected, a greater proportion of male than female *Opheodryx* died in the spring, whereas a greater proportion of females than males died in the summer. However, these apparent sexual differences in mortality could not be demonstrated statistically. The 26–31% of annual mortality that occurred during hibernation is similar to those estimated for two species hibernating at higher latitudes (*Coluber constrictor*, ~33%, Brown and Parker, 1984; *N. sipedon*, 32%, Feaver, 1977). Overwintering survivorship was within the range of values reported for hibernating snakes (Parker and Plummer, 1987).

Few quantitative data are available on sources of mortality for snakes. Known sources of mortality on gravid female green snakes at RL include predation by racers (*Coluber constrictor*), king snakes (*Lampropeltis getula*), and birds (probably bluejays, *Cyanocitta cristata*) (Plummer, 1990*b*). Predation on snakes by birds probably is widespread (Mushinsky and Miller, 1993); although quantitative data are lacking, some studies suggest that such predation on arboreal snakes is intense (e.g., Fitch, 1963; Parker, 1990). Lillywhite and Henderson (1993) suggested that, relative to terrestrial species, arboreal snakes may have more limited access to sites pro-

viding refuge and therefore may be more exposed to potential hazards (e.g., avian/arboreal predators, fire). After a fire at RL in April 1987, I searched the ground and remaining vegetation in the zone from 1000 to 1500 m but did not find any dead *Ophedryis*. Reported sources of mortality for eggs of green snakes at RL include racers, *C. constrictor*, and arboreal skinks, *Eumeces laticeps* (Plummer, 1990b).

Emigration is a possible factor that may have contributed to underestimating survivorship in this study, as well as in many studies of snake population ecology. However, because green snakes normally do not move great distances and limit most of their movements to the vegetation within 5 m of the shoreline around discrete bodies of water, both RL and BKL study populations should have been spatially discrete. Although edge habitats provided by creeks, fencerows, and forest edges could have served as dispersal routes from both areas, there were no known bodies of water within several kilometers of either lake to which green snakes could have emigrated. Thus, known data suggest that the likelihood of emigration having a high impact on estimation of annual survival rates in green snakes is doubtful. Consistent with this conclusion are a few quantitative estimates of the rate of exchange of individuals among noncommunally denning, discrete snake populations (*Thamnophis sirtalis*, *T. sauritus*, *T. butleri*, Carpenter, 1952; *Nerodia sipedon*, Feaver, 1977; *T. sirtalis*, *T. elegans*, Kephart, 1981). However, under conditions of severe environmental stress (e.g., drought), several aquatic snake species (*Farancia* spp., *Nerodia* spp., *Seminatrix pygaea*) are known to respond by emigrating (Dodds, 1993; Seigel et al., 1995). In contrast, *Acrochordus arafurae* normally occurs in discrete populations in individual billabongs. Only in the wet season when billabongs are interconnected does movement occur among populations (Houston and Shine, 1994; Shine and Lambeck, 1985).

Snake Demography

In a comparison of life-table attributes for 16 snake species, Parker and Plummer

(1987) categorized *O. aestivus* as an "early-maturing colubrid," a group characterized by low adult survivorship, low longevity, and high fecundity, but noted that *O. aestivus* had a lower-than-average fecundity for its group. In Plummer's (1985b) life table for the BKL *Ophedryis* population, demographic interaction of fecundity and survivorship yielded a net reproductive rate insufficient to sustain the population over the long term ($R_0 = 0.84$). Field observations made over several years suggested, however, that the BKL population was stable. Unexpected was a low R_0 suggesting that perhaps survivorship, especially for juveniles, was underestimated (Plummer, 1985b). The *Ophedryis* study populations at RL and BKL had similar population densities and age-specific fecundity schedules. As is characteristic for adult snakes in general (Parker and Plummer, 1987), survivorship was age-constant in both populations, but overall adult (age ≥ 1) annual survivorship at RL was 8–11% lower than at BKL. Thus, it would seem that if a life table was constructed for the RL population following the same assumptions and procedures as at BKL, despite the fact that many more captures, especially of juveniles, were made at RL than at BKL, the interaction of fecundity and survivorship would result in an even lower R_0 , and indeed such was the case ($R_0 = 0.60$). Assuming equal parametric variances, the larger sample size at RL should have provided more accurate estimates of survivorship, especially for first-year snakes, which, because of very low sample sizes, at BKL had to be estimated through a back-calculation procedure from the observed number of 2-yr-olds (Plummer, 1985b). Recaptures of marked hatchlings at RL indicated one of the lowest survivorships (15–19%) among 13 colubrid species (Parker and Plummer, 1987), a finding consistent with those obtained by more recent workers who marked and recaptured hatchlings (*Thamnophis sirtalis*, 29%, Jayne and Bennett, 1990; *Nerodia sipedon*, 18%, King, 1987). Despite an initial expectation of being able to directly measure first-year survivorship in the RL population, I was, like most previous investigators

(Parker and Plummer, 1987), relegated to calculating the value from a comparison of eggs likely produced in the population to the number of 1-yr-olds. Furthermore, adult survivorship at BKL was among the lowest reported for 13 colubrid species (Parker and Plummer, 1987), and adult survivorship at RL was even lower. It is likely that survivorship values at RL were low, in part, because they were estimated from a population that was generally declining over the measurement period.

Snakes are excellent models for some types of biological investigations (Seigel, 1993) and it would appear that several attributes would render them tractable for demographic investigations. Green snakes, being small, are less subject to sampling bias with regard to reliably portraying population structure (Shine, 1994). Their existence in high densities in specific, localized habitats, and strongly arboreal habits coupled with a preference for vegetational edges and limited vagility render them easily sampled. Recapture rates for all age classes are unusually high for mark-recapture studies of snakes. However, despite these favorable attributes, in two extensively studied populations of green snakes, it is apparent that survivorship in both populations must have been greater than calculated for long-term viability of the populations. Because several investigators studying snakes previously have found such low survivorship, some have suggested that snakes were poor candidates for studies of population dynamics (e.g., Lillywhite, 1982; Parker and Plummer, 1987; Plummer, 1985*b*; Turner, 1977). Several investigators of the population dynamics of snakes have reported decreases in density over the periods of study (summarized in Parker and Plummer, 1987; R. Henderson, pers. comm.; this study). Parker and Plummer (1987) suggested that, at least for small snakes, handling effects (i.e., measuring, marking) may have contributed to a number of studies in which populations have decreased. Related to this is a discomforting possibility that various aspects of "studying" may stress some snakes to the point of altering behavior and increasing mortality or emigration (e.g., Brown,

1992, 1993). Only long-term data on snake populations can clarify whether observable declines result from natural or anthropogenic factors (Seigel et al., 1995).

Another possible alternative, and one that may be applicable here, is that investigators initially tend to choose populations for study based on the apparent abundance and accessibility of snakes. If the chosen population is at or near peak density, then the probable direction for change in abundance over the course of the study is down. I chose RL as a study site because of the large number of snakes that I caught there on my first visit in June 1986. The same criterion of high abundance was used to select the BKL site in May 1977 after extensive searching elsewhere. A seemingly disproportionate number of snake populations decreasing in abundance over the course of various studies may in part reflect bias in selecting which populations to study demographically. Few investigators have examined populations of snakes during an increasing phase (Parker and Plummer, 1987); perhaps future studies of snakes should address the demographics of sparse populations.

On the University of Kansas's Fitch Natural History Reservation, 49 yr of intensive observations have revealed substantial changes in the relative abundance of snakes associated with rapid habitat succession immediately after establishment of the Reservation (Fitch, 1997). In later years of the Reservation, short-term demographic changes were less apparent indicating that snake populations may be relatively stable in late-successional habitats (Fitch, 1982, 1997, pers. comm.). However, there is no reason to believe that at least some snakes, especially small, insectivorous species such as *O. aestivus*, do not respond rapidly to shorter-term environmental vagaries as similar vertebrates often do generally (e.g., Grant, 1986; Pechmann and Wilbur, 1994). Because low population levels of *Ophedrys* extended at least 3 yr past return of higher precipitation and body condition levels (Fig. 10), it appears that green snake populations respond more slowly to favorable environmental

conditions than they do to unfavorable conditions. This research illustrates the necessity of long-term study to detect such fluctuations in numbers (Seigel et al., 1995). If I had not continued the RL study past 1988, I would have judged the population dense and stable just as I did the BKL population after only 2 yr of intensive demographic study in 1978–1979 (Plummer, 1985b).

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