
Patterns of Feces Production in Free-Living Green Snakes, Opheodrys aestivus
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of females ($\bar{x}$ = 64.1 mm, s^2 = 57.1, range = 48–75, N = 26) was significantly larger than that of males ($\bar{x}$ = 52.5 mm, s^2 = 20.9, range = 42–65, N = 51; t = −8.38; Fig. 2). Pope (1964, p. 128) reported males as larger (SVL) than females; however, on p. 130 he gave measurements for males as smaller than females. We determined that males are smaller than females, as reported by Dickerson (1906), Wright (1914), and Smith (1961). The minimum SVL and mass at reproduction for our population was approximately 42 mm and 6 g for males and 48 mm and 9 g for females.

Wright (1914) reported the first appearance of *Rana palustris* (= immigration) at water temperatures of 7–10 C and maximum air temperatures of 14–26 C. Moore (1939) reported *R. palustris* breeding in water temperatures of 14–16 C in New York. In Illinois, Pope (1964) recorded temperatures of air at 10–19 C and water at 10–18 C. Our results reveal that in northwestern Louisiana, *R. palustris* initiated immigration when the soil surface temperature was 7.4–11.4 C. Air temperatures at the surface of the leaf litter were as much as 4 C cooler than the soil surface, which was protected by the insulation of the leaf litter. However, the leaf litter was warmer (19.0–27.7) than the soil surface (17.9–18.0) later in the season. The air temperature 2.5 cm above the leaf litter, at the level where *R. palustris* would be found, is similar to the soil surface. The temperature of the pond water was always within 0–3.4 C of that of the soil surface. Thus, soil surface temperatures of 7–12 C or pond water temperatures of 7–10 C are probably the best indicators of the initiation of immigration. Study of the microclimatic variation at the air-substrate interface is needed to better understand the effects of environmental temperatures on immigration of terrestrial amphibians.

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Patterns of Feces Production in Free-living Green Snakes, *Opheodrys aestivus*

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Knowledge of the energy ingested by snakes can be useful information for studies of metabolism, growth, and time and ecological energy budgets. In a recent review, Mushinsky (1987) pointed out that despite numerous studies, our knowledge of the foraging ecology of snakes results almost entirely from studies of diet composition obtained from gut contents of dead or living snakes. Although several investigators have studied food consumption of snakes in the laboratory or in seminatural enclosures (e.g., Dmi'el, 1967; Saint Girons, 1979; Diller and Johnson, 1988), the frequency of feeding and amount of food ingested by snakes in nature remain poorly known.

The feeding apparatus of snakes is primarily an adaptation for the ingestion of relatively large prey at infrequent intervals (Gans, 1961). At an extreme, some species eat a substantial portion of their annual energy requirement in a single meal (Pough and Groves, 1983). Despite the typical infrequent ingestion of large prey, several snake species eat relatively small prey at frequent intervals (Greene, 1983). Green snakes, *Opheodrys aestivus*, feed frequently on small invertebrates (Plummer, 1981), and rank among those snake species having the highest frequency of identifiable food items in the digestive tract when collected (Shine, 1986). Frequent foraging behavior by green snakes results in a more or less daily production of feces (pers. obs.). In this paper, I describe mass of

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feces produced by green snakes according to sex, age, and time.

Green snakes were collected from a population at a small lake 2 km west of Denmark, White County, Arkansas. Snakes were collected soon after dark, individually bagged, and stripped of feces the next morning by a standard procedure which involved gently palpating the body at the level of the posterior large intestine and cloaca. Feces so obtained should not include absorbable food materials, since little digestion and absorption of food occur in the large intestine (Skoczylas, 1978). Furthermore, subsequent defecation was not retarded since individual snakes so stripped produced normal feces when stripped again 24 h later in the laboratory or when recaptured in the field. Feces, including those which occasionally were deposited in the bag, were placed in petri dishes and uric acid was removed. Snakes were sexed, measured (snout-vent length, SVL), weighed, and released. Feces were oven dried at 60 C for 24 h and weighed to the nearest 0.1 mg. Prey items in feces were identified from their chitinous remains and were placed into one of five categories: arachnids, lepidopterans, orthopterans, odonates, and miscellaneous. Minimum numbers of prey were tallied in each category. Fecal samples were collected throughout each month from mid-April through September, 1987. Although the data include feces sampled from recaptured individual snakes, I considered each sample to be independent. Snakes were placed into one of two age classes as determined by body size. Those with SVLs less than 280 mm (males) or 360 mm (females) were classified as juveniles; snakes at and above these minima were classified as adults (Plummer, 1984; Aldridge et al., 1990). Differences among mean feces production values (FP = dry feces mass (g)/wet body mass (g)) were analyzed by ANOVA using SPSS/PC+ (SPSS, 1988), and multiplied by 1000 for presentation. Proportional data were transformed to arcsin $\sqrt{x}$ to meet the assumptions of normality and homogeneity of variances. Unless indicated otherwise, data are presented as $\bar{x} \pm 2$ SE.

In late April, only 2 of 29 (7%) adult snakes and none of 3 juveniles contained feces, whereas the mean percent of adults containing feces in monthly samples from May–September was 89.2 ± 2.96% (range 82–97), and for juveniles it was 94.9 ± 1.28% (range 91–98). Since snakes collected in April were not yet feeding, they were excluded from further analyses.

Except for females being heavier in May and June, mean SVLs and masses of adult snakes did not differ among months within sexes (Table 1). Overall FP in juveniles was $\bar{x} = 3.41 \pm 0.181$, whereas that of adults was $\bar{x} = 2.21 \pm 0.078$. Overall FP of adult males was $\bar{x} = 2.38 \pm 0.114$, whereas that of adult females was $\bar{x} = 2.11 \pm 0.107$. Feces production in adults increased from May–June, peaked in July, and decreased through August–September (Fig. 1A). Monthly FP in juveniles paralleled that of adults but was greater in all months (Fig. 1A). Monthly FP of adult males peaked earlier than that of adult females (Fig. 1B). Feces production of gravid females ($\bar{x} = 0.99 \pm 0.214$) was less than that of post-ovipository females ($\bar{x} = 3.08 \pm 0.400$; $F_{1,38} = 18.043$, $P < 0.001$). Age, sex, and month had significant effects on FP, with significant interaction between sex and month (Table 2).

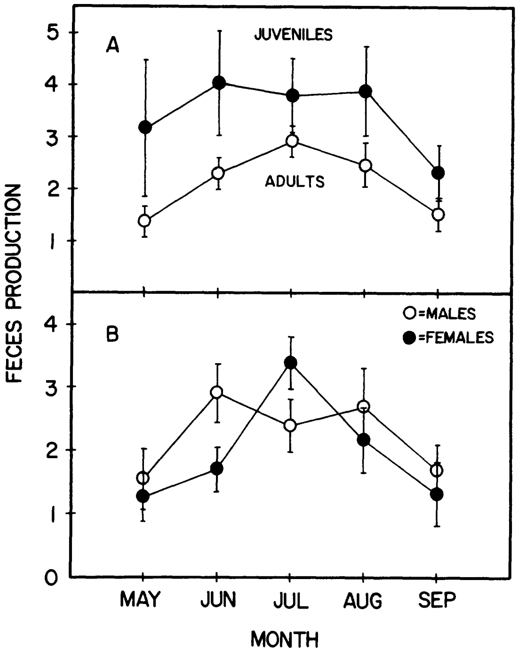

FIG. 1. (A) Feces production (×1000) in juvenile and adult green snakes by month. (B) Feces production (×1000) in adult male and adult female green snakes by month. Plotted are means ± 2 SE.

Spiders, numerically comprising 69% of all identifiable prey and found in over 70% of fecal samples, were clearly the most important prey item (Table 3). Spiders of the genus *Tetragnatha* constituted 66% of all spider prey. "Miscellaneous" prey appeared as minute quantities of unidentifiable amorphous material, occasionally embedded with the remains of various small insects, or in one case, a small fish vertebra. Neither age nor sex affected the frequency of spiders in samples, but month had significant effects (Table 2). The frequency of spiders in feces peaked in July, with a pattern similar to that of FP in adults and juveniles (Fig. 2). The correlation coefficient between bi-monthly FP and the frequency of spiders in bi-monthly samples was 0.69 (N = 10; $P < 0.05$).

In September, 65.7% of hatchling fecal samples (N = 35) and 65.4% of adult samples (N = 55) contained spiders and caterpillars; 97.1% of hatchlings (N = 35) and 74.5% of adults (N = 55) contained feces; FP of hatchlings averaged 2.97 ± 0.381 whereas adults averaged 1.25 ± 0.169.

In September, 18 of 77 adult snakes (23.4%) were either in a pre-shedding or shedding condition. These snakes produced fewer feces (FP = 0.8 ± 0.6) than did non-shedding snakes (FP = 1.8 ± 0.4; $F_{1,76} = 9.59$; $P < 0.01$).

Except for a few items occurring rarely in the stomachs of green snakes, the composition of the diet as determined by nondestructive fecal analysis at the Denmark locality was similar to that determined by destructive stomach analysis in a different population 15 km S at Bald Knob Lake (Plummer, 1981). This similarity supports the use of chitinous remains for

TABLE 1. Mean SVLs and body masses (x̄ ± SE) of snakes by sex and month. Differences among months are indicated (ANOVA; ns > 0.05, *** < 0.001). Vertical lines indicate maximum insignificant subsets of female mass (Student-Newman-Keuls Test).

	Mean SVL (mm)		Mean snake mass (g)	
Month	M	F	M	F
May	372 ± 9	458 ± 7	12.3 ± 0.7	25.4 ± 1.0
June	382 ± 6	448 ± 5	13.5 ± 0.5	23.5 ± 0.8
July	387 ± 7	449 ± 5	14.5 ± 0.6	19.2 ± 0.6
Aug.	379 ± 8	441 ± 8	13.3 ± 0.7	18.6 ± 1.0
Sept.	367 ± 8	442 ± 11	12.3 ± 0.7	20.2 ± 1.6
Sign.	ns	ns	ns	***

assessing diet taxonomically and numerically in green snakes. It appears that, in contrast to some snakes (e.g., *Acrochordus*; Shine, 1986), green snakes eat few prey which cannot be detected in feces.

Inferences regarding food consumption in green snakes assume that mass of feces produced is a function of mass of food eaten, an assumption which has been verified with lizards on constant diets in the laboratory (Avery, 1971; Kitchell and Windell, 1972). In free-living snakes on variable diets, the amounts of feces produced could be affected by the amount of food eaten, as well as by possible differences in efficiency of digesting the different types of food. If differences in diet composition occurred among sex or age classes as occur in many snakes (Mushinsky, 1987), and if differences in digestive efficiency exist among prey types, feces masses would have to be adjusted to make direct comparisons of FP among groups. However, the data show little ontogenetic or sexual differences in diet. Thus, the differences in amount of feces produced between adults and juveniles and between males and females in any given month are primarily functions of the amount rather than kind of food eaten. Because the proportion of spiders in the diet shows a monthly pattern similar to those of FP in both age and sex classes, monthly differences in FP within these groups may be affected both by the amount as well as by the kind of food eaten. This effect also is suggested by the significant correlation between FP and frequency of spiders.

The greater FP of juveniles compared to adults is the expected result based on the greater mass-specific metabolic rate (Bennett and Dawson, 1976), higher rate of growth (Andrews, 1982; Plummer, 1985*a*), and greater food and caloric intake of smaller snakes relative to larger snakes (Dmi'el, 1967; Saint-Girons, 1979; Godley, 1980; Diller and Johnson, 1988).

In many snake species, juveniles ingest an array of prey types and sizes different from that of adults (Mushinsky, 1987). Higher energy demands coupled with a smaller range of suitable prey sizes may result in hatchling snakes being more food-limited than adults (Mushinsky, 1987). Such problems associated with ontogenetic dietary differences and possible constraints on small snakes do not appear to affect green snakes. As judged by FP analysis, juveniles (including hatchlings) apparently forage qualitatively and quantitatively as miniature adults. Most juvenile snakes, including green snakes, suffer high mortality (Parker and Plummer, 1987; Plummer, 1985*b*). The above data suggest that factors other than food limitation, such as more foraging time resulting in higher vulnerability to predation, may be significant contributors to juvenile mortality in green snakes.

TABLE 2. Analysis of variance of feces production and proportion of spiders in the diet by age, sex, and month.

	Feces production			Prop. spiders		
Source of Variation	df	F-ratio	Probability	df	F-ratio	Probability
Main effects						
Age	1	50.936	<0.001***	1	3.543	>0.05 ns
Sex	1	9.015	<0.01**	1	0.393	>0.20 ns
Month	4	19.621	<0.001***	4	15.337	<0.001***
2-way interactions						
Age × Sex	1	1.729	>0.10 ns	1	1.034	>0.30 ns
Age × Month	4	1.849	>0.10 ns	4	0.361	>0.80 ns
Sex × Month	4	7.431	<0.001***	4	0.541	>0.70 ns
3-way interactions						
Age × Sex × Month	4	1.733	>0.10 ns	4	1.936	>0.10 ns
Explained	19	9.060	<0.001***	19	3.973	<0.001***
Residual	785			713		
Total	804			732		

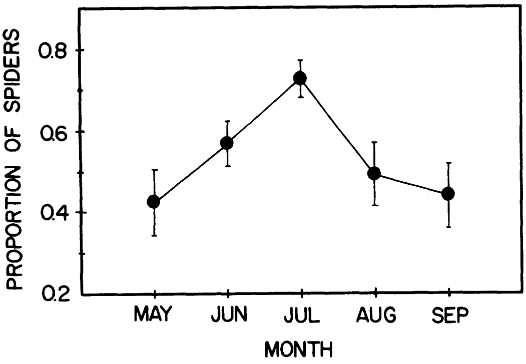

FIG. 2. Proportion of spiders in the diet of green snakes by month. Plotted are means ± 2 SE.

In Arkansas, eggs of green snakes hatch from mid to late August (Plummer, 1984, 1990). Congdon et al. (unpubl. obs.) calculated that hatchling green snakes had sufficient lipid reserves to subsist without feeding for approximately 15 days, the period during which hatchlings must learn to obtain food. The data presented in this paper suggest that hatchlings forage successfully (at least equivalent to that of adults) late in the activity season. With such foraging success, a hatchling green snake may be capable of obtaining a positive energy balance during the approximately 1.5 months between hatching and its first winter period of dormancy.

It is unlikely that allometry could account for the observed monthly and sexual variation in FP of adults. Within sexes, SVLs did not differ among months, and masses differed only for late vitellogenic and preovipository females (Plummer, 1984). Further, the directions of sexual differences in FP were opposite in the two months in which significant differences occurred. If mean monthly FPs are calculated for females in June using mean body mass adjusted for mean clutch burden (mean feces mass/(mean gravid body mass − mean clutch mass)), values remain similar ($FP_{\text{males}} = 2.81$ vs. $FP_{\text{females}} = 1.66_{\text{unadjusted}}$ or 1.95_{adjusted}).

Several non-exclusive explanations may account for the differences in FP between adult males and females in June and July. The smaller FP of females in June is strongly affected by the decreased FP of gravid females. A similar reproductive "cost" (Shine, 1980) occurs in many gravid snakes (Saint Girons, 1979; Gibbons and Semlitsch, 1987; Macartney, 1989). The greater FP for females in July probably reflects increased food intake following the depletion of energy stores during vitellogenesis, search for nesting sites, and oviposition (Plummer, 1984, 1990). Increased feeding after activities requiring high energy expenditures has been reported for female *Vipera* that have just given birth (Saint Girons, 1979), and for lizards in which fat bodies have been experimentally removed (Smith, 1968).

The peak FP of males in June may reflect increased food intake following mating when fat bodies are depleted (Plummer, 1984; Aldridge et al., 1990). Male snakes of many species, including green snakes, are active earlier and more often during the spring than are females (Plummer, 1985*a*; Gibbons and Semlitsch, 1987), and may delay feeding until after mating (Saint-Girons, 1979). Several snake species exhibit a bimodal annual activity pattern with a decrease in activity in summer (Gibbons and Semlitsch, 1987). In green snakes, males decrease feeding in summer as reported for *Nerodia sipedon* (Feaver, 1977). The decrease in feeding of green snakes is coincident with the beginning of spermatogenesis (Aldridge et al., 1990), an interesting observation previously reported by Saint Girons (1982), but one of unknown significance.

After comparing four methods of estimating food consumption in the lizard *Lacerta vivipara*, Avery (1971) found that analysis of feces was the simplest method and that it provided good results. Although the data reported herein for green snakes seem biologically reasonable, I do not generally advocate the method for free-living snakes. Because of the high variance in feces production, large sample sizes were necessary to detect patterns of FP in green snakes. For most snakes, the low frequency of feeding combined with the difficulty of obtaining large sample sizes render the method unsuitable for estimating food consumption. The primary usefulness of these data is the support they provide for questions relative to snake energetics that have been identified in previous studies of snakes. Namely, FP data suggest: (1) a decrease in food consumption by gravid females followed by a substantial increase after oviposition; (2) adjustments in food consumption during both mating activities and spermatogenesis in males; (3) a decrease in food consumption in shedding snakes; and (4) hatchlings and older juveniles forage at least as successfully as do adults. These hypotheses could be tested further by studies incorporating nondestructive field tech-

TABLE 3. Monthly composition of the diet as determined by analysis of feces. Data are number of fecal samples (n_f), nuber of prey items (n_p), percent of fecal samples containing prey taxon, and percent of prey specimens comprising prey taxon (in parentheses).

			Percent of occurrence (percent of specimens)				
Month	n_f	n_p	Arachnids	Lepidopterans	Orthopterans	Odonates	Miscellaneous
May	89	185	60.7 (48.1)	64.0 (43.8)	1.1 (0.5)	6.7 (3.2)	9.0 (4.3)
June	194	423	72.7 (65.2)	33.0 (17.7)	16.0 (7.3)	12.9 (5.9)	8.2 (3.8)
July	204	609	87.3 (79.0)	29.9 (11.2)	12.3 (4.3)	10.8 (3.6)	5.9 (2.0)
Aug.	118	238	61.9 (59.2)	39.8 (23.5)	20.3 (10.1)	5.1 (2.5)	9.3 (4.6)
Sept.	128	184	53.1 (50.0)	35.9 (28.8)	7.0 (4.9)	0.8 (0.5)	22.7 (15.8)
Year	733	1639	70.1 (65.8)	37.5 (20.3)	12.3 (5.6)	8.2 (3.7)	10.4 (4.6)

niques for location of individual snakes and for measurement of metabolic rates and storage of body lipids.

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Satellite Behavior in the Neotropical Treefrog *Hyla minuta*

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Individuals of the same sex may employ alternative mating tactics to increase their reproductive success