

Ecology of a Specialized Predator: *Regina grahami* in Missouri

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ABSTRACT.—I studied the ecology of a discrete population of Graham's crayfish snake (*Regina grahami*) in northwestern Missouri continuously from 1979-1983. As is true of other natricines, females were significantly longer and heavier than males. Snakes were active from April through early November, with peaks of activity in early spring and late autumn. *Regina* in this population were mainly diurnal; nocturnal activity was confined primarily to summer months. In comparison with *R. grahami* from Missouri, snakes in Louisiana began and ended their activity season much earlier and had a unimodal activity pattern. Females in Missouri produced a single brood each year, with a mean brood size of 11.6 (range = 5-16). Larger females produced larger broods. The sex ratio of offspring was skewed in favor of females, and there was evidence of sexual size dimorphism among neonates, with males larger than females in body length but not body mass. All prey items were molting crawfish; feeding frequency was highest among juveniles. Except for sexual dimorphism in offspring size and a biased sex ratio at birth, few major ecological differences were found between *R. grahami* and other natricine snakes.

The crayfish snakes (genus *Regina*) are an ecologically specialized group of four species found in the eastern and central United States. Although their systematic relationships with other natricine snakes have produced a considerable debate (cf. Rossman, 1963, 1985; Price, 1983; Lawson, 1987), all adult *Regina* are highly specialized predators on crawfish (Ernst and Barbour, 1989). Although several detailed field studies have been conducted on various members of the genus (e.g., Hall, 1969; Branson and Baker, 1974; Mushinsky and Hebrard, 1977a, b; Hebrard and Mushinsky, 1978; Godley, 1980, 1982; Mushinsky et al., 1980; Godley et al., 1984), many aspects of the ecology of these unique snakes remain poorly known. Parker and Plummer (1987) and Ernst and Barbour (1989) stressed the need for long-term field studies of single populations of snakes.

The largest member of the genus *Regina* is Graham's crayfish snake, *R. grahami*. Widely distributed in the central and southern U. S., the ecology of this species has been studied in detail only in a swamp system in southern Louisiana (Mushinsky and Hebrard, 1977a, b; Hebrard and Mushinsky, 1978; Mushinsky et al., 1980) with emphasis on feeding ecology, thermal biology, habitat utilization, and activity patterns. Most other data on *R. grahami* are derived from limited field sampling (Kofron, 1979), sometimes combined with data from museum collections (Hall, 1969; Godley et al., 1984). Although museum records are critical in obtaining a broad

overview of the ecology of a particular taxon, they provide limited information on the ecology of single populations. In this paper, I collected data on a single population of *R. grahami* from northwestern Missouri from 1979-1990 to answer the following specific questions: (1) are the distinctive foraging habits of this species associated with any corresponding differences in life-history traits when compared to other natricines?, and (2) are there any apparent geographical differences in life-history traits between *R. grahami* in northwestern Missouri and populations of this species in southern Louisiana?

MATERIALS AND METHODS

All data were collected at the Squaw Creek National Wildlife Refuge in Holt County, northwestern Missouri. The refuge is a 2770 ha area consisting of a central moist cordgrass (*Spartina*) prairie surrounded by a mosaic of freshwater marshes, deciduous woodlands, and agricultural fields. A detailed map and habitat description was given by Seigel (1984, 1986).

Data were collected primarily from August 1979 to April 1983, with sporadic collecting in 1985, 1986, and 1990. Most collecting was concentrated from 0800-2200 h from late March until mid-November. Snakes were collected in three ways: (1) hand-collecting along dike roads which separated the prairie from the marshes; (2) road-hunting along "Loop Road" which surrounded most of the refuge; and (3) drift fences equipped with wire-mesh funnel traps. Drift fences were 5-10 m in length, 0.5 m in height, and were constructed of wood. All snakes found alive were measured (snout-vent length, SVL, and tail length, both to the nearest 1 mm),

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weighed to the nearest 1 g with Pesola or Ohaus scales, and manually forced to disgorge any stomach or fecal contents (Fitch, 1987). Each individual was given a unique ventral scale mark (Brown and Parker, 1976) prior to release at the point of capture. Sex was determined by probing the cloaca or manually everting the hemipenis in males (Fitch, 1987). I gently palpated the abdomen of all females to detect enlarged follicles, and counted the total number of any follicles present three times; when counts differed (rarely), the mean of the counts was used. Farr and Gregory (1991) showed palpation of enlarged follicles was an accurate representation of clutch size in garter snakes (*Thamnophis*).

In late summer, gravid females were brought to the Animal Care Unit at the University of Kansas to give birth. These females were maintained under conditions of constant temperature (ca. 28 C) and photoperiod (12L:12D). Neonates were measured for SVL and body mass within 24 h of birth.

Because sampling intensity varied among months, I made comparisons of monthly activity in this study as follows: I first determined the relative sampling effort per month by dividing the number of days spent in the field each month by the total number of days in the field during 1980-1982, the three years for which I had complete data. Using a null hypothesis of equal activity among months, I then generated the expected number of snakes active each month by multiplying the total number of snakes found active during the study by the relative sampling effort for each month. For example, between 1980 and 1982, I spent 15 d in the field during April, for a relative sampling effort of 0.128 (15/117 field days). If snake activity was equal among months, then the expected number of snakes active (accounting for unequal effort) would be 0.128 times the total number of snakes found active in 1980-1982 (151 snakes). This yields an expected number of 19.3 snakes active in April.

Data were analyzed with SYSTAT (Wilkinson, 1988). All means reported in this paper are followed by \pm one standard deviation. All data were tested for normality and homogeneity of variances prior to using parametric procedures. Because body mass was not normally distributed in adults, I used an equivalent non-parametric procedure to test for sexual differences in this variable. The alpha level for all statistical tests was 0.05.

RESULTS

Population Composition, Body Size and Sexual Dimorphism.—Of 134 individuals that could be assigned to sex or adult/juvenile status, 63 were

TABLE 1. Body sizes of adult male and female *R. grahamii* from Squaw Creek. Males were considered adult at SVL > 38 cm (Hall, 1969); females were considered adult at SVL > 47 cm (see text). The body sizes differed significantly between the sexes (SVL: $F_{1,107} = 17.2$, $P < 0.001$. Body mass: Mann-Whitney $U = 483.0$, $P < 0.001$).

Sex	SVL (cm)	Body mass (g)
Males	54.3 \pm 6.16 N = 63	64.9 \pm 21.80 N = 57
Females	59.2 \pm 6.15 N = 46	116.4 \pm 54.37 N = 43

adult males, 46 were adult females, and 25 were juveniles. The sex ratio of adults did not differ from 1:1 ($\chi^2 = 2.66$, $df = 1$, $P > 0.05$). The mean body size (SVL and body mass) of adult female *R. grahamii* was significantly larger than that of adult males (Table 1). The female-to-male size ratio (FMR; Fitch, 1981) was 1.09 for SVL and 1.79 for body mass. Because size at sexual maturity for males is known from only a single study (Hall, 1969), I also tested for sexual dimorphism by comparing the SVL class containing the upper 10% of individuals of each sex, the upper decile (UDL) of Case (1976). The range of UDL values for males (62.6-65.0 cm) and females (67.0-75.5 cm) do not overlap, supporting the conclusion that females are larger than males in this population.

Seasonal and Daily Activity Patterns.—Over the three years (1980-1982) when *Regina grahamii* were sampled throughout the entire activity season, the earliest and latest dates that snakes were seen were 9 April and 7 November, respectively. The mean overall activity period (defined as the range of capture dates) was 202.0 \pm 8.00 d (N = 3 yr, range 194-210 d). At Squaw Creek, *Regina* showed considerable variation in seasonal activity; 70.1% of all individuals were collected in April, May, and October, while 14.6% of individuals were collected in July through September (Fig. 1). After correction for uneven sampling effort across months (see above), Fig. 1 shows that *Regina* were collected in significantly lower-than-expected numbers in the summer, and in higher-than-expected numbers during May and October (Fig. 1; $\chi^2 = 66.5$, $df = 7$ mo, $P < 0.001$).

Regina at Squaw Creek were primarily diurnal (Table 2); only 8 of 125 snakes (6.4%) whose time of capture was known were found after sunset. *Regina* were exclusively diurnal during April and between August and November. Most activity in all seasons was concentrated between 1200-2000 h (Table 2). However, because the intensity of sampling after dark varied among

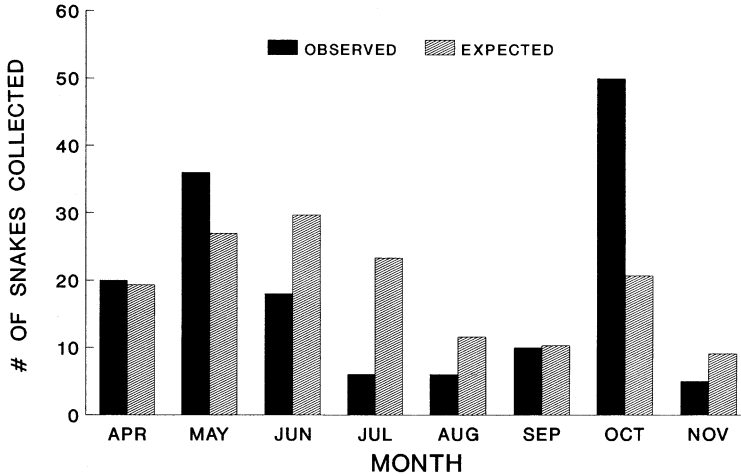


FIG. 1. Seasonal variation in numbers of *Regina* collected at Squaw Creek, 1980-1982. The differences between the observed and expected values were significant (see text for how expected numbers were generated).

seasons ($\chi^2 = 24.6$, $df = 2$, $P < 0.001$), the apparent changes in frequency of nocturnal activity could be the result of sampling bias.

Reproduction.—Summary statistics for reproduction of *R. grahami* at Squaw Creek are shown in Table 3. The smallest gravid female had a SVL of 48.0 cm. Of 16 females found during the reproductive season (late May-mid August) whose SVL was ≥ 48 cm, 13 (81%) were gravid, suggesting annual reproduction. There was a significant relationship between brood size and maternal SVL (brood size = $-9.53 + 0.354$ SVL; $r^2 = 0.59$, $F = 12.7$, $df = 1, 9$, $P < 0.01$). The sex ratio of offspring from five broods that were born in captivity was 44 females:23 males, a ratio significantly different from 1:1 ($\chi^2 = 6.6$, $df = 1$, $P < 0.025$). However, much of this skewed sex ratio can be attributed to a single female

which produced a brood of 13 females and no males; no other female produced a brood that showed a significantly skewed sex ratio. Excluding this all-female brood, the sex ratio of the remaining neonates was 31 females:23 males, a ratio not significantly different from 1:1 ($\chi^2 = 1.19$, $df = 1$, $P > 0.05$).

A two-way ANOVA showed that both maternal identity ($F_{3,46} = 14.6$, $P < 0.001$) and sex ($F_{1,46} = 9.0$, $P < 0.001$) had significant effects on offspring SVL, but there was no interaction between maternal identity and sex ($F_{3,46} = 0.59$, $P > 0.05$). Conversely, only maternal identity had a significant effect on neonate body mass ($F_{3,44} = 47.9$, $P < 0.001$). An analysis of covariance (ANCOVA) using SVL as the covariate showed that the slope of the mass-length relationship differed significantly between male and female neonates (male slope = 0.324, female slope = 0.676, $F_{1,60} = 11.2$, $P < 0.001$).

Because of the apparent effects of both maternal identity and sex on offspring size, these factors are partitioned in Table 4. Within each brood, mean male SVL was always larger than mean female SVL, but differences in body mass showed no clear pattern. Statistical comparisons between sexes within broods are also presented in Table 4, but these are hampered by small sample sizes.

Feeding.—Of 118 snakes that were examined for stomach and/or fecal contents, 31 (26.3%) had fed recently. All identifiable prey items were crawfish (*Procambarus* sp.), and all crawfish found in stomachs ($N = 12$) were recently molted. These 12 crawfish were found in 11 snakes (1.09 crawfish/snake), suggesting that multiple prey items are taken rarely. Because of the small sam-

TABLE 2. Percent of *R. grahami* found active in different time intervals during three seasons of the year. Individuals captured in traps or found dead on the road were excluded if time of activity could not be determined, but these were a small proportion of all records. Seasons correspond to standard calendars; all times Central Standard. N = number of individuals active.

Season	Time interval			
	0800-1200	1201-1600	1601-2000	2001-2400
Spring N = 53	13.2%	37.7%	43.4%	5.7%
Summer N = 11	0.0%	18.2%	63.6%	18.2%
Fall N = 61	8.2%	88.5%	3.3%	0.0%

TABLE 3. Summary statistics on the reproductive biology of *Regina grahami* from Squaw Creek. Data on clutch mass and RCM are from females that give birth in captivity. Mass in g, SVL in cm. Relative clutch mass (RCM) is clutch mass divided by female post-parturient mass.

	Clutch size	Clutch mass	Maternal SVL	RCM
Mean ± SD	11.6 ± 3.07	58.9 ± 12.69	58.8 ± 7.19	0.33 ± 0.033
Range:	5-16	46.4-77.5	48.0-73.0	0.284-0.364
N	11	5	12	5

ple size, I was unable to test for correlations between predator size and prey size. However, there was a significant difference in frequency of feeding among size classes (Table 5; $G = 7.51$, $df = 2$, $P < 0.025$); feeding frequency was highest among individuals < 40 cm SVL. No differences were found in feeding frequencies between the sexes ($\chi^2 = 0.11$, $df = 1$, $P > 0.05$).

DISCUSSION

Comparisons with other Natricines.—As is true for adults of other members of the genus, *R. grahami* at Squaw Creek fed entirely on recently-molted crawfish, a prey item not commonly utilized by any other natricine, or, apparently, by any other snake outside of this genus whose diet is known (Mushinsky, 1987). However, aside from this highly specialized feeding habit, I found relatively little evidence to suggest that any life-history traits of *R. grahami* at Squaw Creek differed greatly from those of other natricines in any of the following characteristics:

- (1) Adult sexual dimorphism—Adult females are larger than males in all natricines examined (Fitch, 1981). Of the 66 taxa examined by Fitch, 18% showed a FMR very similar to that found for *R. grahami*.
- (2) Activity patterns—*Regina* at Squaw Creek were active from April–November, and were

primarily diurnal. Concurrent with this study, I collected data on the activity patterns of six other species of snakes at Squaw Creek, including five natricines (*Nerodia rhombifera*, *Thamnophis proximus*, *T. sirtalis*, *T. radix*, and *Storeria dekayi*) and one viperid (*Sistrurus catenatus*). With minor variations, all showed a bimodal seasonal activity pattern, similar to that of *R. grahami* (Seigel, 1986, and pers. obs.). Such bimodal activity patterns are common in temperate zone snakes (Gibbons and Semlitsch, 1987). However, although all snakes at this locality showed an apparent decrease in activity in summer, that of *Regina* was the most striking. For example, *R. grahami* were never found active during the entire summer and early autumn of 1980 (14 June–1 October), a period of high temperatures and low rainfall, whereas other snakes were active commonly during this period. In addition, *Regina* collected during the early part of the autumn activity peak frequently were coated with mud, much as individuals were when emerging from hibernation in the early spring. My qualitative observations suggest that *R. grahami* at Squaw Creek may avoid high temperatures and dry conditions, and may aestivate during summer. However, if *Regina* became primarily nocturnal during summer (as is true in Louisiana; see below), then the apparent lack

TABLE 4. Sexual dimorphism in body size in neonatal *Regina grahami*. Because both maternal identity and sex affect offspring size (see text), I present the data separately for each of these categories. Means and standard deviations are followed by results of a one-way ANOVA comparing sexes within each brood. Female C produced all females, so no comparisons could be made between the sexes for that brood.

Maternal ID	SVL (cm)			Body Mass (g)		
	Females	Males	F	Females	Males	F
A	20.8 ± 0.40 N = 7	21.5 ± 0.76 N = 6	4.1 $P = 0.06$	4.4 ± 0.26 N = 7	4.3 ± 0.18 N = 6	0.03 $P = 0.85$
B	19.7 ± 0.40 N = 9	20.1 ± 0.51 N = 3	2.1 $P = 0.18$	3.5 ± 0.21 N = 9	3.6 ± 0.10 N = 3	1.1 $P = 0.33$
C	20.4 ± 0.41 N = 12	— —	— —	3.9 ± 0.17 N = 12	— —	— —
D	21.3 ± 0.25 N = 5	21.5 ± 0.77 N = 10	0.31 $P = 0.59$	4.8 ± 0.17 N = 4	4.5 ± 0.29 N = 9	2.7 $P = 0.13$
E	20.8 ± 0.43 N = 10	21.5 ± 0.73 N = 4	5.5 $P = 0.03$	4.7 ± 0.26 N = 10	4.7 ± 0.17 N = 4	0.0 $P = 0.05$

TABLE 5. Ontogenetic variation in frequency of recent feeding in *Regina grahami*. Data on sexes combined. Size classes selected arbitrarily.

Size class (cm)	Percent with food	N
<20-29.9	60.0	5
30.0-39.9	75.0	8
40.0-49.9	18.8	15
50.0-59.9	20.7	58
60.0-69.9	23.3	30
>70.0	0.0	1

of activity in summer could represent biased sampling resulting from limited visibility at night along dikes. Radiotelemetric studies are needed to test these ideas.

(3) Reproduction—The overall frequency of gravid females during the reproductive season (81%) was very similar to that of other natricines (\bar{x} = 80.6%, N = 22 species or populations; Seigel and Ford, 1987). As for 14 of 16 natricines for which data were available, *R. grahami* showed a positive relationship between clutch size and maternal body size. However, *R. grahami* at Squaw Creek did show two unusual reproductive traits. First, the overall sex ratio of neonates was biased in favor of females. Although biased primary sex ratios such as those found in this study are unusual in snakes (Parker and Plummer, 1987), the small sample size from Squaw Creek invites caution in interpreting the significance of these data.

Second, there was evidence for sexual dimorphism in SVL among neonates, albeit not in body mass. Although sexual differences in neonate size are rare for snakes (but see Charland, 1988), this may be an artefact of a limited data set on offspring size (Seigel and Ford, 1987). Unfortunately, interpretation of sexual differences in offspring size are confounded by interactions between maternal size, clutch size, and offspring size (cf. Ford and Seigel, 1989), and my data for *Regina* are too limited to test for such interactions. Larger sample sizes are necessary to adequately determine patterns of sexual dimorphism in neonate size, and such data are needed badly for snakes.

Comparisons with other Populations of R. grahami.—The only other detailed study of a single population of *R. grahami* was conducted in southeastern Louisiana (Mushinsky and Hebrard, 1977a, b; Hebrard and Mushinsky, 1978; Mushinsky et al., 1980), but quantified data on body sizes, population structure, and reproduction are lacking from this location. Both Hall (1969) and Kofron (1979) provided limited data on reproduction from south-central Louisiana, and Hall (1969) reported field data on repro-

duction and activity times for populations in eastern Kansas and Louisiana, respectively. However, given the limited sample sizes and use of museum records from different years and areas in Hall's study, I restrict most of my comparisons to Louisiana.

Kofron (1979) found the minimum SVL at maturity among 20 females to be 60 cm, compared to 42 cm in a combined live/preserved sample of 66 females from eastern Kansas (Hall, 1969). The minimum SVL at maturity in my study was 48 cm SVL. The frequency of reproductive females was 100% in Louisiana (N = 6; Kofron, 1979), 50% (N = 4) in live specimens from Kansas, and 62% in 21 preserved females (Hall, 1969), approximately bracketing the 81% reproductive frequency found at Squaw Creek.

In contrast to the bimodal seasonal activity pattern in Missouri, *Regina* in Louisiana were active from February to August, and showed a unimodal activity pattern, with peak activity in the early spring (March), only limited activity in the summer, and no activity in the autumn, although other natricines were active during this latter period (Mushinsky and Hebrard, 1977a, b; Mushinsky et al., 1980). In addition, Mushinsky et al. (1980) found that *R. grahami* in Louisiana became increasingly nocturnal during summer, whereas I found only limited nocturnal activity in Missouri (but see above for possible bias in my samples).

It is not surprising that snakes from a southern locality showed an apparent higher degree of nocturnal activity than did snakes from a cooler location. I found similar differences in diel activity when comparing *Sistrurus catenatus* from Squaw Creek to other populations (Seigel, 1986). However, few quantified data are available concerning intraspecific differences in seasonal activity patterns in snakes (Gibbons and Semlitsch, 1987). The simplest prediction is that snakes from cooler environments should have shorter activity periods than snakes from warmer areas, and this has been verified in some species (e.g., *Crotalus viridis*, Macartney et al., 1990). However, my data on *Regina* suggest that intraspecific variation in seasonal activity may be more complex than previously believed; *Regina* from both Missouri and Louisiana are active for about seven months, but activity apparently begins and ends earlier in Louisiana, and the pattern of activity (unimodal versus bimodal) also shows considerable intraspecific variation. Additional quantified data on intraspecific shifts in activity patterns are needed for snakes.

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