

ESTIMATING PREY SIZE AND NUMBER IN CRAYFISH-EATING SNAKES, GENUS *REGINA*

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ABSTRACT: Snakes of the genus *Regina* feed almost exclusively on crayfish. The paired, symmetrical gastroliths of crayfish are not digested and are detectable from x-rays of the snake. Gastrolith length is directly proportional to carapace length and can be obtained from x-rays. Carapace length can be converted to kcal of ingested energy. Using these relationships and repeated captures of radio-telemetered *Regina*, estimates of food consumption and energy intake by free-living snakes are feasible. New information on prey selectivity, feeding behavior, and predator-prey size relations in *Regina grahami* and *R. septemvittata* are presented and compared with similar data for other snakes.

Key words: Reptilia; Serpentes; Colubridae; *Regina*; Food habits; Predator-prey size relationships; Crayfish

THE foraging ecology of snakes is less often studied than many aspects of snake biology. Some species are rare and others are secretive; consequently, obtaining adequate samples is a common problem (Turner, 1977). In addition, most snakes eat relatively large prey at infrequent intervals (e.g., Beavers, 1976; Fitch, 1960, 1965; Godley, 1980; Greene, 1983a,b; Schoener, 1977; Seib, 1981), and their digestive tracts seldom contain food. Because of the prey's advanced state of digestion in the hindgut (Brown, 1958; Godley, 1980; Henderson, 1970; Skoczylas, 1970), positive identification of prey species and important measures of prey size often are obtainable only while the prey is in the snake's stomach.

Here we describe an accurate, non-invasive technique for estimating the number and sizes of prey in the entire digestive tracts of crayfish-eating snakes, genus *Regina*. The technique is designed specifically for dietary studies of *R. grahami* and *R. septemvittata*, two species that feed almost exclusively on soft, freshly molted crayfish (Branson and Baker, 1974; Burghardt, 1968; Hall, 1969; Kofron, 1978; Mushinsky and Hebrard, 1977; Strecker, 1926; Wood, 1949). We also provide new information on prey selectivity, feeding behavior, and predator-prey size relations in these species and summarize similar data for other species of snakes.

The technique requires an understand-

ing of specific events in the crayfish molt cycle and the relationship of these events to prey selection in *R. grahami* and *R. septemvittata*. Briefly, individuals of various species of crayfish molt one to 12 times per year depending upon sex, age and environment. Usually less than 15% of a population is molting at any one time (Capelli and Magnuson, 1975; Drach, 1939; Prins, 1968; Stein, 1977; Stevenson, 1975). Prior to molt, calcium is extracted from the exoskeleton and stored in paired, symmetrical gastroliths located in the cardiac stomach (McWhinnie, 1962; Richards, 1951; Stein and Murphy, 1976; Travis, 1960). The gastroliths are resorbed shortly after molt and contribute to the formation of a new exoskeleton. Gastroliths reappear upon initiation of the next molt cycle. Gastrolith growth and resorption are distinct events and are tightly synchronized with other identifiable stages in the molt cycle (McWhinnie, 1962; Stevenson, 1975). As we shall show, these gastroliths provide a convenient, quantitative "marker" for estimating rates of feeding and energy intake in *R. grahami* and *R. septemvittata*, and perhaps in other species that feed extensively on molting crayfish (Neill, 1951; Penn, 1950).

MATERIALS AND METHODS

We estimated the number, size and feeding sequence of crayfish ingested by 36 *R. grahami* (USNM 12864-65, 12891,

12940-70, 13038-39) from New Orleans, Orleans Parish, Louisiana, and two (197638) from Badger Lake, Monona County, Iowa, by exposing identifiable prey with a single ventro-medial incision through the gut wall. The orientation (head or abdomen first) and the ingestion position (dorsal, ventral or lateral) of the crayfish relative to the snake's skull were recorded prior to removal of prey from the snake's stomach. After removal, the crayfish's carapace length (CL = maximum dorsal midline distance from tip of rostrum to posterior edge of carapace) and gastrolith length (GL = maximum longitudinal length of gastroliths) were measured with vernier calipers to the nearest 0.1 mm. Only GL was obtained from intestinal contents; paired, symmetrical gastroliths were assumed to represent the digested remains of a single crayfish. The molt stage of the crayfish (Drach, 1939; McWhinnie, 1962; Stevenson, 1975) also was recorded. Molt stages pertinent to this study are as follows. A_1 —Exoskeleton is soft, gelatinous and easily torn; gastrolith is fully formed; duration is of a few hours. A_2 —Exoskeleton is leathery; gastrolith is reduced to about 50% of former size by end of stage; duration is ca. 24 h. B—Rostrum and cephalic carapace are firmer but flexible; gastrolith is very small to absent at end of stage; duration is of one to three days.

Similar data were obtained from a series of 36 *R. septemvittata* collected in Montgomery Co., Ohio (USNM 128974-98, 129016-27). However, before dissection, each specimen was radiographed in dorso-ventral view. The radiographs were exposed for 30 s at instrument readings of 5 mamp and between 20 and 23 kV depending on snake size. Gastrolith measurements were taken from the radiographs with a dial caliper. Because gastroliths are slightly oblong in shape and the x-rays provided only a single plane of view, the longest dimension of either gastrolith of the pair was chosen to represent the GL. To avoid possible bias, GL measurements taken from the radiographs

were examined after dissection measurements were recorded. Because methods varied between the snake species, results are presented separately.

RESULTS

Regina grahami

Only the remains of crayfish, representing at least three species, *Orconectes palmeri croelanus* (Creaser), *Procamburus clarkii* (Girard) and *P. vioscai* (Penn), were recovered from the stomachs of 38 *R. grahami*. Of these prey, measurements of both GL and CL were obtainable from 17 crayfish (all were in molt stages A_1 or early A_2), CL only from two crayfish (one in stage B, the other in stage A_1 or A_2 but gastroliths broken during processing), GL only from six crayfish (all in stages A_1 or A_2 but carapace partially digested), and two crayfish were represented only by single, very large (57 and 63 mm total length) chaela, each in a different snake. The largest chaela from an intact crayfish (CL = 31.5 mm) in the sample was 36.0 mm, suggesting that the latter two snakes encountered crayfish too large to consume whole and instead removed the only large portion (chaela) that could be disarticulated. In addition, GL measurements from 20 crayfish were obtained from intestinal contents. All of these crayfish appeared to have been in molt stage A_1 or early A_2 .

Although most of the exoskeletons of crayfish were partially digested, the gastroliths seemed normal and unaffected by passage through the snake's digestive tract. In fact, captives of all species of *Regina* defecate gastroliths which macroscopically are indistinguishable from those dissected from live crayfish of a similar molt stage (J. S. Godley, personal observation).

As is typical of freshly molted crayfish (McWhinnie, 1962 for *Orconectes virilis*), GL is a linear function of CL (Fig. 1) and provides an excellent estimate of crayfish size. Most of the variance about this line probably is caused by three sources of experimental error: (1) differences in GL: CL ratios among the three species of cray-

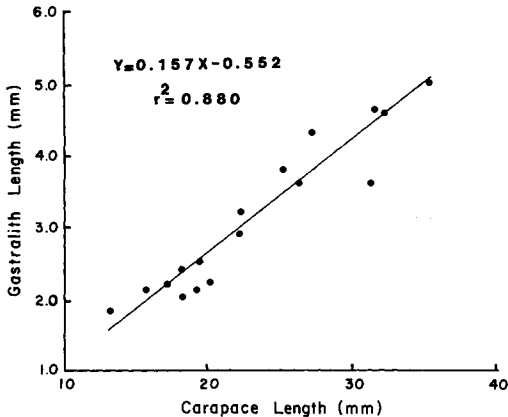


FIG. 1.—Relationship of gastrolith length and carapace length from 17 crayfish removed from the stomachs of *Regina grahami*.

fish represented in the sample, (2) differences in crayfish molt stage, and (3) the difficulties of accurately measuring the CL of soft-bodied crayfish taken from a snake's stomach. In a sample of 18 *Procambarus fallax* from Hillsborough Co., Florida, which were sacrificed within six h of molting, the correlation coefficient between GL and CL was 0.98 (J. S. Godley, unpublished data). The slope of this line was not significantly different from that shown in Fig. 1 ($F_{1,31} = 2.48$, $P = 0.1253$).

Predator-prey size relationships in *R. grahami* can be examined by using GL as an estimate of crayfish size (GL estimated for two crayfish from CL) and snake snout-vent length (SVL) as an estimate of predator size (Fig. 2A). In our data set, the regression of GL on CL (Fig. 1) allowed estimates of size for 27 digested crayfish and increased the usable crayfish sample size 158.8% (from 17–44). Snake SVL explained a significant ($P = 0.0029$, $Y = 1.436 + 0.0046X$) but small percentage ($r^2 = 0.193$) of the variation in the size of prey taken by *R. grahami* (Fig. 2A). Although adult *R. grahami* consumed larger crayfish than juveniles, the minimum size of ingested prey did not change during ontogeny. Of the 25 snakes with

food, 14 contained one crayfish, six had two crayfish each, two contained three, and three had eaten four crayfish. SVL was positively correlated with the total number of prey whether individuals with empty digestive tracts were included (Spearman rank correlation, $r_s = 0.47$; $P = 0.0076$, $n = 38$) or excluded ($r_s = 0.58$, $P = 0.0024$, $n = 25$) from the analysis.

Prey orientation could be determined for 26 of 27 crayfish recovered from the *R. grahami* stomachs; 12 were ingested head first and 14 abdomen first, suggesting no orientation preference ($\chi^2 = 0.08$, $P > 0.75$). Vertical position of prey could be determined for 22 of the 27 prey and was not significantly different from random ($\chi^2 = 4.0$, 2 df, $P > 0.10$) with 12 crayfish ingested on their side with respect to the snake's skull, eight with venters up, and two with venters down. Analysis of covariance with GL as the dependent variable, SVL as the covariate, and prey orientation and position as independent variables showed no significant effects for the latter two variables.

Regina septemvittata

In this species, specimens were x-rayed prior to dissection to determine if radiographs could provide reliable estimates of feeding activity. The two criteria we judged necessary for establishing reliability were: (1) radiographs must detect all crayfish in the digestive tract, and (2) measurements of GL taken from x-rays and those obtained from dissection must show high correspondence.

Gastroliths representing 26 crayfish were identified from the radiographs of the 36 *R. septemvittata*. The same number of prey was found when the snakes were dissected. A representative radiograph is shown in Fig. 3. A strong correlation exists between GL based on radiographs and GL based on dissections (Fig. 4).

Only four of the 26 crayfish in the *R. septemvittata* were in the stomachs. These four prey (*Cambarus diogenes* Girard) were partially digested and no CL mea-

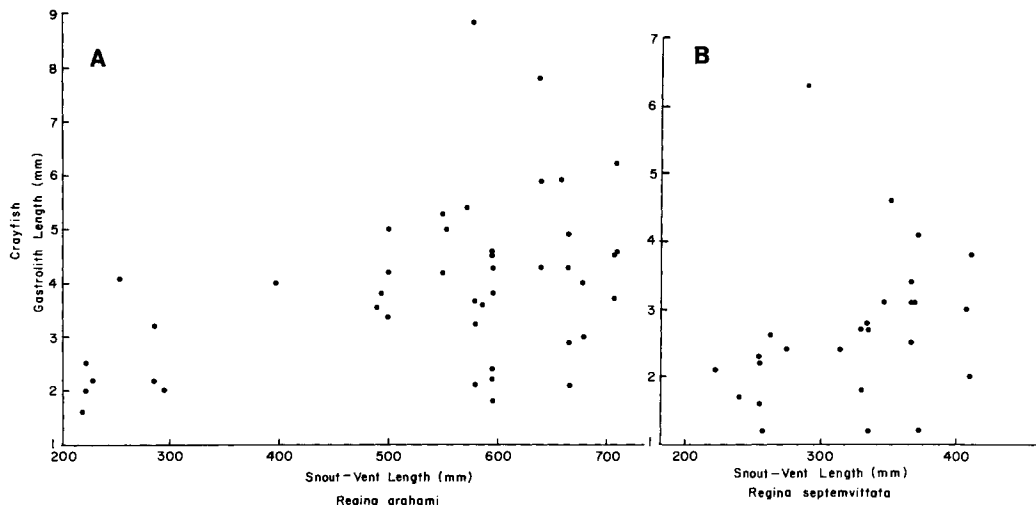


FIG. 2.—Size relationship between snakes and their respective crayfish prey. (A) *Regina grahami* ($n = 44$). (B) *Regina septemvittata* ($n = 26$).

surements were obtained; all were in molt stage A_1 and were ingested abdomen first. Judging from the condition of the gastroliths (representing 22 crayfish) found in the intestines, these crayfish also were in molt stage A_1 or A_2 when eaten. The scatter plot of crayfish GL on *R. septemvittata* SVL (Fig. 2B) was similar to that observed in *R. grahami* (Fig. 2A), but the regression was not significant ($r^2 = 0.09$, $P = 0.139$).

DISCUSSION

Our work has revealed an accurate, nondestructive technique for estimating the number and size of prey in two species of *Regina* based on the following observations. (1) *Regina* feed almost exclusively on crayfish. (2) The paired, symmetrical gastroliths of crayfish are not digested. (3) GL is directly proportional to CL. (4) GL is obtainable from x-rays of *Regina* that have fed on crayfish.

Insight into several poorly known aspects of snake foraging ecology and digestive physiology could be gained using this technique. For example, little is known about the effects of different feeding, temperature and activity regimes on

clearance times and rates of digestion in snakes of different size, sex and reproductive condition (see Dandrifosse, 1974; Godley, 1980; Skoczylas, 1978 for reviews). Here a major difficulty has been the lack of a convenient, natural marker to follow the course of prey digestion. X-rays made at appropriate intervals of crayfish-eating snakes would provide such a system under controlled laboratory conditions. Perhaps the greatest use of this technique lies in its potential field application. By using the relationships developed above, a portable x-ray unit, and repeated captures of *Regina* equipped with transmitters that measure heart rate or body temperature, accurate estimates of the energy budget of free-living snakes are possible (the energy content of crayfish is known, see Godley, 1980; Stein and Murphy, 1976). Concurrent x-rays of non-telemetered animals from the same population could serve as a control for possible effects of experimental procedures.

Our results show that crayfish are subject to predation by *Regina grahami* and *R. septemvittata* only while they are in molt stages A_1 or A_2 . Further, the low variance in GL for crayfish of any size (Fig.



FIG. 3.—Radiograph of *Regina septemvittata* (USNM 128998) from Ohio. This snake contains three pairs of gastroliths and a pebble (arrow).

1) and the rapid temporal decline in GL following molt (McWhinnie, 1962) suggest that most crayfish are eaten by these snakes within 6 h of molt (stage A_1). This extreme molt-stage selectivity may have important ecological consequences. In three species of crayfish found within the range of *R. grahami* or *R. septemvittata*, freshly molted individuals comprise less than 15% of the population averaged over the year (Prins, 1968; Stein, 1977). In addition, all of these species seem to have a "mass, synchronized molt" (Prins, 1968: 678) which would further limit the biomass of snakes that could be supported on a given population of crayfish. In contrast, morphological and behavioral adaptations of *Regina alleni* (Franz, 1977; Godley, 1980) and *R. rigida* (Kofron, 1978) enable these species to exploit crayfish in all stages of their molt cycle. Available density estimates for *R. septemvittata* (Branson and Baker, 1974) and *R. alleni* (Godley, 1980) support this contention.

Variation in molt-stage selectivity among species of *Regina* also is reflected in their feeding behavior. Covariance analysis suggests that in *R. grahami*, orientation and positioning of crayfish is random with respect to the snake's skull and

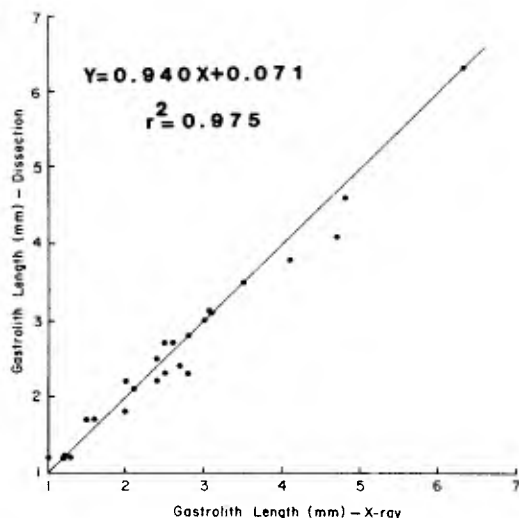


FIG. 4.—Relationship between gastrolith length as measured from gastroliths removed from gut and those measured from x-rays of *Regina septemvittata* ($n = 25$); one gastrolith was damaged during processing and excluded from this comparison.

is independent of crayfish size (see also Hall, 1969). However, *R. septemvittata*, which feeds on crayfish of similar molt stages, apparently ingests crayfish only abdomen first (see also Branson and Baker, 1974; Wood, 1949), suggesting that these two closely related species (Rossman, 1963) have diverged behaviorally while maintaining similar molt-stage selectivity. *R. alleni* consumes crayfish abdomen first and lateral with respect to the snake's skull regardless of crayfish size, molt-stage or snake feeding experience (Franz, 1977; Godley, 1980 and unpublished). The feeding behavior of *R. rigida* is unknown but probably is similar to that of *R. alleni*.

Snake SVL proved to be a relatively poor predictor of the size of crayfish eaten by *Regina grahami* ($r^2 = 0.19$, $P = 0.0029$) or *R. septemvittata* ($r^2 = 0.09$, $P = 0.139$) (Fig. 2). In reviewing similar data for 17 other species of snakes distributed among five families (Beavers, 1976; Godley, 1980; Greene, 1983a,b; Mushinsky et al., 1982;

Reynolds and Scott, 1982; Seib, 1981; Shine, 1977; Voris and Moffett, 1981), we found four common, intraspecific trends. (1) Larger snakes can consume absolutely larger prey than smaller individuals. (2) The variance in prey size tends to increase with increasing snake size. (3) A least squares regression of prey size on snake size usually yields a positive, significant slope but rarely accounts for more than 50% of the variation. (4) The slope of the boundary line for minimum prey size is much lower than that for maximum prey size such that the size of the smallest prey is similar for adults and juveniles of the same species. As did Voris and Moffett (1981), we define prey boundary lines as the approximate lower and upper size limits of prey eaten by a snake during its ontogeny.

We are concerned with the increasing tendency among some workers to interpret the shape of predator-prey size trajectories in snakes as a reflection of prey size selection seemingly without consideration of alternative hypotheses. Constraints imposed by head morphology alone would restrict the range of prey sizes ingested by gape-limited snakes (Gans, 1961; Greene, 1983a) and could produce each of the four intraspecific trends noted above. A morphological-constraint hypothesis also could explain why, in our opinion, experimental attempts to demonstrate prey selection based on size in snakes have failed (Czaplicki and Porter, 1974; Godley, 1980; Reynolds and Scott, 1982; Smith and Watson, 1972). Although we do not doubt that ecological factors influence prey choice in snakes, it remains to be shown that any species of snake selects a smaller range of prey sizes than the limits imposed by its morphology.

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