Size and Proportion Relationship between the Beaked Sea Snake and Its Prey

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ABSTRACT

Size comparisons are made between the beaked sea snake, *Enhydrina schistosa*, and its usual prey, an ariid catfish, *Tachysurus maculatus*. Of 108 catfish found in as many snake stomachs, most were partially digested. Estimates of catfish length, maximum diameter, and weight were made using linear regression relationships between these measures and index measures determined on entire specimens. Maximum prey diameters were one to two times the neck diameters of the snakes. Prey selection is implicated along both the upper and lower limits of prey size. Large snakes take a disproportionately large number of relatively small fish. This may be a function of prey availability alone.

OPTIMAL FORAGING THEORIES have encouraged ecologists to look at feeding behavior and habits much more rigorously than in the past. To test theories of selective feeding it is necessary to define and gather data on factors such as foraging time, processing time, net energy gain, feeding frequency, etc. (see Schoener 1971, for a review of optimal foraging theory). Among terrestrial vertebrates snakes are the only major group which specializes in swallowing whole relatively large prey. The prey size of snakes relates directly to prey-handling factors as well as energy considerations.

There are numerous reports in the literature on the taxonomic identity of the food of marine snakes (Klawe 1964, McCosker 1975, Voris 1972). The bulk of the data indicates that most species are specialists on some variety of fish. A study of the food and feeding behavior of the beaked sea snake, *Enhydrina schistosa*, in Malaysia (Voris *et al.* 1978) revealed behavioral specializations for ingesting spiny catfish (Ariidae). In this paper the relationship between the size and body proportions of *E. schistosa* relative to its catfish prey is explored.

MATERIALS AND METHODS

Beaked sea snakes (*Enhydrina schistosa*) were collected at Muar, Malaysia (2°3′20″N, 102°34′20″E). Details of habitat and collection techniques are available elsewhere (Jeffries and Voris 1979). The measurements of snout-vent (s-v) length, girth at the neck, and girth at 3/4 the s-v length were made on snakes relaxed with sodium pentobarbital. The latter two girth measurements represent the minimum and maximum girths respectively for *E. schistosa*. The neck of *E. schistosa* is round, and thus girth measurements were converted to diameters by dividing each circumference by π. All specimens were weighed several months after they had been preserved in formalin and stored in 70 percent ethanol. The stomach contents were removed from the relaxed snakes and preserved in 10 percent formalin. Several months later the fish were transferred to 70 percent ethanol. At Muar the most frequent prey of the beaked sea snakes was the ariid catfish, *Tachysurus maculatus* (Voris *et al.* 1978), and this paper deals mainly with this species. Measurements and weights were made on preserved catfish. Body length was measured from the most anterior part of the head to the base of the tail where the fin rays emerged from the body. The maximum diameter, excluding the extended dorsal or pectoral spines, was across the body at the base of the pectoral fins and will be hereafter referred to as the diameter. Tail height was measured as the depth of the caudal peduncle, excluding the fin rays, at the base of the tail. The dorsal fin to tail length was the distance from the posterior junction of the dorsal fin and the body to the base of the tail medio-laterally, where there was a small notch at the base of the tail.

E. schistosa swallow catfish head first (Voris *et al.* 1978), and thus the posterior end of the fish is the last to undergo digestion. Fish lacking some part of the forebody comprised 75 percent of the stomach contents. Of the 108 catfish removed from stomachs, the length, diameter, and weight were measured directly for 27, 16, and 11 specimens respectively. For the remaining partly digested fish, tail height and dorsal fin to tail length measurements were used to estimate the original body dimensions and weight. This was done after first analyzing a series of 50 complete specimens to determine the relationship between the two index measurements (tail height and dorsal fin to tail length) and the length, diameter, and weight of the catfish.

A linear relationship exists between tail height and body length, thus the linear regression was used

TABLE 1. *Data on relationships between catfish index measurements (dorsal fin-tail length and tail height in centimeters) and catfish parameters used in comparisons with snakes.*

	Body length			Maximum diameter			Body weight (log)		
x	n	y	r	n	y	r	n	y	r
Fin-tail length	50	1.87x − 0.11	1.00	42	0.38x + 0.04	0.99	35	3.29x − 1.27	0.99
Tail height	50	10.03x + 0.91	.99	41	1.97x + 0.27	0.98	34	2.86x + 1.25	0.98

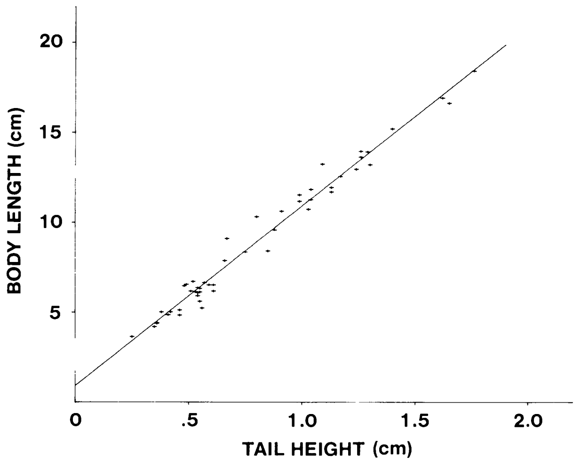

FIGURE 1. The relationship between tail height and body length for 50 *Tachysurus maculatus*. The slope and correlation (r) data are given in table 1.

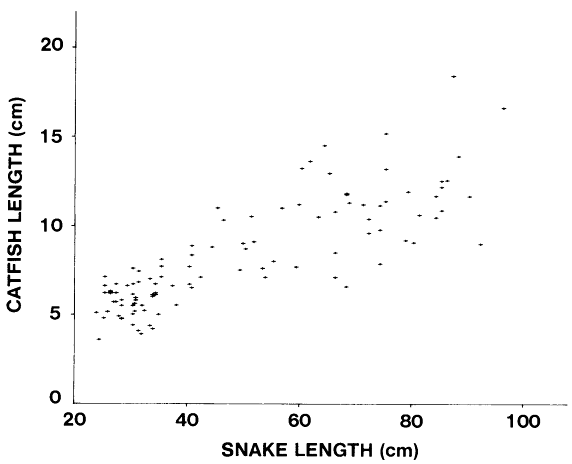

FIGURE 2. The relationship between snake s-v length and the length of its catfish prey for 106 snakes. The least squares linear regression data are: $y = 2.41 + 0.12x$. The correlation coefficient (0.83) is significant at $p < 0.01$.

to estimate fish length from tail height measurements (figure 1 and table 1). The relationship between each index measurement and weight is linear after performing logarithmic transformations on the index measurements and weight. The values predicted using the dorsal fin to tail length were used in preference to those given by tail height whenever possible. For most fish, however, only the tail height was measurable.

RESULTS

The three measures of catfish size were plotted against comparable measures from the snakes. Snake s-v lengths (fig. 2) ranged from about 20 to 100 cm. The smaller snakes (20-28 cm) were newborn while the snakes over about 70 cm long were two or more years old and sexually mature (Voris and Jayne 1979). The catfish found in the snake stomachs ranged from about 4 to 18 cm in length. The smallest fish were probably very young, based on the fact that yolk sacs were observed on museum specimens which were only slightly smaller (*ca* 3.5 cm). The ages of the larger catfish are unknown. Figure 2 shows that juvenile snakes of less than 40 cm s-v length prey upon relatively small catfish. Larger snakes eat larger catfish as well as rather small catfish. For example, a recently born snake (25 cm s-v length) contained a 7 cm catfish while a two-year-old snake (68.0 cm s-v length) had eaten a 6.5 cm catfish. The correlation between catfish size measurements (length, diameter, and weight) causes a similar pattern to emerge when snake-fish diameters (fig. 3) and weight (fig. 4) are plotted.

Larger snakes eat a wider range of fish sizes. In the plot of snake weight vs fish weight (fig. 4) the range of prey weight taken by large snakes is particularly striking. However, relative to the size of the snakes, small snakes take a broader range of prey sizes. This finding can be seen in figure 5, which gives the relative prey weight for each snake stomach content.

The dotted slopes in figure 3 follow the upper and lower boundaries. The upper slope (1.95) is based on 10 uppermost points, and the lower slope (0.87) is based on 11 low points. The decision as to which points to use to form the boundaries was arbitrary. The purpose of generating these slopes was to

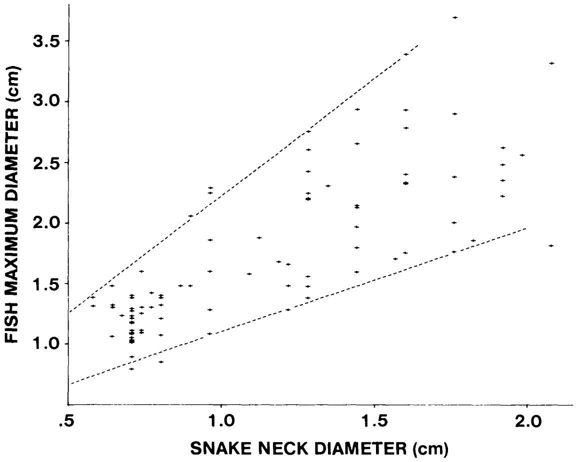

FIGURE 3. The relationship between snake neck diameter and prey maximum diameter for 94 snakes. The linear regressions for all data are: $y = 0.45 + 1.15x$. The dashed lines represent regressions for 10 points along the upper boundary ($y = 0.28 + 1.95x$, $r = 0.99$) and 11 points along the lower boundary ($y = 0.23 + 0.87x$). See text.

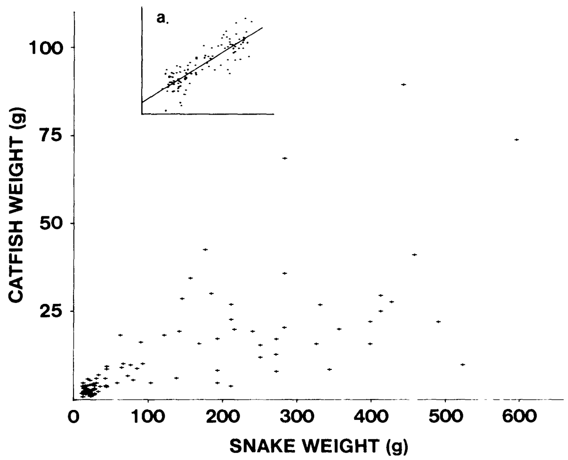

FIGURE 4. The relationship between snake weight and the weight of its prey for 104 snakes. The least squares linear regression is $y = 2.13 + 0.07x$. The correlation coefficient (0.72) is significant at $p < 0.01$. Inset "a" gives the log-log plot of the same data. The least squares regression line (drawn) has the equation $0.77x - 0.58$, with $r = 0.85$.

obtain lines that approximate the upper and lower diameter limits of prey. Prey taken along the lower limit are about nine-tenths of the respective snakes' neck diameters, and those taken along the upper limit are about twice the snakes' neck diameters.

In figures 2, 3, and 4, there is also a common distribution pattern with respect to the size of catfish taken by snakes of different sizes. To demonstrate this, the following transformation was made on the

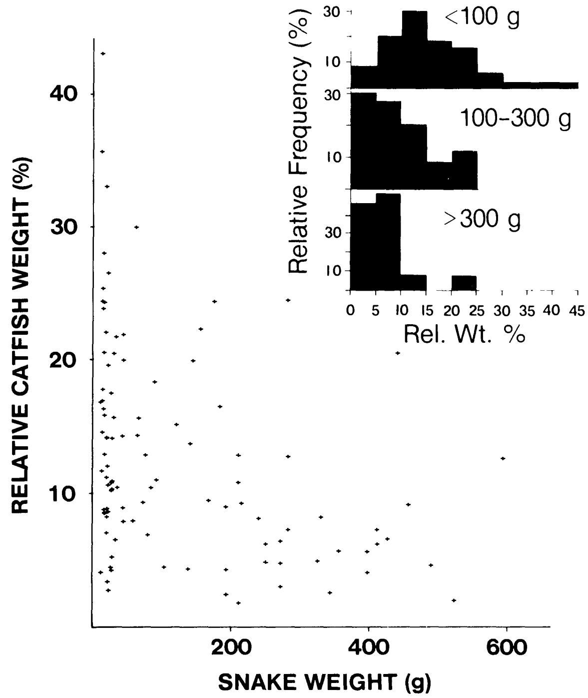

FIGURE 5. The percent by weight that each prey item is of the predator weight (catfish weight/snake weight x 100) is plotted against snake weight. The inset shows the distribution of relative prey weights taken by snakes of different weights.

points in the plot of snake neck diameter vs fish diameter (fig. 3):

$$\frac{(\text{Diameter of fish eaten } (Y)) - \text{Min}}{\text{Max} - \text{Min}}$$

$$= \frac{Y - (0.87X + 0.23)}{(1.15X - 0.45) - (0.87X + 0.23)}$$

$$= \frac{Y - 0.87X - 0.23}{0.28X + 0.22}$$

'Max' and 'Min' represent the maximum and the minimum fish diameters which could be consumed by a snake (X) which ate a particular fish (Y). These maximum and minimum diameters were estimated by using the equations for the upper and lower boundaries respectively from figure 3. This operation facilitates the analysis of prey sizes eaten by different-sized predators, assuming the upper and lower boundaries are reasonably well defined by the boundaries given.

Following the transformation, the distribution of points on the Y-axis is normal ($p < 0.01$) for small (< 1.0 cm neck diameter) snakes but skewed downward for the large (> 1.50 cm neck diameter) snakes ($p < 0.01$). When equivalent transformations were made on the points in the length and weight plots (figs. 2 and 4), statistical analysis gave the same results ($p < 0.01$ or $p < 0.05$). The bar graph in figure 5 emphasizes the tendency for large snakes to take relatively small prey.

DISCUSSION AND CONCLUSIONS

In general, studies of the food habits of reptiles have neglected the size of the prey. In the few studies where prey size has been considered, rarely was there any attempt to estimate the size of the partially digested prey. Shine (1977) provided plots of elapid snake vs frog prey snout-vent lengths using only entire stomach contents. However, he provided no analysis of these data except to suggest that, because prey size is small relative to snake size, feeding is unselective. Beaver (1976) used average adult weights for each rodent prey species to increase his sample size in a study on the diet of *Crotalus atrox.*

Our study uses linear regression as a prey size estimation technique, an approach more commonly used on invertebrate taxa (e.g., Thompson 1978). The very high correlations between measurements such as catfish tail height and body length ($r = 0.99$) indicate the reliability with which one can estimate the prey size from partially digested specimens removed from digestive tracts. In this study the technique increased the usable sample size from 27 to 108 items.

It seems intuitively obvious that since snakes are incapable of shearing or masticating their prey before swallowing, a relatively abrupt upper limit will be set on the diameter of prey which can be swallowed. Prey of a greater diameter are unavailable. If a larger prey was caught it could not be swallowed and would have to be released at the loss of the snake's time and energy. However, there is no apparent reason why *E. schistosa* of a given size would be incapable of taking longer or heavier fish than shown in figures 2 and 4, based on prey length or weight alone. In figure 2 it may be seen that the largest catfish consumed by a snake of any given size is only a small fraction of the snake's s-v length. In comparison, many other sea snakes feed exclusively on eels or eel-like fish among which the length is much greater, and the diameter much less, than for catfish of the same weight. If the prey diameter is always very small relative to prey length, then the length of the prey may set an upper limit on prey size.

It seems likely that the absence of catfish with diameters greater than approximately twice the snake's neck diameter, among the stomach contents, is a result of mechanical limitations which prohibit the ingestion of wider prey. The upper boundaries on the weight and length graphs are attributable to the strong correlations between snake neck diameter and these measurements (figs. 2 and 3). The boundary points in these graphs usually represent the same fish.

If the snakes of all size classes took catfish down to the smallest size available (i.e., those still having yolk sacs), the lower boundary line in the length, diameter, and weight plots would have a zero slope. However, a positive slope is evident in the lower boundary of each of these plots (figs. 2, 3, 4) although it is least pronounced in the weight plot. The fact that beaked sea snakes, which are early in their second year of life (about 50 to 65 cm s-v length), do not feed on the smallest catfish (about 4 to 6 cm long), which are eaten by the newborn snakes (fig. 2), strongly suggests that some kind of prey discrimination is taking place along the lower size boundary.

A lower size limit for prey could reflect mechanical limits of the snake-feeding mechanism or possibly sensory limitations. However, it is not clear why juvenile and subadult *E. schistosa* (s-v length 40 to 70 cm) could not perceive, capture, and manipulate catfish less than about 6 cm long. Thus it is possible that the limit of prey size taken reflects behavioral discrimination based on energy budget factors.

Although in this study the factors important in defining the lower size limit of prey can not be specified, it can be said with some assurance that it is not a result of prey availability alone. According to Wilson (1976), if the species feeds according to the optimal foraging theory, then the boundary of marginally acceptable food items directly estimates the overall energy available to the animal in the environment. Preliminary observations on feeding in young snakes (Voris *et al.* 1978) indicate considerable variance in search and ingestion times which, if measured, could help begin to determine whether beaked sea snakes are screening prey within the framework of optimal foraging theory.

One comment is necessary on the non-normal distribution of prey sizes taken by large snakes (fig. 5). This distribution may to a large degree be a simple function of prey availability. The disproportionately large number of young catfish taken by large snakes was mirrored in the net catches and would be expected simply on the basis of natural population structure of the catfish.

Puff fish (Tetraodontidae) make up only about 5 percent of the diet of *E. schistosa*, but an abbreviated analysis proved interesting. Measurements of tail height and uninflated diameter on 22 complete puff fish specimens defined the relationship for predicting the diameter of partially digested puffers. Of the nine puff fish found in stomachs, five came from small snakes (neck diameter less than 1.0 cm) and had diameters which placed them within the boundaries in figure 3. However, four fish came from larger snakes ($>$ 1.25 cm neck diameter), and these puff fish diameters were below the lower boundary in figure 3. This circumstance may reflect the snakes' ability to compensate for the puff fish's habit of expanding its body when attacked by the snakes (Voris *et al.* 1978).

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