

Foraging Theory and Prey-Size–Predator-Size Relations in Snakes

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Introduction

The aim of this chapter is to encourage additional studies of prey-size–snake-size relations. The fascinating evolutionary vistas sketched by Greene (1983), Mushinsky (1987), Pough and Groves (1983), and Voris and Voris (1983) have not been explored as assiduously as they might. In this chapter I focus on one tantalizing result from the recent literature on snake diets in the hope of encouraging more work. The result is that in many of the snake species studied so far larger snakes drop small prey items out of their diet. The implication is that snakes pass over, perhaps even avoid, some of the smallest prey items they encounter. Foraging theory is used to devise some hypotheses to explain this apparently enigmatic result. In trying to use foraging theory to this end, I was constantly plagued by the lack of relevant data. However, the lack of data is undoubtedly a reflection of our failure to adapt theory to snake biology. Perhaps even a provisional application of theory to the problem will help break the logjam.

Trend in the snake diet literature

A progressive trend is apparent in the literature on snake diets, with later papers providing ever more detailed information. The earliest reports (and some later ones) provide only simple lists of prey with no indication of relative importance (Surface, 1906; Wright and Wright,

1957; Mori et al., 1989). Beginning in the 1940s investigators reported the relative importance of prey types in the diet. Relative importance has been variously based on number, weight, volume, or energy content of prey; on the number of snakes that have eaten particular prey types; or on indices that are functions of two or more of these variables (Fitch and Twining, 1946; Hamilton, 1951; Carpenter, 1952; Hamilton and Pollack, 1956; Fitch, 1960; Catling and Freedman, 1980; Arnold, 1981; Shine, 1986; Hasegawa and Moriguchi, 1989). Surprisingly, the uses, virtues, and limitations of these different modes of representing relative importance seem not to have been comprehensively discussed in the snake literature. Such a discussion is, however, beyond the scope of the present chapter. In the 1960s investigators began reporting the relative importance of different prey types as a function of snake size (Fitch, 1963, 1965; Godley, 1980; Saint Girons, 1980). In the simplest cases, the diets of juveniles and adults are compared. In the late 1970s workers began reporting prey size, as well as relative importance, as a function of snake size (Shine, 1977; Voris and Moffett, 1981; Mushinsky et al., 1982; Henderson and Horn, 1983; Plummer and Goy, 1984; Seib, 1984; Henderson et al., 1987; Shine, 1987; Henderson et al., 1988; Slip and Shine, 1988; Cobb, 1989). Finally, in the last few years workers have used field studies of prey-size-snake-size relations to motivate laboratory studies of prey handling and swallowing ability (Jayne et al., 1988; Shine, 1991).

How can we make foraging theory work for us?

Foraging theory (MacArthur and Pianka, 1966; Schoener, 1971; Stephens and Krebs, 1986) apparently did not promote the progressive trend in the snake diet literature. Optimal foraging theory is occasionally mentioned in snake diet studies, but it seems to have been used post hoc rather than to inspire (but see Shine, 1991). The progressive trend appears to have been propelled as much by herpetological craft and tradition as by theoretical developments outside the discipline. Within the discipline, Greene (1983) argued persuasively that prey diameter in relation to snake head size (ingestion ratio) and prey mass in relation to snake mass (weight ratio) are the keys to understanding snake evolution and ecology. The connection between Greene's key variables and foraging economics needs to be drawn out so that we can evaluate his propositions. More generally, how do we make foraging theory work for us?

Foraging theory could motivate studies of snake diet in three ways. We might test the theory's assumptions or its predictions, or we might use the theory to highlight certain data trends and generate

new hypotheses. I will concentrate on the third approach, but first I will review some important assumptions of the theory.

An Economic Perspective on Prey-Size—Predator-Size Relations in Snakes

Crucial assumptions of optimal foraging theory

Optimality is one of the most hazardous assumptions of foraging theory. Important lessons can be drawn from the theory, however, while avoiding the pitfalls of the optimality assumption. The goal of foraging theory is to predict how animals should feed (Schoener, 1969, 1971; Pyke et al., 1977; Krebs and McCleery, 1984; Stephens and Krebs, 1986). To make predictions we need to evaluate foraging alternatives. The use of optimality to evaluate alternatives has three aspects: (1) the choice of a currency; (2) the choice of a cost-benefit function that specifies the relationship between foraging and the currency; and 3) the solution of the function for the foraging traits that maximizes the currency (Schoener, 1971). The third aspect is a straightforward mathematical problem, but the first two aspects involve potentially hazardous assumptions and implications. From a practical standpoint the best choice for a currency is amount of energy gained, time spent foraging, or some combination of the two. Time and energy are both readily measured and natural currencies for the various activities or stages of foraging. From an evolutionary standpoint, however, fitness (the number of progeny produced in a lifetime) is the natural currency (Crow and Kimura, 1970). To use energy and time as a currency for evolutionary predictions we must know or specify the relationship between our currency (based on time and/or energy) and fitness. The standard assumption is that the relationship is linear or monotonically increasing. Either version is equivalent to saying that the currency is under perpetual directional selection with no intermediate optimum. The second hazardous assumption is that the population will (and has) evolved to the optimum specified by the cost-benefit function. Frequency-dependent selection and various kinds of genetic constraint can cause violations of this assumption (Lewontin, 1978; Gould and Lewontin, 1979; Lande, 1979). One posture is to argue that these two assumptions are not hazardous. Another posture is to acknowledge the potential pitfalls of the two assumptions and use foraging theory in a way that avoids those pitfalls.

The pitfalls of optimality can be avoided by using foraging theory to characterize selection rather than to predict evolutionary outcome. We can think of selection as the statistical relationship between a phenotypic trait (such as a foraging tendency) and fitness (Lande, 1979; Lande and Arnold, 1983). If we visualize the relationship as a

pathway, we can recognize two parts: the path from our foraging trait to our energy and time currency and the path from the currency to fitness (Arnold, 1983, 1988). Foraging theory gives prescriptions for measuring the first part of the pathway, the energy gradient (Arnold, 1988). In other words, foraging theory guides measurement of part of the phenotypic selection that acts on foraging. In principle, we could also measure the second part of the path (the fitness gradient), which is often and conveniently assumed to be linear, and so characterize the total selection that acts on foraging. If we have not accomplished this second task (i.e., the fitness gradient remains unknown) then we must qualify our conclusions by recognizing that we have measured only a part of the selection. If we had measured total selection, we still would need to measure genetic constraints to predict the outcome of selection. But even if we use foraging theory just to make statements about selection, it can be an informative tool.

Prey size versus snake size

Ontogenetic shift in lower size limit for prey. In this section I will review studies in which prey size is plotted as a function of snake size. In all the studies it is apparent that larger snakes tend to eat larger prey. Furthermore, regression line intercepts for plots relating prey dimensions to snake dimensions are often appreciably different from zero (Voris and Moffett, 1981; Plummer and Goy, 1984; Seib, 1984; Cobb, 1989). Such nonzero intercepts mean that prey-size-snake-size ratios will vary within a species as a function of snake size. In the two studies in which the regression slope was estimated for log prey mass as a function of log snake mass, the allometric slope was less than one (Voris and Moffett, 1981; Jayne et al., 1988), indicating that prey mass does not increase in proportion to snake mass (Schmidt-Nielsen, 1984). The range of prey is also larger for larger snakes. These important trends may be universal in snakes and have been discussed by Shine (1991). I will not remark on these trends as I survey published studies. Instead, I will focus on the lower size limit for prey as a function of snake size. Two patterns are apparent in the snake literature and are shown diagrammatically in Fig. 3.1. In some species the lower limit does not increase, so that the prey of small snakes is a subset of the prey sizes eaten by large snakes (Fig. 3.1A). The range of prey sizes eaten by smaller snakes telescopes within the range of larger snakes. In most species, however, the lower limit increases with snake size (Fig. 3.1B). In other words, in most species larger snakes delete small prey from their diets. In Figs. 3.2–3.10 N refers to the number of snakes in the sample and n refers to the number of prey.

Shine (1977, 1987) used museum specimens to study the diets of three genera of terrestrial elapids in Australia. *Notechis scutatus* is a

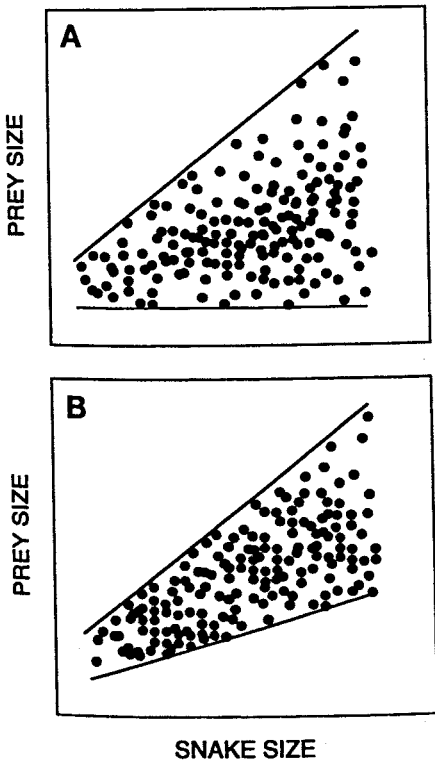


Figure 3.1 Patterns of prey-size-snake-size relationships. (A) Ontogenetic telescope. (B) Ontogenetic shift in lower size limit.

swamp dweller that feeds on frogs and nestling birds (Shine, 1977). Frog length is plotted against snake length in Fig. 3.2A. *Pseudechis porphyriacus* is a riparian forager that feeds on frogs and lizards (Shine, 1977). Frog length is plotted against snake length in Fig. 3.2B. Australian Copperheads (*Austrelaps*) are active searchers that feed on lizards and frogs (Shine, 1987). Lizard (mainly scincids) length is plotted against snake length in Fig. 3.2C. The data in Fig. 3.2C are pooled from three species of *Austrelaps* (*A. labialis*, *A. Ramsayi*, and *A. superbus*). In all three genera of Australian elapids there is no indication that larger snakes delete small prey from their diets. Shine (1977) argues that large elapids continue to eat small prey because capture and ingestion costs are small in relation to energy content of prey and because envenomation of prey eliminates risks.

Seib (1984) used special collections and museum specimens to study the diets of three colubrid snakes in the genera *Drymobius* and *Mastigodryas*. All three species are frog and lizards predators. Seib

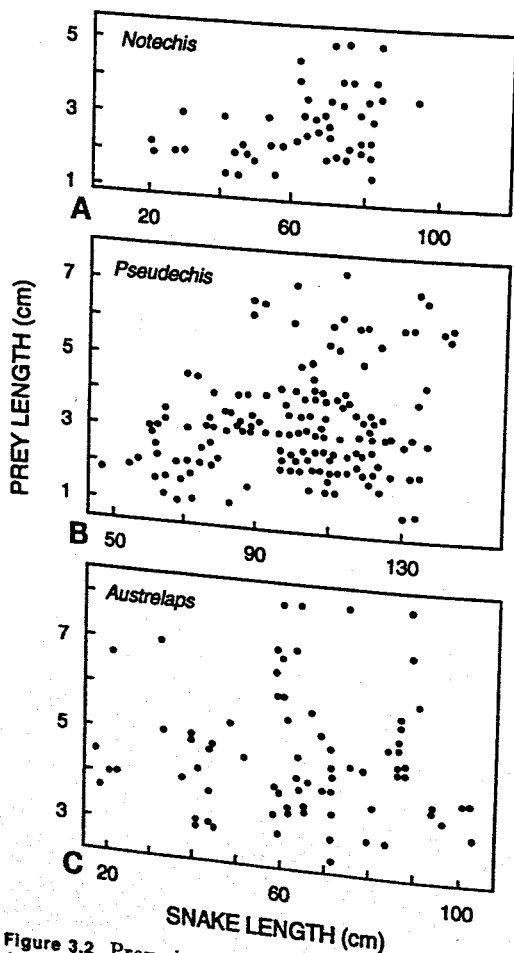


Figure 3.2 Prey-size–snake-size relationships in Australian elapids. (A) *Notechis scutatus* feeding on frogs ($n = 83$) (data from Shine, 1977). (B) *Pseudechis porphyriacus* feeding on frogs ($n = 198$) (data from Shine, 1977). (C) *Austrelaps* (three species) feeding on lizards ($n = 147$) (data from Shine, 1987).

plotted the cube root of prey mass against the cube root of snake mass for all three species (Fig. 3.3). This transformation should make variance about regression more homogeneous than on the original scale, but variances are still heterogeneous on the cube-root scale. It appears that larger specimens of *D. chloroticus* and *M. melanolomus* continue to eat small frogs (Fig. 3.3A,B). Larger specimens of the third species (*D. margaritiferus*), however, appear to drop small animals out of the diet (Fig. 3.3C). That trend is especially clear when prey length is plotted against snake head length (Fig. 3.3D).

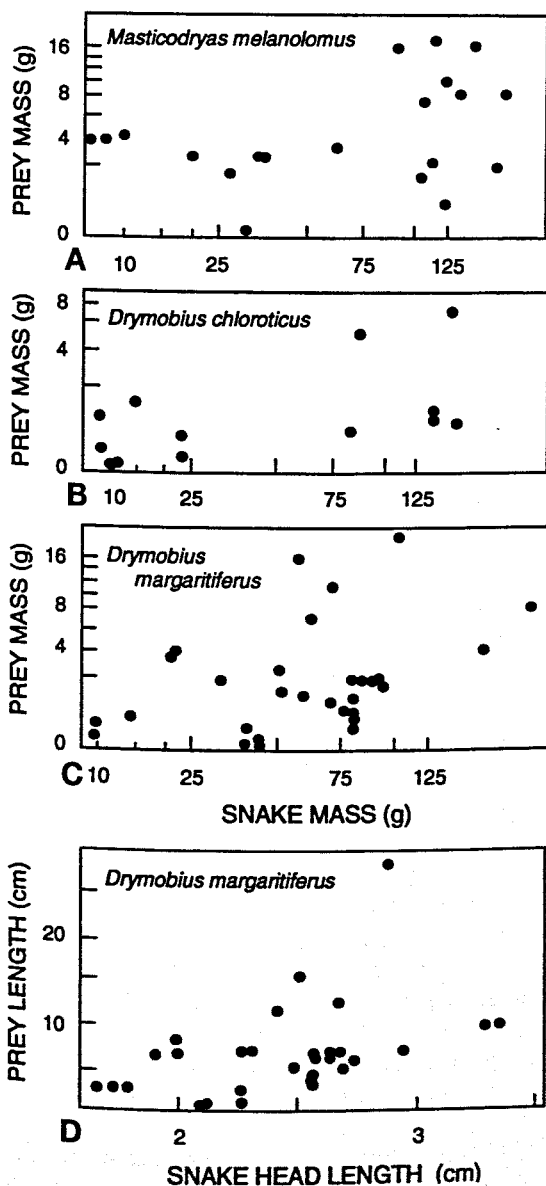


Figure 3.3 Prey-size—snake-size relationships in neotropical racers (data from Seib, 1984). (A) *Mastigodryas melanolomus* feeding on frogs, lizards, snakes, and mammals ($n = 20$). Cube-root scales on both axes. (B) *Drymobius chloroticus* feeding on frogs ($n = 13$). Cube-root scales on both axes. (C) *Drymobius margaritiferus* feeding on frogs and lizards ($n = 30$). Cube-root scales on both axes. (D) Same specimens as C. Linear scales on both axes.

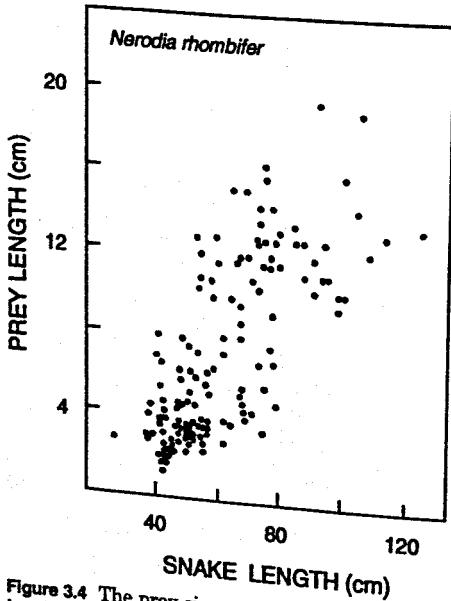


Figure 3.4 The prey-size-snake-size relationship in the Diamondback Water Snake (*Nerodia rhombifer*) ($N = 134$) feeding on fish ($n = 194$) (data from Plummer and Goy, 1984).

Plummer and Goy (1984) studied the diet of a large, freshwater natricine (*Nerodia rhombifer*) at a catfish hatchery. Channel Catfish (*Ictalurus punctatus*) dominated the diet, but Fathead Minnows (*Pimephales promelas*) and centrarchids were also eaten. A plot of fish length versus snake length (snout-vent length, SVL) shows a striking tendency for larger snakes to drop small fish from their diet (Fig. 3.4).

Godley et al. (1984) studied the diets of two crayfish-eating natricines (*Regina grahamii* and *R. septemvittata*). They found that crayfish gastroliths were a good predictor of crayfish size and used radiography of museum specimens of *Regina* to determine the gastrolith sizes of partially digested prey. Larger specimens of both species of *Regina* showed no tendency to drop small crayfish from the diet (Fig. 3.5).

Henderson et al. (1987, 1988) used museum specimens to study the diets of three species of semiarbooreal colubrids (*Uromacer*) in Hispaniola. *Uromacer frenatus* is a slender-bodied, sit-and-wait forager that feeds only on lizards. Larger individuals of *U. frenatus* add *Leiocephalus* and *Ameiva* to their diets but continue to eat small *Anolis* (Fig. 3.6).

Cobb (1989) studied the diet of the Flathead Snake (*Tantilla gracilis*), a small, secretive colubrid, in Texas. The diet was dominated by

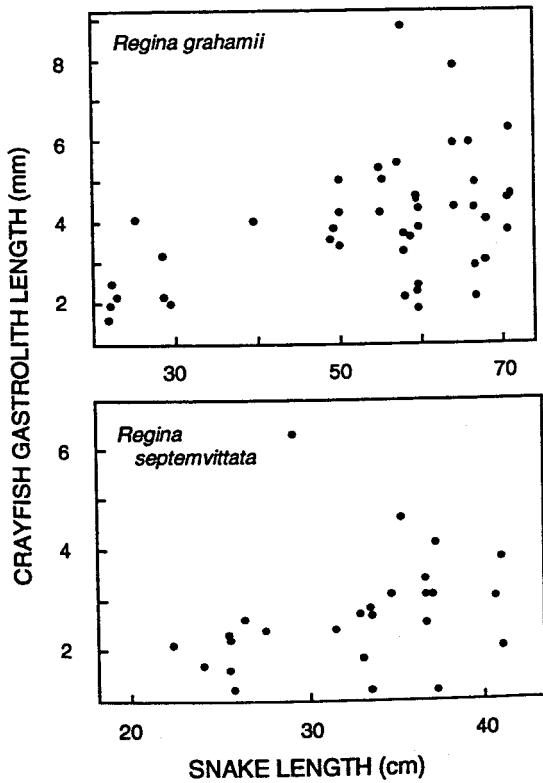


Figure 3.5 Prey-size–snake-size relationships in the crayfish specialists *Regina grahamii* ($N = 25$, $n = 44$) and *R. septemvittata* (N not reported, $n = 26$) (data from Godley et al., 1984). Crayfish body length is highly correlated with gastrolith length ($r = 0.94$).

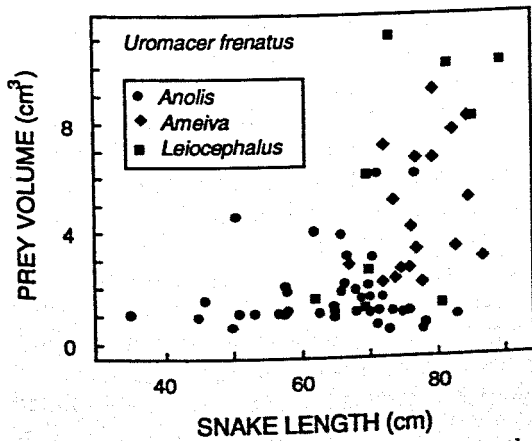


Figure 3.6 Prey-size–snake-size relationship in the Tree Snake *Uromacer frenatus* feeding on lizards ($n = 108$) (data from Henderson et al., 1987).

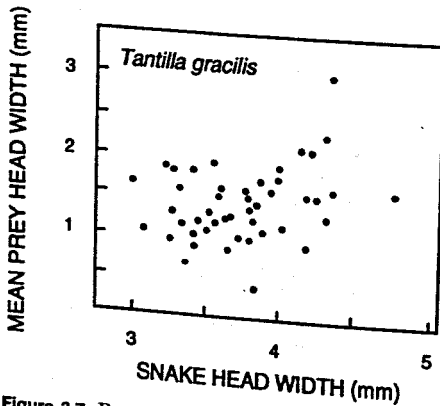


Figure 3.7 Prey-size-snake-size relationship in the colubrid snake, *Tantilla gracilis* ($N = 65$) feeding on arthropods and molluscs ($n = 158$) (data from Cobb, 1989).

beetle larvae (82% of items) and centipedes (11% of items). Diameters of snakes and their prey are compared in Fig. 3.7. Larger snakes take larger prey and appear to drop small prey from their diet.

Voris and Moffett (1981) studied the diet of Beaked Sea Snakes (*Enhydrina schistosa*) in Malaysia and produced an exemplary analysis of snake-size-prey-size relationships. One species of arid catfish (*Tachysurus maculatus*) dominated the diet of the sea snakes. The authors reconstructed the original size of partially digested fish using measurements of intact fins and regression equations. Three measures of fish size (diameter, length, and mass) were plotted against three comparable measures of snake size (Fig. 3.8). In all three plots it is apparent that small fish are missing from the diet of larger snakes. Notice that a log transform yields uniform variance about regression in the fish mass versus snake mass plot.

Jayne et al. (1988) studied the diet of the homalopsine snake *Cerberus rynchops* in mangrove habitat in a river mouth in Malaysia. The diet was exclusively fish and was dominated by four species of oxydercine gobies. The authors analyzed total mass of prey for each snake as a function of snake mass. A log-log transformation was used to make variance about regression uniform. The resulting plot (Fig. 3.9) indicates that larger snakes have a larger mass of prey in their stomachs. The plot also suggests that larger snakes drop small prey from their diets, but this needs to be confirmed by plotting the sizes of individual fish against snake size. Because Jayne et al. (1988) found that larger snakes showed no tendency to have more fish in their stomachs, a plot of individual fish as a function of snake size should look very much like Fig. 3.9.

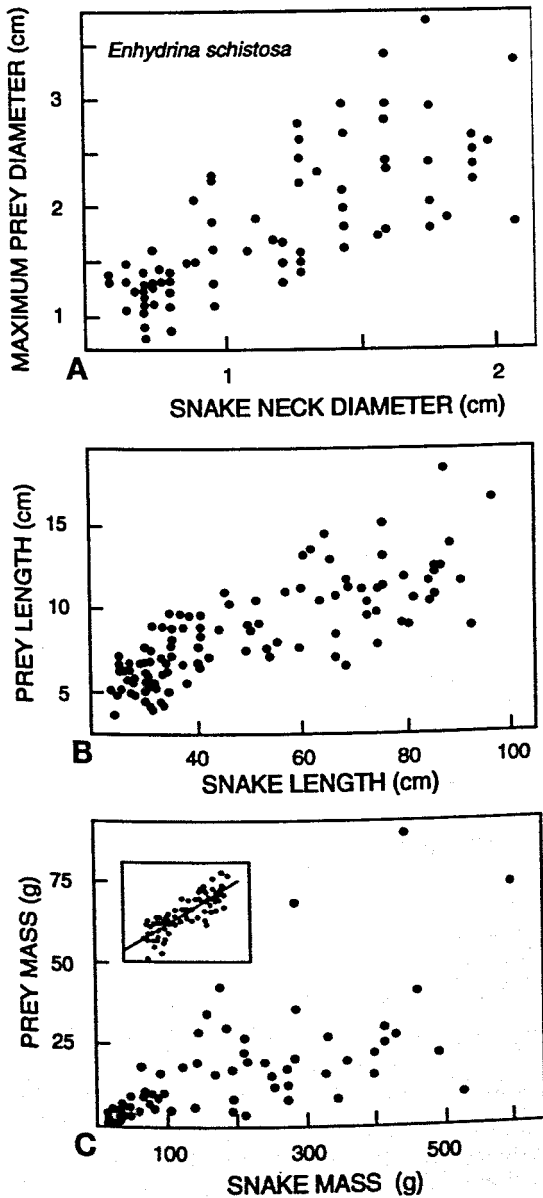


Figure 3.8 Prey-size-snake-size relationships in the Sea Snake *Enhydrina schistosa* feeding on catfish (data from Voris and Moffett, 1981). (A) Maximum prey diameter as a function of snake neck diameter ($N = 94$). (B) Prey length as a function of snake length ($N = 106$). (C) Prey mass as a function of snake mass ($N = 104$). Inset shows data after log-log transformation.

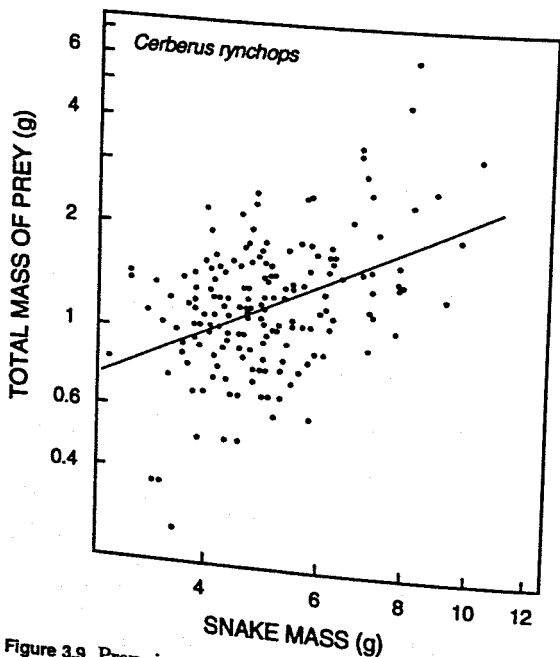


Figure 3.9 Prey-size-snake-size relationship in the homalopsine snake *Cerberus rynchops* ($N = 181$) feeding on fish (data from Jayne et al., 1988). Logarithmic scales on both axes.

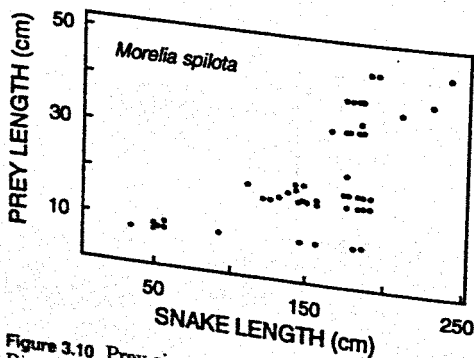


Figure 3.10 Prey-size-snake-size relationship in the Diamond Python *Morelia spilota* ($N = 49$, $n = 57$) feeding on rodents (data from Slip and Shine, 1988).

Slip and Shine (1988) found that Diamond Pythons (*Morelia spilota*) in Australia fed predominantly on mammals (mainly *Rattus*). A companion study of radiotelemetered snakes suggested that *M. spilota* is an ambush predator. Stomach analyses (Fig. 3.10) indicated that large snakes continued to eat small prey.

In summary, as most snake species grow larger they drop small prey from their diets. This deletion trend is apparent in all the studies just reviewed with the exception of Australian elapids (Shine, 1977, 1987), a boid (Slip and Shine, 1988), crayfish-eating natricines (Godley et al., 1984), and possibly some neotropical racers (Seib, 1984). A tendency for larger snakes to drop small kinds of prey from the diet has been noticed in a large number of studies in which snake size was measured but prey size was not (Fitch, 1963, 1965; Godley, 1980; Saint Girons, 1980; Mushinsky et al., 1982). In the next section we shall consider possible explanations for the prey-deletion phenomenon and how they might be tested. But before leaving empirical studies of snake-size-prey-size relations, let us consider some methodological issues.

It could be argued that larger snakes continue to eat small prey but the lower limit for prey size increases as a statistical artifact. William Magnusson (personal communication) has pointed out that if we plot the average prey size in each snake's stomach as a function of snake size, then we expect the lower limit for prey size to increase with snake size even if snakes continue to eat small prey. The reason for the illusion of prey deletion is that the variance of the mean decreases with sample size (Sokal and Rohlf, 1981, p. 183). If larger snakes have larger samples of prey in their stomachs, the lower limit of prey size might increase as a simple statistical consequence. This explanation, however, does not appear to apply to any of the studies reviewed above (with the possible exception of Cobb, 1989). Apparently, the data points in all the plots (except Cobb, 1989) represent individual prey items, not the averages of items in individual stomachs. In the study by Jayne et al. (1988) the total mass of stomach content was plotted against snake mass, but the authors also report that prey number is unrelated to snake size. Magnusson's interpretation should be considered, however, in future studies of prey-size-snake-size relations. Although visual inspection of a plot based on individual prey items is a good first start at determining whether the lower prey-size limit increases with snake size, such a plot is not the best form of data for describing the average relationship between prey size and snake size.

Perhaps the best procedure for estimating the regression slope relating prey size to snake size is to use the average prey size for each snake. This approach takes account of the likely possibility that the sizes of prey within each snake are correlated. In other words, the individual snake stomachs can be treated as independent data points even though all the individual prey items may not be independent data. One can account for the variation in number of items per stomach by using a weighted regression. Since the variance in mean prey size is inversely related to the number of items per stomach, a nat-

ural weighting scheme is to weight each snake stomach by the number of items it contains (Neter et al., 1990). Weighted regression is available in some computer packages (e.g., SAS™).

In all of the studies we have reviewed, variance in prey size increases with snake size. While biologically interesting, such inconsistency of variance violates a modeling assumption that is made for the purposes of testing the statistical significance of the regression slope. Transformations such as the log-log transform used by Voris and Moffett (1981) may make the variance about regression uniform and so render tests of significance more trustworthy. Another advantage of such log-log plots (known as allometric plots) is that scaling relationships can be easily interpreted from the regression coefficients (Schmidt-Nielsen, 1984).

The quantitative characterization of the lower or upper prey-size limit as a function of snake size is a difficult statistical problem. Voris and Moffett (1981) and Seib (1984) quantified the lower limit by using only the 10 or 11 prey items along the lower limit in a regression of prey size on snake size. The problem with this approach is that the decision of which points to include is arbitrary. Maller et al. (1983) discuss two other approaches that might be applicable to the problem. (I am grateful to W. Magnusson for this reference.)

Quantifying the prey-size-snake-size relationship from a field collection (Figs. 3.2 to 3.10) can tell us whether large snakes delete small prey from their diet but it cannot tell us why the deletion takes place. Once the field study has performed the important function of identifying which prey types of what size are deleted from the diets of which-sized snakes, we can use insights from foraging theory to formulate hypotheses that might answer the *why* question.

Why are small prey deleted from the diet of large snakes?—The conversion of worthy prey to worthless prey with increasing predator size. Schoener (1971) gives a useful model for the costs and benefits of foraging that can be modified to reflect snake biology. Let us recognize three possible outcomes for a snake that has encountered a prey item: (1) no capture but no ingestion (e.g., the prey escapes during the ingestion process); and (3) capture, ingestion, and digestion. These three outcomes are mutually exclusive and hold for each of the various prey types that the snake might encounter. To evaluate the economics of feeding on various types of prey we need to know the probabilities of the three outcomes for each prey type, as well as their costs and benefits. The three probabilities can be expressed usefully as functions of the probabilities of transition between the various possible events (Fig. 3.11). Thus, the probability of an outcome from a given encounter is the product of the various transition probabilities that lie along the relevant path in Fig. 3.11. For example, the probability that the snake

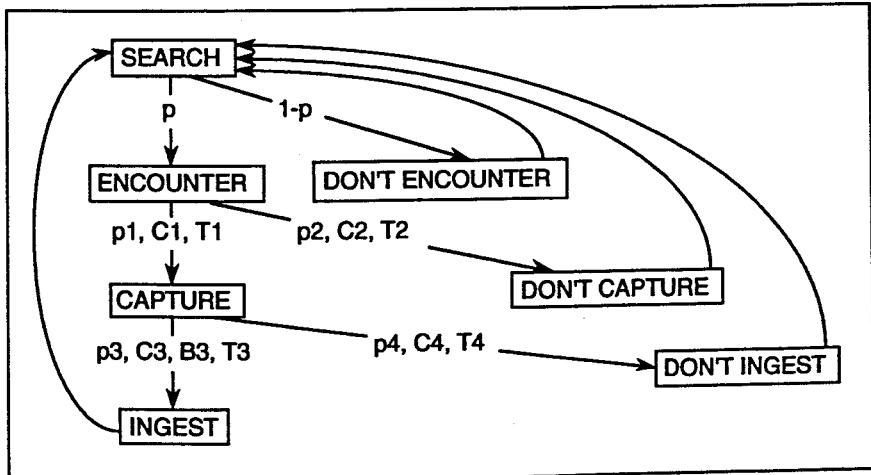


Figure 3.11 Foraging activities in the model and possible transitions between them. p and $p1-p4$ are transition probabilities. $C1-C5$ are energetic costs. $B3$ is benefit or energetic gain. $T1-T5$ are times spent in various activities.

will not capture the prey it has encountered is $p2$. The probability of encounter, capture, but failed ingestion is $p1 p4$. The probability of capture, ingestion, and digestion is $p1 p3$. These three probabilities correspond to the three possible outcomes given an encounter and so sum to one. Symbols for the benefits and costs of various transitions are also shown in Fig. 3.11. Only successful prey ingestion benefits the snake. Benefit is denoted $B3$ after capture in Fig. 3.11. All of the various events could incur costs in the form of energy expenditure and are denoted $C2$ for pursuit costs, etc. The various events could also incur costs in terms of time expenditure and these are denoted $T1, T2$, etc.

The ingredients just listed can be used to express the net energy expected from a particular prey type,

$$\begin{aligned}
 e_i &= [\text{expected energy gain from successful ingestion} = p1 p3 B3 \\
 &- \text{expected cost of successful prey pursuit} = p1 p3 C1 \\
 &- \text{expected cost of successful prey ingestion} = p1 p3 C3 \\
 &- \text{expected cost of prey digestion} = p1 p3 C5 \\
 &- \text{expected cost of failed capture attempts} = p2 C2 \\
 &- \text{expected cost of failed ingestion attempts} = p1 p4 C4].
 \end{aligned}
 \tag{1}$$

The first four terms (involving $B3, C1, C3$, and $C5$) represent the net benefit of a successful prey encounter that goes all the way to digestion. Similarly we can express the expected time devoted to pursuing, ingesting, and digesting the i th prey type as

$$\begin{aligned}
 t_i = & \text{[expected time spent in successful pursuit} = p_1 p_3 T_1 \\
 & + \text{expected time spent in successful ingestion} = p_1 p_3 T_3 \\
 & + \text{expected time spent in prey digestion} = p_1 p_3 T_5 \\
 & + \text{expected time spent in failed capture attempts} = p_2 T_2 \\
 & + \text{expected time spent in failed ingestion attempts} = p_1 p_4 T_4].
 \end{aligned} \tag{2}$$

All of the variables in the preceding expressions should carry an i subscript to indicate that they pertain to the i th prey type, but those subscripts have been left off for simplicity.

The ratio e_i/t_i represents the net energy expected per unit time from the i th prey item given encounter. This ratio can be used to rank all prey items on the basis of their profitability. Even with a ranking of all prey items, however, it would be hard to predict where the cutoff point should be. What is the least profitable prey type that should nevertheless be included in the diet? A useful mathematical approach is to cast the issue as a standard maximization problem. As Schoener (1971) put it, we need to choose a currency and an appropriate cost-benefit function and then solve for the maximum. We need a function that includes more than e_i and t_i for each prey type. In particular, we need to take the relative availability of prey into account and also the costs of prey search. The simplest way to incorporate search costs is to assume that the snake searches for all prey types simultaneously (i.e., that there are no special search costs associated with different prey types). Schoener (1971) proposed maximizing the following function:

$$\frac{\sum_{i=N_1}^{N_2} p_i(e_i) - C_s T_s}{\sum_{i=N_1}^{N_2} p_i(t_i) + T_s}, \tag{3}$$

where p_i is the probability of encountering the i th prey type, C_s is the cost per unit time of searching for prey, T_s is the expected time between prey encounters (whether or not they result in prey capture). Thus, $C_s T_s$ is the expected energy expended in prey search for each prey encountered. The numerator gives the expected net energy gain from search, pursuing, ingesting, and digesting all the prey types that are included in the diet. The denominator gives the expected time spent in these activities. We wish to maximize their ratio, which is the rate of energy gain for a particular diet. N_1 denotes the most prof-

itable prey type (i.e., the prey with the highest e_i/t_i). The maximization problem is to find the least profitable prey type (denoted N_2) that should be included in the diet.

Some insights can be gained without amassing all the relevant data needed to solve the diet optimization problem for a snake population. Many models of optimal foraging, including the present one, predict that a greater range of prey types should be taken when the overall food abundance is lower (longer T_s) (Schoener, 1971). Also, larger predators should take larger prey when one assumes exponential forms for handling and ingestion times (Schoener, 1971). Finally, some prey should be dropped from any diet because they are absolutely worthless or net the snake too small an energy gain. We can recognize a number of varieties of worthless prey using Eqs. (1)–(3).

Varieties of worthless prey

The first four varieties that we will consider are absolutely worthless. That is to say, the expected energy gain from these prey is zero or negative. On the average the snake gains nothing or actually loses energy in the process of hunting, pursuing, and trying to ingest these prey. In other words, Eq. (1) or the term that occurs in the numerator of Eq. (3) and pertains to a particular prey type is zero or negative.

Hard-to-find prey. Finding such prey involves a special and possibly costly search (large prey-specific $C_s T_s$ term). This search is special in the sense that the snake cannot search for or encounter other prey while looking or waiting for the prey in question (see Shine, 1991). Prey that occur only in localized habitats fall into this category. For this aspect of prey to raise the lower prey limit as snake size increases, larger snakes must incur larger search costs than small snakes.

For many fish-eating snakes an ontogenetic shift to larger fish may mean deleting small fish from the diet because large and small fish occupy different habitats. At Eagle Lake in northern California, for example, small minnows that are preyed on by juvenile Western Terrestrial Garter Snakes (*Thamnophis elegans*) are found most abundantly in shallow, warm water at the lake's edge. In contrast, larger minnows are found only in deeper water. Because adult snakes ambush and pursue large minnows at a depth of 1–2 m, they necessarily miss encounters with schools of small minnows.

Hard-to-catch prey. Such prey are unprofitable because they are likely to escape once encountered or because the cost of a failed capture

attempt is high (large p3 C1 or p2 C2). Elusive prey such as fish fall into the first category. Racers and other active pursuers (e.g., *Coluber*, *Masticophis*, *Psammophis*) may incur substantial costs in pursuing prey but we need actual data to test this possibility. An ontogenetic shift away from elusive prey could occur if large snakes are more inept at catching small prey than are small snakes or if large snakes incur greater costs.

Hard-to-eat prey. Such prey are unprofitable because ingestion is likely to be unsuccessful or costly (large p3 C3 or p4 C4). Anguid lizards, for example, can thwart snake predation by grasping some part of the snake's anatomy or even their own tail in their jaws (Fig. 3.12; Fitch, 1935). Slugs and salamanders can impede or even thwart ingestion with sticky secretions (Figs. 3.13, 3.14; Arnold, 1982). The most likely circumstance that could cause an ontogenetic shift away from such prey is if large snakes are more inept at prey handling than small snakes. Such a circumstance is not inconceivable, but it seems more likely that large snakes would be more capable of overwhelming the defenses of hard-to-eat prey than small snakes.

The analysis of trials involving hard-to-eat prey could be accomplished in the laboratory. Events leading up to prey encounter depend on a large number of special ecological circumstances, but predatory outcome after prey capture can be accurately scored and measured in the laboratory if a little care is taken. Special ecological factors that need to be controlled are the body temperatures of the snake and its prey, their psychological states, and perhaps the substrate (which might adhere to sticky prey). Arnold (1982) discusses scoring predatory outcome and statistical analysis. The anaerobic costs of prey handling can be assessed by dropping the snake into liquid nitrogen at the end of the encounter and later measuring its lactic acid content (Feder and Arnold, 1982). The aerobic costs of prey handling could be assessed by staging encounters in sealed containers and measuring oxygen consumption, as in the study by Pough and Andrews (1985) of the lizard *Chalcides ocellatus*.

Feder and Arnold (1982) used the liquid-nitrogen technique to stop the metabolic action after predatory encounters between Western Terrestrial Garter Snakes (*Thamnophis elegans*) and Woodland Salamanders (*Plethodon jordani*). Anaerobic costs were measured directly and other costs were estimated. The average time to ingest a salamander was 14.4 min. A typical 16-g snake that ingested a 2.2-g salamander with an energy content of about 2000 cal might expect to pay as much as 6.7 cal in aerobic metabolism and 2.4 cal in anaerobic metabolism during capture and ingestion plus another 6.1 cal to pay off the incurred oxygen debt and 260 cal in digestion costs. Thus, the

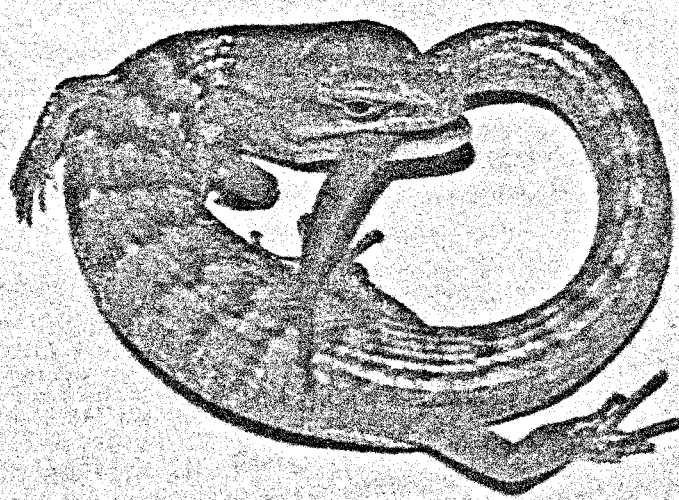
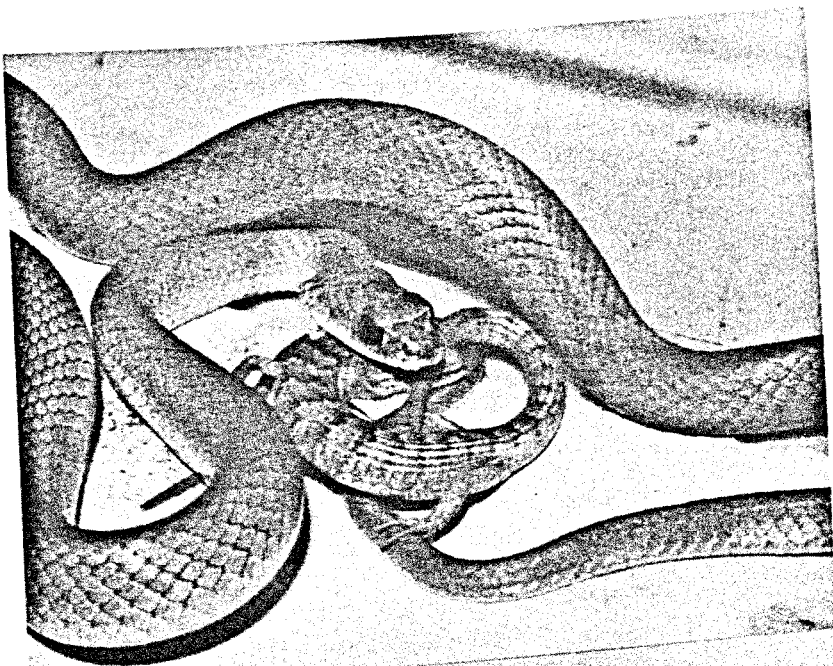


Figure 3.12 A Racer (*Coluber constrictor*) during an unsuccessful attempt to swallow an anguid lizard (*Gerrhonotus multicarinatus*) that thwarts ingestion by holding its tail in its mouth.

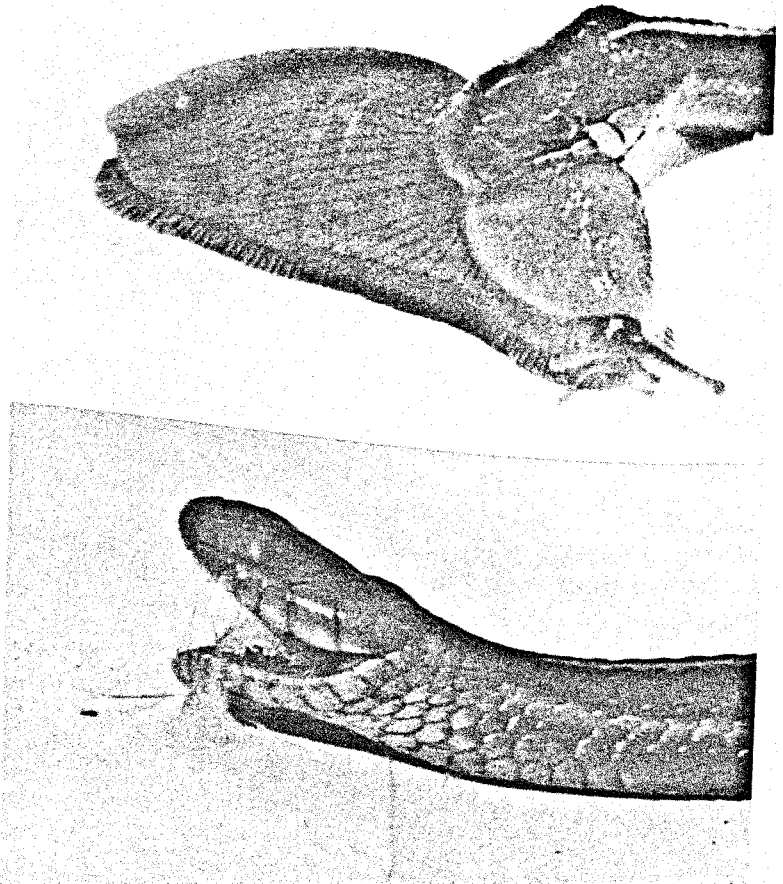


Figure 3.13 Predation by the Western Terrestrial Garter Snake (*Thamnophis elegans*) on the slug (*Ariolimax columbianus*). (A) The snake during attack on the slug. (B) After ingestion the snake's mouth is filled with slug mucus, which also causes the snake's head to adhere to the substrate.

total energetic costs of the encounter are no more than 15.2 cal, while the energetic content of the prey (subtracting digestion costs) is at least 1740 cal. Thus, the energetic cost of the encounter is less than 1% of the energy assimilated from the prey (Feder and Arnold, 1982).

We can use the preceding results to estimate how elusive salamanders would have to be for them to be deleted from the diet on energetic grounds. From our discussion so far we have $B3 = 2000, C1 + C3$

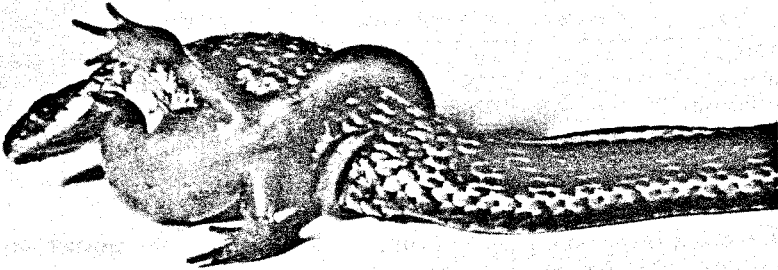


Figure 3.14 A plethodontid salamander (*Ensatina eschscholtzii*) thwarts ingestion by a Western Terrestrial Garter Snake (*Thamnophis elegans*) by wrapping its tail around the snake's neck. Sticky secretions have been released from the salamander's tail, causing it to adhere to the snake's neck.

= 15.2, and $C5 = 260$. Feder and Arnold (1982) found that salamanders escaped from snakes in 32% of encounters, so $p4 = 0.32$ and $p3 = 0.68$. Let us assume that the cost of a failed capture attempt is about 1% of the costs of successful capture and ingestion ($C2 = 2$) and that the cost of a failed ingestion attempt is about the same as the costs of successful capture and ingestion ($C4 = 15.2$). Using Eq. (1) we can solve for probability of successful capture given an encounter ($p1$) that will make net energy gain positive ($e_i > 0$). We find that even if only 1 in 1000 capture attempts is successful, salamanders should still be retained in the diet. In other words, salamanders would have to be so elusive that they escaped capture in more than 99.915% of encounters to be deleted from the diet. While it seems unlikely that salamanders could ever be this elusive, fish may very well have such high escape rates from snakes.

Low-energy prey. Such prey are unprofitable because even when ingestion is successful, net energy gain is small. In particular, the net gain may be small or negative when the usable energy content of the prey ($B3$) is low and/or the costs of capture, ingestion, and digestion ($C1-C5$) are high. Low-energy prey are candidates for ontogenetic shifts if large snakes experience larger capture, ingestion, or digestion costs, because those costs may overwhelm the possible energy gain from such prey.

Some snake prey have a relatively low-energy content. A slug with the same live weight as a mouse has only about one-quarter the energy content (Table 3.1). Adult *Thamnophis elegans* in at least some populations appear to drop slugs from their diet while adding

TABLE 3.1. Average Energy Content of Major Prey Categories (Data from Cummins and Wuycheck, 1971). Values Flagged with Asterisks Are Based on Small Samples

Prey	Ash-free dry weight, cal/g	Wet weight, cal/g
Mollusks	5492	480
Annelids	5628	782*
Arthropods	5673	2315*
Fishes	5296	1493*
Tetrapods	6542	1853

mice (C. R. Peterson, personal communication). An energetic comparison of slug and mouse predation in this snake species might be an informative exercise.

Marginal prey. The snake turns a profit from these prey but the gain rate (e_i/t_i) is so small relative to other prey types that the snake's overall energy budget is improved by dropping marginal prey from the diet. In contrast to the first four varieties of unprofitable prey, marginal prey are not absolutely worthless. The two important causes of marginal status are low net energy gain and large time expenditure. In the preceding categories we discussed the energetic aspect of predation but not time expenditure. When search, capture, or ingestion are energetically costly they are likely to be time consuming as well. Time spent in these activities cannot be spent in predation on more profitable prey, in thermoregulation, in mating, or in other activities. Perhaps more importantly, time spent in predatory activities exposes the snake to predation. At present we do not know whether exposure to predation constitutes a sizable hazard. Brodie's (1993) recent work with snake models, however, provides a field protocol for measuring at least part of the hazard. It may be that predatory costs are so trivial [as Feder and Arnold's (1982) results suggest] that time is the informative currency for evaluating the economics of snake predation.

Pough and Groves (1983) measured swallowing time in a series of trials in which snake size and prey size were varied systematically. These authors used number of maxillary protractions as an index of handling time because that index was not sensitive to disturbance of the snake. During feeding trials the authors noted that snakes would sometimes cease all swallowing movements for several minutes. If such bouts of inactivity are not induced by human interference, they should be included in swallowing time if the aim is to pursue an energetic model of the type specified in Eq. (3). Nevertheless, it is interesting to note that the number of maxillary protractions shows a linear relationship to prey size over a more than fivefold range in prey diameter (Fig. 3.15A).

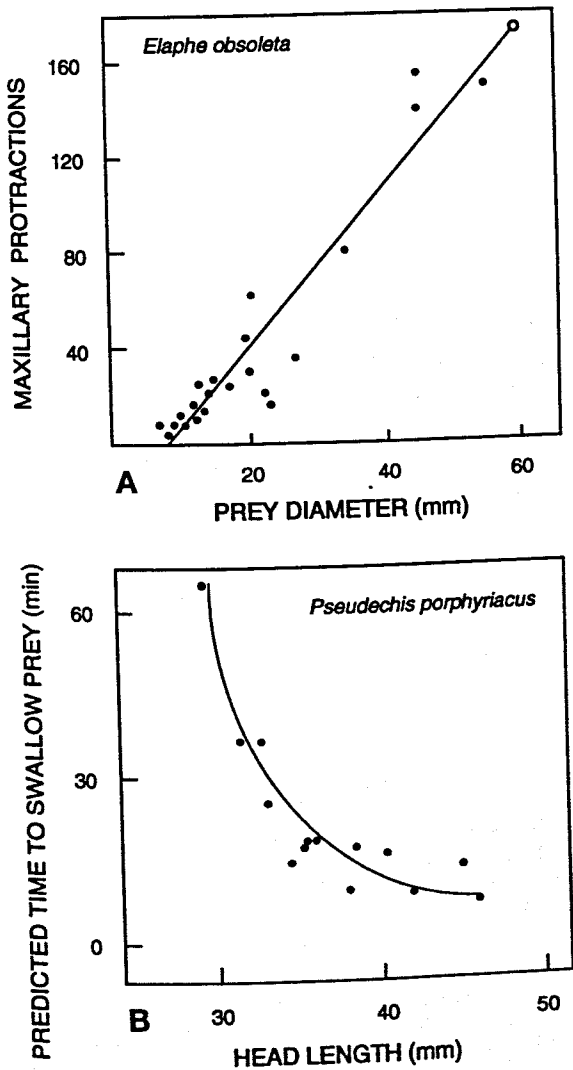


Figure 3.15 Swallowing time as a function of prey size and snake size. (A) An individual Rat Snake (*Elaphe obsoleta*) feeding on rodents (data from Pough and Groves, 1983). Swallowing time is measured as the number of maxillary protractions during ingestion. Solid circles denote successful ingestion of prey. The single unsuccessful ingestion attempt is shown with an open circle. (B) Predicted time to swallow a 50-g mouse as a function of snake head length in Black Snakes (*Pseudechis porphyriacus*) (data from Shine, 1991). Curve was fitted by eye.

Jayne et al. (1988) measured handling times for the homalopsine snake *Cerberus rynchops* feeding on live fish (*Periophthalmus chrysopilus*). These workers recognized three phases of prey handling: (1) an initial quiescent phase (during which the motionless snake holds the fish in its mouth); (2) positioning time (the time from the onset of jaw-walking until the snake positions the fish's snout in its mouth); and (3) swallowing time. Fish size and snake size were significant predictors of the durations of all three phases of prey handling as well as total handling time (in all cases larger fish increased handling durations and larger snakes decreased handling times). The duration of fish struggling affected only the duration of the initial quiescent phase, while the initial position where the fish was seized affected only the duration of the positioning phase.

Shine (1991) conducted a particularly illuminating study of ingestion times in Black Snakes (*Pseudechis porphyriacus*) and Diamond

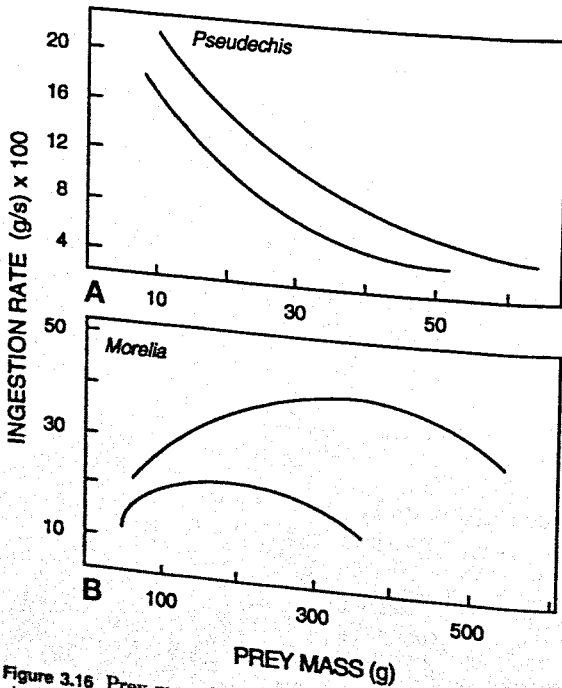


Figure 3.16 Prey mass ingestion rates as a function of prey size for individual Black Snakes (*Pseudechis porphyriacus*) and Diamond Pythons (*Morelia spilota*). Curves were fitted by eye to the data of Shine (1991). (A) Ingestion curves for two individual Black Snakes. (B) Ingestion curves for two individual pythons.

Pythons (*Morelia spilota*) handling dead mice and rats. In both species ingestion times increased with prey size and decreased with snake size (Fig. 3.15B). Shine's most surprising result was that the ratio of prey mass to ingestion time for individual snakes declined steadily with increasing prey mass in *Pseudechis* but showed an intermediate peak in *Morelia* (Fig. 3.16). Thus, individual Diamond Pythons were relatively inefficient when ingesting both very large and very small prey.

One of the many unresolved issues involving swallowing time is snake performance in the vicinity of the breaking point. Arnold (1982) defined the breaking point as the smallest size of prey that the snake is incapable of ingesting. For example, Pough and Grove's (1983) results for a Rat Snake (Fig. 3.15A) suggest that its breaking point is in the vicinity of 55–60 mm prey diameter, although more trials with prey 55 mm and larger would be required to establish this. Does swallowing time increase disproportionately fast as the breaking point is approached? Shine's (1991) results for Black Snakes (*Pseudechis porphyriacus*) suggest that swallowing time increases exponentially as the breaking point is approached (Fig. 3.15B).

Behavioral Basis of Ontogenetic Shifts in Diet

We can imagine that an ontogenetic diet shift simply reflects the experience and changing fortunes of the growing snake. Such a purely ecological perspective on diet shifts is challenged by an important study conducted by Mushinsky and Lotz (1980). By rearing Water Snakes (*Nerodia*) on specified diets and periodically testing their chemoreceptive responses to various prey, Mushinsky and Lotz were able to show that the intrinsic perceptual program of at least one species shows an interesting maturational change. Young *N. erythrogaster* show a strong tongue-flicking reaction to fish odor that persists for several months whether the snakes are reared on fish or frogs. At 8–9 months of age *N. erythrogaster* show a strong reaction to frog odor, regardless of their rearing diet. In particular, even snakes reared on fish show a strong reaction to frog odor at 8–9 months. Analysis of stomach contents indicates that *N. erythrogaster* show an ontogenetic diet shift from fish to frogs (Mushinsky et al., 1982). Mushinsky and Lotz's (1980) results indicate that an intrinsic maturational change is the proximate factor determining the diet change in the field. Of the many species that show ontogenetic shifts in diet, *N. erythrogaster* and *N. fasciata* are apparently the only species in which maturational reactions to prey have been studied.

Summary and Future Research

In the last decade a number of snake ecologists have succeeded in quantifying the relationship between prey size and snake size in a number of snake species. Although the number of studies is too few to reveal broad ecological or phylogenetic patterns, several trends stand out. Larger snakes tend to eat larger prey species. More specifically, larger snakes take larger individual prey items, and they often add larger prey species to their diet. The range and variance in prey size also increase with snake size. An enigmatic result is that in many snake species larger individuals drop small prey items from the diet. To date this trend seems characteristic of fish-eating snakes.

Foraging theory can be used to erect hypotheses to explain why the lower prey-size limit increases as a function of snake size. To test these hypotheses we will need to measure the costs and benefit of prey pursuit, capture, and ingestion, while varying both prey size and snake size. Various experimental studies with lizards (DeMarco et al., 1985; Pough and Andrews, 1985) and snakes illustrate how particular aspects of such a program could be tackled. What is particularly needed is an allometric approach to snake-feeding performance and predatory costs that is firmly rooted in field results. In particular, field studies of diet could be used to identify the prey types and sizes to manipulate in the laboratory (Jayne et al., 1988; Shine, 1991).

The behavioral basis of ontogenetic diet shift is another potentially important but neglected topic. One pathbreaking study illustrates how to combine experimental and observational approaches.

Acknowledgments

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