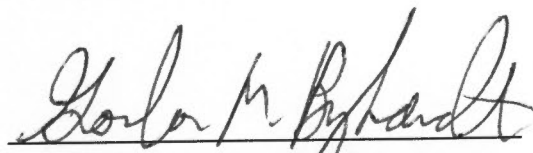
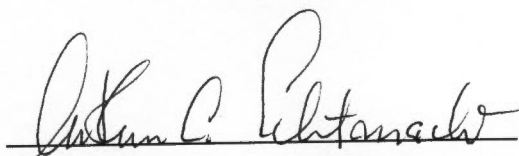


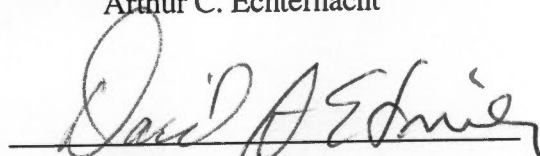
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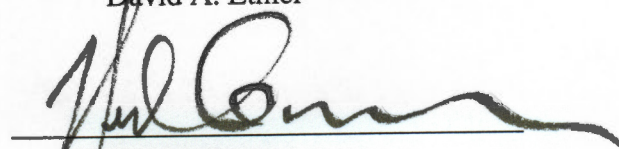
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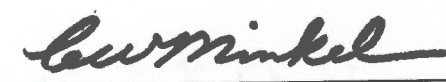
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CONTROL OF FOOD INTAKE AND EXPRESSION OF HUNGER
IN THE NORTHERN WATER SNAKE, Nerodia sipedon (L.)

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Paul Timothy Andreadis
December 1998

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DEDICATION

This work is dedicated to Roger H. Peterson,
my first and best teacher of natural history.
Perhaps it was no coincidence that I ended up
doing my dissertation "down in Tennessee."

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Every Acknowledgements section which I have ever read mentions persons too numerous to thank. Viewing this as an unqualified cop-out, I intend to thank everyone who has aided my intellectual growth, or otherwise helped me to get to where I am. In chronological order, more or less:

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ABSTRACT

Most of what is known about the control and expression of appetite comes from studies of laboratory rodents. Such animals, which take small, frequent meals, are located at one end of a spectrum of feeding frequencies. The theme of the present work was to explore appetite in an animal that takes relatively large meals at long intervals. I studied some of the factors that control food intake and influence the expression of hunger in Northern water snakes, Nerodia sipedon; Serpentes: Colubridae). Subjects were collected in streams in eastern Tennessee, especially the Little River in Blount County.

In order to establish criteria for satiety, I examined feeding in single meal sessions. After ingesting a large prey item, Northern water snakes exhibit a behavioral satiety sequence that closely resembles that in mammals: feeding is followed by grooming, then locomotory activity, and finally, by resting. However, satiety sequences were qualitatively similar after meals of 10 and 30% of snake mass. Because of ambiguity in interpreting this sequence, a temporal criterion derived from satiation curves was used to establish satiety.

Neonate water snakes eat much smaller meals when offered an excess of small prey than when offered a single large prey. At prey sizes from 5-20% of body mass, meal size of neonates was 23.5% (average of 6 litter means). In contrast, neonates can readily ingest single prey equal to 40% of their mass, and sometimes as large as 55%. Thus, the largest meal that these snakes can take is a single, maximal item. Since snakes exhibited this response in their first feeding, the response is unlearned.

Because snakes are competent foragers over a large range of body sizes, they are ideal models for investigating ingestive allometry. When prey size (in %) is held constant, the meal size of hungry water snakes scales as an isometric function of body mass (log-log slope=0.97). Over a body mass range of 2.5-449.0 g, meal size averaged 22.4% of body mass.

An ad libitum feeding study was conducted with four Northern water snakes (mean mass=70 g) offered live minnows (mean mass=2 g). All feeding events were recorded with time lapse video. On this ration, snakes converted 24% of ingested mass into body tissue. Log survivorship analysis indicated that these snakes fed prandially, i.e. in temporally discreet meals. Median meal sizes were 2.7-6.0% of initial snake mass. Snakes typically took much smaller meals (44-71% of meals consisting of one fish) than their maxima (4-17 fish). Median intermeal intervals were 22.7-32.8 h, and the shedding cycle did not appear to affect the timing of meal taking. Intermeal intervals of approximately one and two days were prevalent, with the likely cause being a strong diel cyclicity. Feeding was significantly nocturnal, and more specifically, crepuscular (19-78% of meals initiated during first hour of darkness). Most meal pattern correlations were not significant.

Using the method of Diana (1979), I estimated the feeding frequency of adult female Northern water snakes in the field. The time needed at 26 °C to complete gastric digestion of a prey of typical size was 49 h. The proportion of adult females with food was 18/34, or 52.9% . I estimated that adult female water snakes feed, on average, once every 3.9 d (95% discrimination interval=2.9-5.0 d).

Given the importance of timing factors, I investigated the influence

of the lunar cycle on snake foraging activity in the field. I conducted field censuses along a standardized transect in the Little River . There was a significant positive correlation between number of snakes seen and water temperature. After accounting for thermal differences, I found a significant effect of lunar phase on snake foraging activity. More snakes were seen during phases when the moon was dark in the early evening. Predation both by and upon the snakes may be relevant to understanding this phenomenon. Changes in the timing of lunar ascent/descent may be an important part of lunar rhythmicity in addition to changes in illumination.

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Northern water snake (Nerodia sipedon)
swallowing a banded sculpin (Cottus carolinae),
Little River at Peery's Mill, Blount Co., TN.

CHAPTER I

INTRODUCTION

A. The value of comparative study.

The control and expression of hunger have generally not been studied from a comparative perspective. Most of our knowledge of the proximal control and behavioral correlates of appetite has come from the detailed study of a few species. Much taxonomic territory lies between the only two thoroughly studied taxa: the Blowfly, Phormia regina (summarized in Dethier, 1976), and the domestic Norway rat, Rattus norvegicus (summarized in Le Magnen, 1985). Differences in the internal mechanisms controlling feeding in these taxa have been noted, such as the greater complexity and redundancy of controls in rats (Grier and Burk 1992). However, in terms of the feeding performance of the whole animal, and in the categories of inputs that are important, students of appetite have emphasized that flies and rats function quite similarly. Thus, in comparing the control and expression of feeding behavior in rats and flies, Dethier (1976) noted mainly similarities. Both respond to food deprivation with increased appetitive searching, the appetites of both are responsive to peripheral and central nervous stimulation, both have analogous autonomic endocrine systems that can influence feeding, and both have satiety mechanisms to prevent overconsumption (see also Bolles 1980). Even with regard to motivation, a psychological concept that has historically been treated mainly in highly encephalized, vertebrate animals, Dethier downplayed differences. He discussed (Dethier 1981) the supporting

evidence for, and lack of contrary evidence against, invertebrates possessing such hallmarks of motivated behavior as expectancy and overt expression of affect (emotion). The importance of associative learning in rat feeding behavior was the greatest point of divergence. Dethier narrowed that distinction by closing with the observation that some insects (e.g. honeybees) could indeed be conditioned. It has more recently been claimed that even blowflies can be classically conditioned (Zawistowski and Hirsch 1986, Ricker et al. 1987).

Dethier's comparison suggests that the general characteristics of feeding behavior bridge vast phylogenetic distances. This view recalls the traditional psychological approach to animal behavior, namely, that general principles governing all behavior are revealed by careful experimentation on a single, tractable laboratory subject such as the rat. Truly comparative studies might, thus, be construed as unnecessary. However, the comparative approach has been and continues to be a useful tool in organismal biology (Burghardt and Gittleman 1990, Brooks and McLennan 1991, Harvey and Pagel 1991). The generalities of Dethier notwithstanding, a comparative scope has great potential to inform the study of food intake. The diversity of animal feeding ecologies, even when considering only quantitative aspects of ingestion, promises to both test the generality of existing ideas, and to reveal unrecognized phenomena. A brief review of variations in feeding ecology can serve to introduce this discussion.

The most basic characteristic responsible for variations in feeding ecology is undoubtedly body size, the influence of which extends to all aspects of an animal's biology (Peters 1983, Calder 1984, Schmidt-Nielsen

1984). Both prey size and rate of food intake show strong scaling effects (Peters 1983, Vezina 1985). The characteristics of the diet and the means by which it is procured comprise another important source of variation in feeding ecologies. Jørgensen (1982) outlined a taxonomy of feeding ecologies. One dimension of the classification is diet type in terms of macronutrient content, e.g. detritivory, herbivory, omnivory, and carnivory. In a quantitative sense, these dietary types can be identified as points on a continuum of digestibility and availability. Animal tissue is a readily assimilable and distributionally clumped food source with a relatively low biomass, while plant food provides a large standing crop of more uniform distribution and low digestibility. Feeding types can further be subdivided as to ingestion mechanism: fluid/suspension feeding, microphagy, and macrophagy (Jørgensen 1982). This distinction is essentially a spectrum of food particle sizes. Correlated with this dimension, but probably deserving of its own axis, is the temporal distribution of food intake. Animal feeding frequencies can be placed on a broad spectrum ranging from continuous to intermittent (Rozin 1964). Fábry (1969) incorporated this idea in his studies of physiological adaptation (i.e. acclimation) to different feeding frequencies. He noted (op. cit., p. 104) that the responses of various species to a given feeding schedule depended on "how and to what extent the experimental regimen differs from the specifically and oecologically conditioned normal regimen of the animal."

Many of the variations in animal feeding ecology can be reduced to the two basic questions of "How much?" and "How often?" As such, they can be depicted as a series of quantitative axes. My conception of this

feeding ecology hyperspace is depicted in Figure I-1. The axes are (1) body size, (2) feeding frequency, and (3) amount ingested per feeding. The interpretations of axes 2 and 3 are somewhat variable, depending on whether or not feeding consists of bouts of ingestion of multiple items. In the easiest case, the animal in question is a carnivore that consumes a single prey item in its entirety during each feeding episode. For this example, axis 3 is thus equivalent to prey size, and axis 2 is unambiguous. If, however, typical feedings consist of multiple prey, such as an anteater taking a meal of thousands of termites, then axis 3 might be more meaningfully considered as total meal size. Axis 2 would then refer to bout frequency, not the frequency with which individual termites are consumed within a bout of feeding. In general, herbivory would also be described by the second example, with individual bites of foliage being the analog of individual termites. Before leaving this topic, I should emphasize that I do not think that variation in prey size is unimportant. One could scarcely

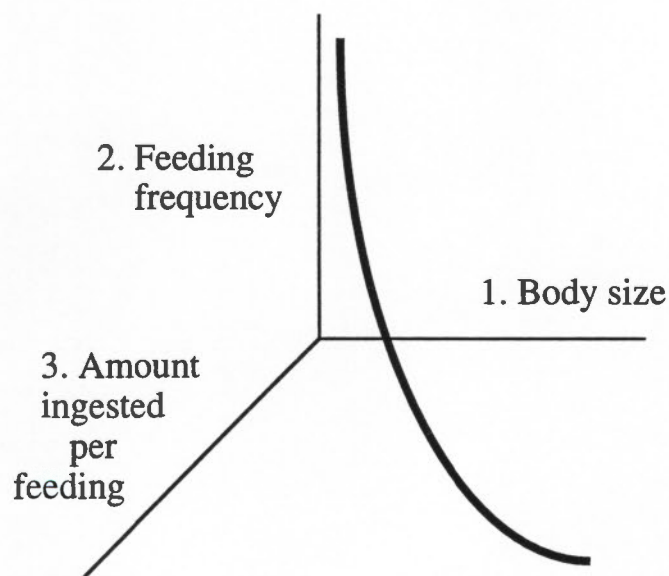


Fig. I-1. A three dimensional quantification of feeding ecology.

deny that the difference in prey sizes of giant anteaters and jaguars has important correlates and consequences for appetite control. For simplicity, however, I do not extend the hyperspace beyond three dimensions here.

Over a broad range of body sizes, these axes are correlated with each other such that they may be considered a one dimensional spectrum of feeding ecologies. Assuming that standard scaling principles apply (see Peters 1983, Calder 1984, Schmidt-Nielsen 1984), amount ingested per feeding would scale positively with body size, while feeding frequency (i.e. bouts per unit time) would scale negatively with body size. The raw variables would be power functions of one another, with the single function correlating all three being linear if logarithmic axes are used. This multiple correlation should not be taken to mean that there is no residual scatter about the axis. Indeed, variations in feeding amounts and frequencies at a given body size may provide some of the most interesting objects of comparative study. For example, Peters (1983) used the scaling of prey size and long term rate of food intake to estimate feeding frequencies for four classes of predators: large-prey eating homeotherms, large-prey eating poikilotherms, small-prey eating homeotherms, and small-prey eating poikilotherms. At a given body size, estimated predation frequency (number of kills per day) varied by as much as a thousand fold between these four classes. Such variation is exactly the sort that we might expect to lead to unique features in how appetite is controlled and expressed.

To what extent do variations in "How much?" and "How often?" entail differences in the control mechanisms of food intake? Are the behavioral expressions of hunger universal among animals with diverse

trophic lifestyles? The answers to these questions require a comparative database which is still lacking, in spite of early attempts (e.g. Rozin 1964) to summarize and stimulate study of animals with diverse trophic lifestyles.

The utility of a comparative perspective is seen in the phenomenon of postfasting food compensation. After having been deprived of food, many animals eat at accelerated rates once food is available. In the face of privational challenge, this behavioral and physiological compensation serves to reverse the negative deviation from the animal's typical energy budget. Given a finite and unpredictable environment, such hyperphagia would seem to be a homeostatic and universally adaptive trait for any animal. Surprisingly, while several rodent species do exhibit postfasting food compensation (Mrosovsky 1964, Hamilton 1969, Kutscher 1969), one does not. Kutscher (1969) reported that the food intake of Golden hamsters (Mesocricetus auratus) given access to food for two hours per day was only 10-15% of that when they were fed ad libitum. Kutscher found that Norway rats, in contrast, could readily adapt to ingesting their entire 24 h ad libitum intake in two hours. Silverman and Zucker (1976) subsequently confirmed that Golden hamsters did not show a compensatory adjustment in food intake after deprivation. After 24 h without food, refed hamsters ate at the same rate as they did when they had ad libitum access. Continued maintenance on a schedule of alternate days of feeding and fasting led to pronounced weight loss and eventual death of the deprived subjects. While the reasons for this unusual pattern remain unclear, Silverman and Zucker suggested that the ultimate explanation might lie in food storing behavior. Hamsters are prodigious food hoarders. Given a constant, nonlimiting food supply in the form of their larder, hamsters may

have experienced relaxed selection for ingestive compensatory mechanisms. Ecologically, they may never experience food deprivation in the wild. After the initial descriptions of these unique attributes, a series of investigations of hamster appetite physiology followed (Ritter and Balch 1978, Borer et al. 1979, Lowy and Yim 1982, Rowland 1982, Angel and Taranger 1991, Mercer et al. 1996). Some of these studies found Golden hamsters to be useful animal models for human appetite dysfunctions, i.e. anorexia nervosa and its attendant weight loss. Kutscher's (1969) original report initiated a body of clinical work on appetite and body weight regulation that can best be researched with hamsters.

B. Snakes as trophic extremes.

If variation in feeding ecology can yield insight into the proximal control of food intake, what variations are biologically interesting? In his past presidential address to the American Society of Zoologists, George Bartholomew (1982) discussed scientific innovation and creativity. Among various prescriptions for enhancing scientific creativity, Bartholomew advised researchers to study nonstandard organisms and, particularly, those displaying extremes of evolutionary adaptation. Golden hamsters fit the description of such an extreme, and studies of their food intake have indeed provided novel insight. In the context of appetite research, what animals represent a Bartholomaic ideal?

Among vertebrates, snakes represent such a trophic extreme, occupying one end of the prey size/feeding frequency spectrum. The evolutionary history of snakes has entailed a shift from the saurian condition of frequent feeding on small, arthropod prey (Pough 1980,

Greene 1982) to taking relatively large prey at infrequent intervals (Greene 1983). The consequences of this shift are evident in all aspects of snake trophic biology. Snakes have pronounced morphological adaptations for ingestion of large prey (Gans 1961, Cundall 1987). Historically, studies of snake trophic biology have focused on describing these anatomical features (e.g. Gans 1952, Haas 1952, Dullemeijer 1956, Albright and Nelson 1959a,b, Bolt and Ewer 1964, Frazzetta 1966). Later work involved other disciplines, notably physiology, ethology, ecology, and evolutionary biology (Burghardt 1970, Ruben 1977a,b, 1979, 1983, Greene and Burghardt 1978, Savitzky 1980). An American Society of Zoologists symposium in 1983 on snake feeding adaptations (see Pough 1983b), and a review of foraging ecology (Mushinsky 1987) summarized the most recent developments in snake trophic biology, including behavioral studies of the ontogeny and genetics of prey preference, and ecological work on niche partitioning.

Despite the widespread recognition of snake feeding ecology as trophically extreme, food intake and related phenomena are poorly known. Lists of prey species are not lacking in the herpetological literature (summary in Mushinsky 1987). However, little information exists with which to address the "How much?" or "How often?" questions of food intake research. Greene (1986) lamented the paucity of diet studies that even report relative prey size (RPS; = ratio of prey mass to predator mass), an appropriate parameter in dietary studies, and one with obvious relevance to studies of appetite. A few researchers have estimated long term rates of food intake in the wild (Fitch 1982, Godley 1980). However, the mechanisms and manifestations of appetite remain largely unstudied.

Only one study has addressed the proximal control of food intake in snakes. Myer and Kowell (1971) examined feeding patterns of four Florida kingsnakes, Lampropeltis getula floridana, under laboratory conditions of ad libitum food availability. A perfect example of Batholomew's advice to study nonstandard animals, Myer and Kowell observed the responses of snakes to conditions that had previously only been applied to standard laboratory animals. Once per day, snakes were offered live mice and allowed to feed till satiated. Myer and Kowell reported that snakes generally ate 3-4 mice per meal (range 1-10), taking meals every 4-6 days (range 1-15). These snakes were, thus, feeding prandially, i.e. taking temporally discrete, satiating meals.

What is perhaps most unexpected about this finding is the fact that Myer and Kowell's subjects were not taking small meals (i.e. a single mouse). Rather, snakes tended to defer feedings, at which times a larger meal was accommodated. In his extensive review of predation, Curio (1976) indicated that most ectothermic animals do not display such a feeding pattern. Rather, after an initial tanking-up when food is first made available, most ectotherms thereafter take small meals at short intervals. The pattern Curio described is suggestive of a system in which rate of gastric evacuation largely determines food intake. As soon as space for a single prey is created in the stomach, the predator eats a new item. However, the animals that Curio had in mind when he characterized the ectotherm feeding pattern are considerably more microphagous than snakes. Curio (1976) drew heavily from the work of Tugendhardt (1960) and Beukema (1968) on Three spined sticklebacks (Gasterosteus aculeatus). These fish were fed Tubifex worms which averaged about 0.3 % of fish

mass each. To achieve the average daily intake of about 12% of their mass, sticklebacks would thus consume about 36 worms. In contrast, some snakes can ingest single prey equaling 35-40 % of their mass (Pough and Groves 1983), with a maximum ingested prey size of 160% of snake mass reported for one pit viper (Greene 1992). The prey of a small colubrid (Diadophis punctatus; mean mass = 4 g) and a larger viperid (Agkistrodon contortrix; mean mass = 108 g) averaged 12.0% and 18.5% of snake mass, respectively (Fitch 1982). Curio's generalizations about "the" ectotherm feeding pattern may not apply to ectotherms adapted for macrophagy.

In addition to their uniqueness as trophic extremes, snakes offer several advantages to the study of food intake. Since the vast majority of appetite research is directed at understanding human nutrition and ingestive disorders, most of the animal species used are omnivorous. Omnivore diets are extremely varied in nutrient content, obliging the researcher to incorporate the influences of particular foods, e.g. nutrient-specific appetites and satieties (Le Magnen 1985). The phenomenon of desatiation in rats is one example. Having fed to satiation on a glucose solution, rats trained to expect a feeding at the time of day that followed the glucose test would avidly eat a second, full sized meal if any food other than glucose solution was provided (review in Mook 1990). This phenomenon may be a characteristic primarily of omnivores and euryphagous predators. Dietary variations thus make the study of ingestion in omnivores fascinating, complex, and logistically difficult. The diets of carnivores, in contrast, are much less variable in nutrient quality, thereby reducing the number of variables that need to be controlled. All snakes are carnivorous, with the majority of species specializing on some restricted set of vertebrate prey

(Mushinsky 1987). The availability of an acceptable prey species assures that a nutritionally complete diet is being provided, and allows the researcher to focus on quantitative aspects of food intake. In their treatment of comparative studies of food intake, Hainsworth and Wolf (1990) largely restricted their discussion to nectarivorous birds and insects. The one-dimensionality of the diet makes these systems logistically tractable and amenable to experimentation.

A second advantage to using snakes is that they, like all nonavian reptiles, are competent foragers and feeders shortly after hatching/birth. Unlike those species with postparturient/posthatching parental care, the food intake characteristics of snakes are unaffected by learning from their parents. Indeed, the first feeding actions of neonate reptiles may not be affected by learning from any source. This facet of snake biology led to the demonstration that the characteristic diets of several colubrid snake species are evolved, innate traits, being correctly predicted by the response pattern of neonates to chemicals from arrays of potential prey (Burghardt 1966, 1970). The use of ingestively naive subjects is a powerful tool in ingestion research, as one school of thought argues forcefully that appetite and food intake are primarily learned phenomena (Weingarten 1985, Booth 1980, 1987). The main research program exploiting this paradigm in standard laboratory animals studies is study of the early ontogeny of ingestion in newborn rat pups (Phifer and Hall 1987, Hall 1990).

One of the principal themes developed by Rozin (1964) was that the feeding behavior of poikilotherms is understudied. Most animals are poikilothermic ectotherms. A truly comprehensive theory of the control of feeding can only be achieved by incorporating knowledge from such

species. Indeed, two important factors can not be effectively addressed with endothermic subjects: scaling, and thermal dependence of food intake. Because of lactation and parental care, many mammals and birds become capable of feeding themselves at a body size near to that of adults. Many ectothermic vertebrates, in contrast, are capable foragers shortly after hatching/birth. However, neonates are often orders of magnitude smaller than the largest adults of each species (Zug 1993). Previous studies of the scaling of food intake rate and prey size have been interspecific studies (summary in Peters 1983). For example, Farlow (1976) showed that long term ingestion rate scaled with similar exponents to metabolic rate (i.e. allometric slopes = 0.69-0.82). Vezina (1985) reported that prey mass of both large-prey eaters and small-prey eaters scaled with positive allometry (log-log slopes = 1.16-1.18). However, the interpretation of results from interspecific scaling studies can be complicated by the nature of the data. Heusner (1982) suggested that the much-debated meaning of the 0.75 exponent of metabolic rate scaling in mammals was a statistical artifact. Intraspecifically, many of the constituent species show shallower scaling curves consistent with a surface area explanation (i.e. exponent = 0.67). Intraspecific studies of the scaling of ingestive parameters are best accomplished with an ectotherms that is a competent forager over a large range of body sizes.

Endotherms metabolically maintain a high and relatively constant body temperature. Thus, the effect of body temperature variation on ingestive performance has not been addressed in laboratory mammals. This situation is akin to the demonstration of the adaptive significance of fever in fighting infection. Such studies can not be readily done with

endotherms because fairly invasive measures are needed to prevent infected subjects from developing fever. The first study to indicate that fever could increase the survival rate of an infected animal was done with desert iguanas (Dipsosaurus dorsalis; Kluger et al. 1975). By infecting the subjects with a pathogen and then placing them at various temperatures, Kluger et al. were able to quantify the effect of body temperature on physiological function. In the absence of difficult surgical or pharmacological intervention, endotherm body temperatures can not be modified. Thus, the thermal dependence of food intake and ingestive performance are best studied in ectotherms. Snakes show a strong thermal dependence of digestion rate (Naulleau 1983, Stevenson et al. 1985, Hailey and Davies 1987). The only measurements of temperature's effect on ingestive parameters is Hailey and Davies's (1986) study of Natrix maura. Prey handling time was found to be similar at 15 °C and 25 °C, but significantly shorter at 35 °C.

The following comments summarize snake feeding ecology as it pertains to control and expression of hunger (see also Savitzky 1989). Snakes are typically specialists on relatively large, vertebrate prey. Many snakes can probably ingest single, large prey that are satiating. Since snakes are obligate carnivores, their prey are probably nutritionally complete. Snake diets are often highly specialized and are largely under genetic control. Neonates are equipped from hatching/birth to hunt and feed. Snakes vary greatly in body size over their postnatal lifespan. As ectotherms, snakes are subject to the effects of temperature on physiological and behavioral function, controlling these influences by behavioral thermoregulation. Under ad libitum conditions, limited

evidence indicates that snakes feed prandially, and the time interval between feedings is larger than would be expected if hunger were controlled primarily by gastric fill and evacuation.

What are the correlates and consequences of the trophic lifestyle of snakes? What does it mean for a snake to be hungry? How is hunger in snakes manifested behaviorally? Are the physiological mechanisms controlling appetite the same as those in more frequent feeders? Are snakes physiologically constrained to feeding rarely? These questions are themes for the work I describe below.

C. Components of basic analysis.

An analysis of the control of food intake traditionally focuses on two events, the initiation and termination of feeding bouts. Concerning the former, the proximal factors that produce the condition of hunger are sought. What external stimuli and internal influences interact to create the appetite for food? In order to explore this question, the researcher must also identify observable, behavioral features which reflect the animal's internal state. Such behaviors are what Craig (1918; p. 92) referred as "signs or 'expressions' of appetite." In more familiar terms, these questions about mechanisms and manifestations of hunger can be phrased as "What turns feeding on, and how can you tell?"

The second focal event is the termination of feeding. What are the proximal mechanisms that cause feeding to stop once it has been initiated? These control processes have been referred to as satiety mechanisms. As above, the observer needs an external means to establish whether the animal is satiated. What are the symptoms of satiety? One way that such

behaviors have been described is as the cessation of appetitive behavior that follows the completion of a consummatory act (Craig 1918). Thus, for the second part of the analysis, "What turns feeding off, and how can you tell?"

Although I have used the terms "hunger" and "satiety" above, there is no unanimity regarding what these terms mean. Kennedy (1987) argued that motivation as a distinct psychological state does not exist, and strongly criticized the application of terms like "hunger" to nonhuman animals.

Kennedy opined that zoologists, in borrowing such "mentalist" terminology from psychology, promote serious confusion of the ultimate causation of behavior with its proximate causation. In contrast to Kennedy, who argues that motivation as a separate class of proximate cause does not exist, Mook (1990) considers feeding as a textbook example of purposive, voluntary, motivated action. The position I adopt in the present work lies between these extremes, but is closer to that of Mook. If nothing else, the reality of motivational phenomena can at least be considered via introspection (cf. critical anthropomorphism; Burghardt 1985). Kennedy's caveats notwithstanding, I judge that the convenience of such terms will outweigh the potential for confusion in the present analysis. I have followed Halliday (1983; p. 105) in using such terms as hunger, appetite, and satiety as "labels for unknown physiological processes." My only amendment to Halliday's usage would be to describe the internal, physiological processes as "incompletely known."

1. Individual meals. An appropriate place to begin a study of food intake is the description of a single feeding episode, i.e. the meal. Before proceeding, it is necessary to define what is meant by a meal. In most appetite research, "meal" has a fairly specific meaning that differs

somewhat from common usage. A meal is a bout of ingestion that ends with the subject being satiated (Le Magnen, 1985). This definition is somewhat circular, and further begs a definition for satiation. However, it incorporates the idea succinctly phrased by Le Magnen (1985: p 15) that "Feeding, in all animal species, is essentially periodic in nature." Many animals feed in temporally discrete bouts, and the cessation of such a bout may, under certain circumstances, allow the inference that the animal has reached a state of satiety. For example, an experimental animal is given unlimited access to a highly palatable food. It then eats for a period of time, and stops. In the absence of any interruptions or aversive factors, and assuming that the animal has had sufficient time, the researcher can conclude that the subject stopped feeding because it became satiated. And thus, the bout of feeding that produced this state of satiety was a meal.

Since meals end in satiety, and satiety is an internal state, overt behavior must be used to define meal termination. Initial observations are made to identify a behavioral criterion of satiety. Such criteria can be either qualitative or quantitative. Antin et al. (1975) established what they termed the "satiety sequence" for lab rats. In this qualitative definition of meal termination, satiated rats exhibit a fairly repeatable, behavioral sequence. They cease feeding, then groom for a period of time, engage in locomotory activity, then go to sleep. When this behavioral sequence was observed, Antin et al. concluded that the animal was satiated. Qualitative satiety sequences have since been established for laboratory mice, rhesus monkeys, and humans (references in Smith and Gibbs 1979).

An alternative to such a definition of satiety is to use a quantitative criterion. It is implicit in the definition of "meal" above that the animal

has had sufficient time to ingest a satiating meal. If the experiment involves only scheduled access to food, the time course of a bout of feeding is monitored. A criterion is then chosen for the length of time that would be sufficient for the animal to complete a meal. This session duration is based on satiation curves which plot the cumulative amount eaten over the bout (McCleery 1977). The time needed for these satiation curves to asymptote is estimated, and a minimum session duration is found (Fig. I-2).

Once meal termination can be reliably established, measurements of meal size can be made in one of two experimental paradigms: the session paradigm or the free feeding paradigm. In the session paradigm, the factors affecting the size of single meals are observed. The factors that control size of individual meals in snakes may be quite different from those in laboratory rats. Prey size and predator size are two factors which would seem to be of particular relevance to snakes.

Snakes consume entire prey without mastication (Gans 1961), and most species can undoubtedly ingest a single prey item that is large enough

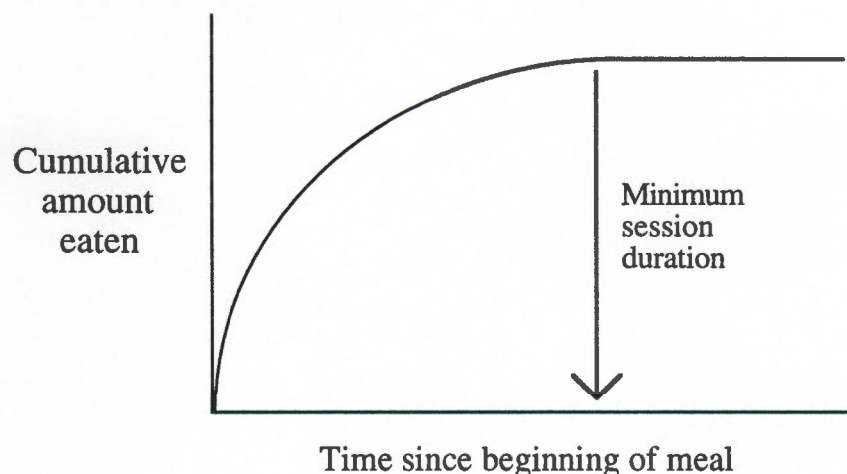


Fig. I-2. A representative satiation curve.

to be satiating. For example, Pough and Groves (1983) reported that the relatively largest prey item consumed by a viper in their study was a rodent equaling 36% of the snake's mass. I presume that the snake was satiated after that meal. If not, it is difficult to imagine that the small Bothrops atrox that ate a lizard weighing 1.6 times its own mass (Greene 1992) was not sated. Since mammals mechanically reduce food by chewing, they do not have to consume items in their entirety. Snake meal sizes, however, may depend on the size of prey offered, with meal sizes ranging from the single smallest to largest items that they can ingest. Maximum meal size is, thus, presumably constrained by the anatomical limits of the snake's head.

At the other extreme of prey size, it is not clear that a meal of multiple, small items would sum to the same total mass as a single, maximal item. A snake's food storage capacity is delimited by the space in the stomach plus the posterior esophagus (Skoczylas 1978). On one hand, one could posit that smaller items can be packed more efficiently into this space than could one large item. Alternatively, each ingestion of a small item may incrementally sum such that satiety is achieved sooner. Such a phenomenon in rat pups has been described as oral habituation; the subjects ingest smaller meals when given repeated, brief tastings of food before the test (Swithers-Mulvey et al. 1991, Swithers-Mulvey and Hall 1992). The satiating influence of oral stimuli has been implicated in a study of an unusual snake subject, a two headed rat snake (Andreadis and Burghardt 1993).

Brown (1958) conducted satiation feedings in captive Northern water snakes, Nerodia sipedon. Although the hunger level, prey size, and session

duration were not specified, it appears that Brown offered hungry subjects ample time to ingest their fill of multiple, nonmaximal prey. Brown obtained a mean satiation meal of 26% of body mass (limits 11-43%, $n=19$ snakes). Tu and Hutchison (1995) fed five large Nerodia rhombifer to satiety with multiple, nonmaximal prey, reporting an average meal size of 23% of snake mass (limits 17-27%). In contrast, Uhler et al. (1939) reported that one wild caught N. sipedon had consumed a single bullhead catfish (Ameiurus sp.) equaling 40% of the snake's mass. Brown (1979) reported that two wild caught N. sipedon had eaten single items, apparently Bullfrogs (Rana catesbeiana), that were 40% and 56% of the respective snake's masses. Thus, it seems likely that sizes of multiple-prey meals in snakes are smaller than single-prey, maximal meals.

Certain characteristics of snakes underscore the importance of scaling effects (see I.A above) in determining meal size. Snakes generally lack postprandial parental care (Shine 1988, Somma 1990). Thus, neonates must be competent foragers. But, some reptiles may increase in mass by two orders of magnitude or more from hatching/birth to maturity (Zug 1993). Shine (1991) has asked "Why do larger snakes eat larger prey?", and it is also relevant to consider how meal size changes with body size. A 1000 g snake will eat an absolutely larger meal than a 10 g snake, but do large and small snakes consume meals that are a constant proportion of their mass? In other words, does meal size in snakes scale isometrically? This question can be explored in a session paradigm by measuring meal sizes of snakes of a wide range of body sizes.

The other experimental paradigm in which to explore meal taking is free feeding (*ad libitum*). Numerous consecutive meals are monitored in a

smaller number of subjects. This paradigm, which focuses on meal patterning over longer time frames, has been the focus of extensive work in lab animals, and is considered in depth in the following section.

2. Ad libitum feeding patterns. Since most animals feed prandially, meal patterns are determined by two parameters: the amount of food consumed per meal, and the time between meals (Brobeck 1955). The most common reference condition under which to measure meal patterns in mammals and birds has been that of a free feeding paradigm with ad libitum food availability (Le Magnen 1985, Clifton 1987). The relevance of studying snake feeding under such conditions might not be apparent. After all, a seemingly definitive characteristic of the snake trophic strategy is infrequent feeding. Yet, to thoroughly explore food intake patterns, the range of food availabilities must be spanned. The ad libitum treatment allows one to define a limit or constraint on what the subject animal is capable of. How much and how often will a snake feed when it can feed whenever it chooses? In addition to delimiting a feeding constraint, the ad libitum method may allow direct comparison of snake meal patterns with those of previous studies of endothermic vertebrates. Although ad libitum feeding has been examined in taxa such as Goldfish (Carassius auratus; Rozin and Mayer 1961) and Florida kingsnakes (Myer and Kowell 1971), no analyses of prandial patterning have been reported for any vertebrate ectotherm.

Clifton (1987) summarized the methodology and data analysis of ad libitum meal pattern studies. The subject, most commonly a laboratory rat, is trained to actuate a food dispenser when hungry. Food units of a standard size are used (e.g. 45 mg Noyes rat pellets), and automated

recording equipment registers the time of delivery of each item. Interpellet intervals are then subjected to spectral analysis in order to establish the temporal criterion of a meal. Interpellet intervals less than the criterion are considered to be the short pauses within a meal, while those longer than the criterion reflect the satiety between meals. Once the criterion for a meal is chosen, the entire feeding record of each subject is recoded as meals and intermeal intervals.

Once meals can be defined, the distributions of meal sizes and intermeal intervals are determined. It may be possible from the distribution of meal sizes to infer a possible mechanism controlling meal size in snakes. If the mean meal size is not significantly different from the mass of a single prey item, it may be that gastric evacuation determines hunger and meal size. In other words, a snake might eat a single prey item every time, and as soon as, an equivalent mass is emptied from the stomach. If, however, mean meal sizes are significantly larger than mean prey size, then subjects are not eating as soon as space for a single item is created. In such a case, gastric evacuation is unlikely to be the primary factor controlling meal size and the return of hunger (see discussion of Myer and Kowell [1971] in I.B above).

The initiating of a free feeding experiment affords an opportunity to explore another phenomenon. The meal sizes of traditional laboratory animals vary depending on the procurement costs, e.g. the number of operant bar presses to receive a unit of food. High costs cause animals to reduce meal frequency, but increase meal size (Collier and Rovee-Collier 1981). Ideally, free feeding should represent the animal's feeding behavior in a costless environment. Collier and colleagues have explored the idea

that the taking of small, frequent meals under low procurement costs is an adaptive solution to an essentially ecological problem. Their hypothesis is that there is a cost to taking large, infrequent meals (Collier 1985).

However, the nature of the cost is obscure. One possibility is that periodic gorging, like all feeding, is a potentially harmful perturbation of homeostasis. In this regard, it is pertinent to consider the Eating Paradox, a concept which contrasts the necessity of eating with the potential danger from surges in absorbed nutrients (Woods 1991). Pathological conditions like diabetes mellitus underscore what happens, in a lesser scale, after each meal an animal takes. Given these possibly harmful aftereffects, Woods reasons that all animals should, theoretically, take small, frequent meals. Herein may lie the explanation for why animals take small, frequent meals when presented with unlimited food and low procurement costs. Given the opportunity, animals feed so as to homeostatically regulate absorbed nutrients with minimal perturbations in concentration. If this hypothesis is generally true, what about snakes? The evolutionary origin of snakes entailed an ecological shift from small, frequent meals to large, infrequent ones. By their very lifestyle, snakes defy the Eating Paradox. Does this mean that snakes suffer no homeostatic risks of binge feeding? Has natural selection culled this cost from the snake lineage, as compared to clades of more frequently feeding animals? This idea can be explored by examining meal sizes of snakes in a free feeding paradigm. In particular, how do average meal sizes of snakes under ad libitum conditions compare to maximal meals?

While the preceeding topic considered the implications of feeding for homeostasis, some important influences on food intake are not proximately

homeostatic. Richter (1927, 1947) was the first researcher to study meal patterns in freely feeding domestic rats. He considered these patterns to be driven by depletion and repletion of the animal's metabolic state. However, Richter also discovered the important influence of such nonhomeostatic factors as the time of day, i.e. circadian rhythms in appetite. Such diel cycles are now well studied phenomena in appetite research on laboratory rodents (review in Le Magnen 1985). Norway rats take multiple meals during the day and during the night, but nighttime meals are larger, last longer, and are taken much more frequently than daytime meals (Le Magnen 1985). While diel cyclicity and endogenous rhythms in activity have been examined in a number of reptile species (Jones 1974, Underwood 1992), including some snakes (Heckrotte 1962), the effect of such factors on feeding behavior of snakes has not been addressed.

A major goal of employing the free feeding paradigm is to examine the temporal structure of feeding, i.e. the meal pattern. To this end, various prandial correlations are calculated. In the appetite literature, the term "prandial" pertains to meals (as defined on p. 16). Thus, "postprandial" is not synonymous with "postingestive", and I follow this convention here. In a free feeding experiment, a preprandial correlation is that between meal size and time since the last meal. A postprandial correlation is that between meal size and the time to the next meal. A final calculation is the autocorrelation between the sizes of consecutive meals. In most meal pattern studies of rodents, there is no significant preprandial correlation, but there is a postprandial correlation (Le Magnen 1985). In other words, under ad libitum conditions, the time between meals is

dependent on the size of the last nutrient load, while size of a meal is itself an unpredictable parameter. Autocorrelation in meal sizes (e.g. feeding in runs of large meals, or alternating large meals with small) is generally not found.

As noted above, prandial correlations have apparently never been studied in an ectothermic subject. Similarly, most of the traditional laboratory subjects in which meal patterns have been investigated are "nibblers" that typically take many, relatively small meals in a day (Collier and Rovee-Collier 1981, Le Magnen 1985). Do comparative "gorgers" like snakes exhibit the same characteristics, e.g. a significant postprandial correlation? The situation is unclear in the domestic cat (Le Magnen 1985), the closest ecological equivalent (both are obligate carnivores) to snakes among the laboratory mammals that have been tested.

D. The ecological context for snake feeding

In order for laboratory studies of snake feeding to achieve external validity, their relevance to the snake's feeding behavior in a natural environment must be established. Thus, Curio (1976; p. 10) noted: "Under laboratory conditions food supply is usually held constant and prey density high.... The question arises as to whether the rules thus observed also prevail in the wild." In terms of individual meals, how do the meal sizes measured in the lab compare to typical amounts consumed during one foraging bout in the field? Such a comparison is hampered by ignorance of whether or not a field caught animal was foraging at the time of capture. Sometimes, the number of prey in the stomach can be a surrogate for such knowledge. Brown (1958) examined the stomach contents of 207 Northern

water snakes collected in the field (i.e. not at fish hatcheries). He found that 88% of the snakes contained a single prey item in the stomach. The high percentage suggests that these snakes most commonly take one prey item per foraging bout. If this interpretation is true, the average size of a prey item would equal (1) the average mass of food in the stomach, as well as (2) the average amount of food eaten per foraging bout. For his field caught sample, Brown (1958) did not report masses of either prey items or stomach contents; thus, other sources were consulted for this information. King (1993) measured the mass of stomach contents in field collected N. sipedon ranging from 5.0 g neonates to 890.0 g adult females. He found that stomach contents averaged 6.4% of body mass. This figure can be compared to meal sizes measured in captivity. Brown (1958) reported meal sizes of hungry N. sipedon in the laboratory to average 26% of body mass (elaborated on in C.1 above). To the extent that foraging snakes in the field are as hungry as Brown's captives, this species typically catches about one quarter of a satiating meal per foraging bout. Until a greater comparative database becomes available, the generality of this finding can not be established. In addition, it would facilitate future comparisons if field and laboratory meal sizes are made as comparable as possible, i.e. subjects for field and laboratory studies should be taken from the same population and fed comparable prey in the lab to what is taken in the field. Further, it would be informative to know what typical meal sizes are under ad libitum conditions, and not just when snakes are hungry.

1. Feeding frequency in the wild. For validating laboratory studies of snake appetite, no question is more important to have answered than "How often do snakes feed in the wild?" Although snakes undoubtedly

feed less frequently than many other vertebrates, only rarely has an attempt been made to measure just how infrequently. Godley (1980) used stomach contents and food clearance times to estimate feeding rates of the Striped crayfish snake (Regina alleni), a small, aquatic, crayfish specialist. Godley found that adults (mass = 45 g) under the most favorable conditions took, on average, meals of 7.5% of their mass every 3.0 d. The general consensus of herpetologists would likely be that this is a high frequency. Pough (1980, 1983a) has emphasized that survival, growth, and reproduction of ectothermic tetrapods are not as limited by fluctuating food availability as is the case for endotherms. Their low rate of metabolism essentially permits ectotherms to do without. Pough's seminal papers are dogma to students of amphibian and reptile ecology, but may, to one extent, have done the field a disservice. Pough's view of the advantages of ectothermy may have distracted researchers from the idea that natural selection will favor those individuals that excel in obtaining food. Avery's (1971) study of food intake in the lizard Lacerta vivipara is an example of how well an ectotherm can perform in obtaining food. Avery found that the mass of stomach contents in field caught lizards under warm climatic conditions was very close to the mass consumed by laboratory subjects fed ad libitum! This result is not expected if one views reptiles as animals that, by virtue of ectothermy, do not need to eat much or often. If food is at all available, selection should favor those that can obtain it. Among vertebrates, snakes are the exemplary taxon that should not need to feed very often. Measurements of feeding frequency in the wild are thus of some interest.

Ichthyologists have used stomach contents of field collected fish and

rates of gastric evacuation to measure feeding frequency and ration size in the field (review in Gerking 1994). The model of Diana (1979) estimates feeding frequency of Northern pike (Esox lucius), a top consumer that eats vertebrates (other fish) and typically has a small number of items in the stomach at one time. The parameters needed for the estimation are the time needed to evacuate an average prey item from the stomach, and the proportion of snakes in the field that have food in the stomach. Godley (1980) used a variety of this method to obtain his estimate of feeding frequency in Striped crayfish snakes. As with the comparison of field and lab meal sizes, the extent to which this measure of feeding frequency is unusual can not be evaluated at the present. Certainly, however, feeding once every three days is a much lower frequency than would be expected in an endotherm of comparable mass (e.g. mouse, passerine bird).

2. Biological rhythms in foraging. As with free feeding in the laboratory (see I.C.2), natural, temporal cycles may influence appetite and the expression of hunger (i.e. hunting behavior) in the field. Many of an animal's activities recur with a characteristic frequency. The biological rhythms with daily and annual periodicities are the best studied examples (see Aschoff 1981). However, other ultradian (shorter than 24 h) and infradian (longer than 24 h) rhythms have been found to have major significance in certain biological systems. Lunar cycles, for example, are particularly well studied in the nearshore marine environment, where the gravitational pull of the moon is responsible for tidal fluctuations (Neumann 1981). Other lunar rhythms are a consequence of the variation in intensity of lunar illumination as the moon changes phase. Brightness varies from 0.0009 lux at the new moon (=just starlight) to 0.2150 lux at

the zenith of the full moon (Austin et al. 1976). Moonlight dependent effects on nocturnal animals are often reported in the context of visually mediated predator-prey interactions (Lima and Dill 1990). Lunar light levels may impact the ability of nocturnal foragers to both find prey and evade predators. Such effects of lunar light level raise both ultimate and proximate questions. In terms of fitness, do predatory success or predator avoidance vary with lunar phase? Proximately, are moonlight fluctuations important in understanding the mechanistic control of food intake in nocturnal animals? In those animals that exhibit lunar rhythms, is there an endogenous circalunar clock? Alternatively, are responses elicited solely by external stimuli?

Among studies of vertebrate behavioral rhythms, there is a paucity of work on reptiles and amphibians (Rusak 1981). The reptile studies that have been done have primarily addressed rhythms in locomotor activity (e.g. Heckrotte 1962) and behavioral thermoregulation. Underwood (1992) reviewed the literature on endogenous rhythms in reptiles, but focused primarily on daily rhythms and circadian clocks. Perhaps the only documented case for an endogenous lunar rhythm in reptiles is Wikelski and Hau's (1995) study of Marine iguanas, Amblyrhynchus cristatus (Iguanidae). They reported that the forays of iguanas to and from their algal grazing beds both tracked and anticipated the ebb and flow of the tide. In nonmarine (i.e. nontidal) situations, the changes in light level that accompany different moon phases might also influence the activity of nocturnal reptiles. Viewing foraging behavior as an expression of hunger level, one can propose that the appetite of actively foraging nocturnal reptiles might fluctuate with the lunar cycle.

E. Study animal and field sites

In the present work, I examined the control and expression of hunger and satiety in the Northern water snake, Nerodia sipedon (Linnaeus). This species is a nonvenomous, semiaquatic member of the Family Colubridae, with adults typically ranging between 61-107 cm in total length (Conant and Collins 1991). It is an extremely abundant snake in varied aquatic habitats of the eastern U.S.A. (Ernst and Barbour 1989a). In eastern Tennessee, this snake is commonly found in clear, rocky, fast flowing streams and rivers (personal observation). The active season of N. sipedon is approximately from April to October (Ernst and Barbour 1989a, Mitchell 1994, pers. obs.). Mating takes place from mid April through early July (King 1939, Bauman and Metter 1977, Ernst and Barbour 1989a, Mitchell 1994). This species is viviparous, with births occurring from mid-August to mid-October (Bauman and Metter 1977, Mitchell 1994, Palmer and Braswell 1995, pers. obs.). Average litters consist of about 25 neonates (Bauman and Metter 1977, Mitchell 1994, Palmer and Braswell 1995).

The diet of N. sipedon has been well sampled in various portions of its range. Indeed, in terms of diet, N. sipedon is one of the best studied snakes in the world (Table I-1). Fish predominate in the diet, with amphibians comprising a typically lesser, but appreciable proportion. Rare occurrences of crayfish, mammals, and insects are reported. Brown (1958) found that the most important prey taxa in streams of central New York, the sampled habitat most closely resembling the streams of eastern Tennessee, included minnows (Cyprinidae), darters (Percidae), sculpins (Cottidae), suckers (Catostomidae), and lampreys (Petromyzontidae).

Table I-1. Literature survey of Northern water snake diets. Some values were not reported ("-") or could not be calculated ("?").

Source	Location (postal code); habitat	Prey Volume		No. of Prey items		No. of snakes w/ food		
		% Fish	% Amphib.	% Fish	% Amphib.	n	% w/ Fish	% w/ Amphib.
King 1939	TN, NC; stream	-	-	-	-	48	60.4	35.4
Uhler et al. 1939	VA, WV; stream?	60.9	34.7	57.9	39.5	30	-	-
Lagler & Salyer 1945	MI; stream	85.6	12.8	89.3	6.0	106	?	7.5
Lagler & Salyer 1945	MI; lake	47.4	52.6	80.0	17.1	18	?	33.3
Raney & Roecker 1947	NY; stream	95.8	4.2	-	-	59	89.8	15.3
Barbour 1950	KY; stream	66.7	16.7	-	-	8	-	-
Hamilton 1951	ON; great lake	53.9	46.1	-	-	23	56.5	52.2
Diener 1957	MO, AR, OK; stream	100.0	0.0	100.0	0.0	25	100.0	0.0
Brown 1958	NY; stream	82.7	17.3	84.5	15.5	120	?	17.3
Brown 1958	NY; inland lake	46.4	53.6	48.0	52.0	15	?	60.0
Brown 1958	MI; inland lake	49.2	50.8	86.7	13.3	48	?	16.7
Brown 1958	MI; great lake	81.0	19.0	89.3	10.7	19	89.0	15.8
Bush 1959	KY; stream	71.4	28.6	71.4	28.6	7	71.4	28.6
Zelnick 1966	IL; inland lake	-	-	78.0	16.0	60	?	25.0
Brown 1979	NC; stream & canal	-	-	24.4	75.6	30	-	-
Camp et al. 1980	GA; stream	46.7	51.9	50.0	41.7	10	40-60	41.7
Collins 1980	NC; various?	-	-	-	-	10	10.0	100.0
King 1986	OH, ON; great lake	-	-	-	-	37	91.9	8.1
King 1993	OH, ON; great lake	-	-	82.2	17.8	31	77.4	22.6
King 1993	OH, ON; marsh	100.0	0.0	100.0	0.0	14	100.0	0.0

Most of the snakes used in these studies were collected in eastern Tennessee, particularly in the three contiguous counties of Blount, Knox, and Sevier. My principal sites for collection, as well as for studying feeding behavior in the field, are along the Little River in Blount Co. The Little River originates in the Great Smoky Mountains, flowing northwest to join the Tennessee River just southwest of Knoxville, TN. Unlike most rivers in East Tennessee, the Little River has not been subjected to large impoundments. It is one of the cleanest and most faunistically diverse rivers in eastern Tennessee (Etnier and Starnes 1993). Many water snakes can be found either basking on overhanging perches, hidden under rocks, or foraging in the water, especially at night (personal observations). Water snakes from Little River have been the subjects of previous studies. Gove and Burghardt (1975) compared the tongue flicking responses of water snakes to chemical cues from indigenous and exotic prey. Drummond (1979, 1980) experimentally examined the stimulus control of predation in Little River water snakes. Both Gove (1971) and Drummond (1980) gave brief descriptions of field behavior, including foraging activities, of water snakes in Little River.

Although I collected snakes at several localities along the river, the site where I did the majority of my collecting was Peery's Mill (35° 40.2' N, 83° 50.5' W). This was also the study site for the investigation of lunar cycles. A map of this field site is provided in Chapter V. The other important collecting sites were on the West Prong of the Little Pigeon River, east of Sevierville, Sevier Co., and in Love Creek, east of Knoxville, Knox Co.

F. Objectives.

The studies below of snake feeding are organized in four chapters according to the location (laboratory or field) and principal methods used. I have outlined several objectives of these studies, including basic description, parameter estimation, and hypothesis testing of predictions from other sources.

Chapter II. Individual meals in the session paradigm.

- Does N. sipedon possess a behavioral satiety sequence?
- What is meal size in N. sipedon?
- Does prey size affect meal size in N. sipedon?
- How does meal size scale with body size in N. sipedon?

Chapter III. Meal patterns in the free feeding paradigm.

- Does N. sipedon feed prandially?
- Is meal size reduced under ad libitum feeding conditions?
- What are typical meal sizes and intermeal intervals?
- Does timing of N. sipedon meals involve a diel cycle?
- Does N. sipedon exhibit a postprandial correlation?

Chapter IV. Gastric evacuation and feeding frequency.

- How often do N. sipedon feed in the wild?

Chapter V. Biological rhythms: Lunar cycles in foraging.

- Does the incidence of foraging change with moon phase?

CHAPTER II

INDIVIDUAL MEALS IN THE SESSION PARADIGM

A. Introduction.

The two most basic questions in the study of appetite are "What initiates feeding?" and "What terminates feeding?" Since the termination of a bout of eating determines the amount consumed, the latter question is often stated as "What determines meal size?" The session paradigm (Collier 1985) is the most common approach used to study the control of meal size. The investigator manipulates a variable (e.g. drug dosage, ambient temperature) and monitors multiple subjects to see the effect on the amount consumed in a single feeding session, i.e. a single meal. Perhaps the earliest application of the session paradigm was Skinner's (1932) descriptive work on the time course of meal ingestion. Later, such satiation curves were studied as examples of general models of motivated behavior (McCleery 1977). Single session feedings also came to be used extensively in studies of satiety mechanisms, i.e. the neural and hormonal signals of satiety and the location in the body where such signals are transduced and processed (Smith and Gibbs 1979). Much recent clinical work devoted to the study of eating disorders has used the session paradigm to investigate the phagostimulating or anorectic effects of various drugs (e.g. Willner et al. 1990, Halford and Blundell 1996).

The studies described in this chapter use a session paradigm to examine meal ingestion in snakes. The trophic lifestyle of snakes is very different from that of the laboratory rodents which dominate appetite

studies (see I.B above). The present chapter is organized into three major sections, each with distinct, but interrelated topics. In Part A, I begin by describing attempts to identify a satiety criterion. I assessed whether or not a qualitative indicator of satiety was present (Experiment 1), and how the postingestive behavior of snakes differed depending on the amount eaten (Experiment 2). I also examined a quantitative measure for assessing satiety by constructing satiation curves of individual meals (Experiment 3).

Given a criterion for establishing satiety, in Part B I describe two studies (Experiments 4 and 5) on the effect of prey size on meal size. Since snakes swallow their prey whole, it is unclear whether meals of small prey would sum to the same total size as when a snake ingests large prey. For logistical reasons, the experiments on prey size effects used a single size class of snake. I chose to use ingestively naive neonates. Naive snakes have been used extensively since the pioneering work of Burghardt (1966; review in 1970) to examine innate responses in the absence of learning. One school of thought argues that meal size is primarily a learned parameter (see I.B). The use of naive snakes, thus, also serves a general goal of appetite studies: to separate the roles of learned and unlearned factors in meal size determination.

Lastly, in Part C I investigated the effect of predator size on meal size (Experiment 6). Over the large mass range between very young and old snakes, does meal size display isometric scaling?

B. Satiety Criteria.

A set of three experiments investigated both qualitative and quantitative indices for establishing satiety.

1. Methods.

Experiment 1: Qualitative satiety sequence. The subjects were five juvenile water snakes ranging in mass from 20.4-30.0 g (mean=23.1). Prior to testing, the subjects had been in captivity for 1-2 months, during which time they were individually housed in 31 x 16 x 9 cm plastic cages. A 13:11 light:dark cycle and an air temperature of 24-26 °C were maintained prior to and throughout the study. A clear, plastic water dish (18 x 13 x 3 cm) held water at all times. Either a red brick or a chunk of limestone was supplied for the snakes to perch on and rub against during shedding. Snakes were fed commercially obtained Fathead minnows (Pimephales promelas: Cyprinidae) 1-2 times per week, and all snakes were reliable feeders.

The experiment was conducted on 28-29 July 1992. All subjects were tested in their home cages. The prey items for this initial observation were Longnose dace (Rhinichthys cataractae: Cyprinidae) which had been frozen when fresh, then thawed shortly before the feeding trials. Between 1630-1940 h, snakes were fed by placing a thawed dace (mean=28.4% of snake mass) in their water bowls. Although water snakes are capable of ingesting larger prey than this (Uhler et al. 1939, Brown 1979, Andreadis, unpublished data), the mass of prey items in the stomachs of wild caught snakes is typically much smaller (approximately 4-8% of body mass; King 1993). Trials were videotaped with a Canon A1 Hi 8 camcorder. Because of variability in the duration of prey manipulation, I did not begin videotaping until the snake reached the snout of the prey item and began to engulf it. The snakes were videotaped for approximately 40 min.

Coding of the videotapes followed previous studies of laboratory

rodents (Antin et al. 1975, Kushner and Mook 1984). Four behavioral states were scored: Ingestion, Grooming, Locomotion, Resting (summarized in Table II-1). "Ingestion" included the alternating maxillary protractions and retractions, head turning, prey lifting, and neck kinking behavior that effect swallowing. "Grooming" is a functional interpretation of two behavior patterns which often followed ingestion. The most frequent form included the pressing of the chin or lateral head surfaces against horizontal or vertical cage surfaces and sliding the head forward (cf. Cunningham and Burghardt, In press). This behavior was topographically distinct from the nosing of the glass that indicated the snakes were seeking escape (see below). In Grooming, there is a shallow, acute angle between the long axis of the head and the surface being rubbed, while in escape movements the head is at more of a perpendicular angle to the surface being rubbed. Furthermore, there is a single forward slide that often extends the entire length of the cage; in escape behavior the snake moves repeatedly back and forth, pressing against the same spot. The less frequent form of Grooming involved drawing the head backwards across the lip or corner of the water dish. The postingestive head rubbing of snakes is trivially familiar to most individuals who keep snakes, but has largely not been scientifically investigated. My observations of the topography and context of the behavior are consistent with an interpretation of grooming (cf. Dunn and Chiszar 1993, Cunningham 1996). The presumed proximate function is to remove fish scales and mucus adhering to the snake's head scales.

Two behavior patterns were scored as "Locomotion." I considered a snake to be Locomoting if the snake's midpoint moved > 3 cm without

Table II-1. Behavioral categories scored in the satiety sequence of juvenile Northern water snakes. One-zero sampling of one min intervals was used.

Behavior	Description and Criteria
Ingestion	Manipulation of prey from beginning of swallowing of fish's snout until deglutition completed; includes body kinking associated with prey reaching "neck" region.
Grooming	Chin or lateral surface of head rubbed against wall or floor with a forward, sliding motion; also includes drawing head backwards across edge of water bowl or rock/brick.
Locomotion	Midpoint moves more than 3 cm without pausing, or, if center of gravity is stationary, head moves more than 5 cm. Exclusive of Grooming.
Resting	Does not move, except for minor postural adjustments of head, for 60 consecutive s. Exclusive of all other categories.

pausing, and if the snake was not Grooming. Locomotion was also scored if the snake's head made large excursions (> 5 cm) while its midpoint remained stationary. The latter behavior was noted when the snakes were nosing the cage walls and investigating the cage lid, apparently seeking escape. In satiety sequences of rats, a period of activity involving locomotion and rearing on the hind feet is usually termed "exploration" (Antin et al. 1975, Kushner and Mook 1984). I am less confident in applying this functional description to the locomotory movements of snakes, but given the behavior that often followed it, a parsimonious interpretation is that the snakes were seeking a retreat. A snake was scored as "Resting" if its midpoint was immobile for a period of 1 min and its head made no more than slight repositionings (i.e. comfort movements). Resting was mutually exclusive of the other three categories.

Beginning with the start of Ingestion, each snake's behavior was scored in one min intervals with one-zero sampling (Altmann 1974). Thus, I recorded whether or not each category occurred at any time within each one min period. If a snake was scored as Resting in a given interval, it could not, by definition, have performed the other behavior categories in that interval. However, Ingestion, Grooming, and Locomotion could all potentially co-occur within the same interval. This sampling method, although controversial (Altmann 1974), was adopted because it was been used previously in studies of rat satiety sequences (Antin et al. 1975, Kushner and Mook 1984). Another methodological feature of the rat studies was that observations were pooled into time blocks, apparently to reduce the noise in the behavioral data. A preliminary inspection of the data for water snakes indicated that a pooling interval of 5 min, as used in

many rat satiety studies, was too coarse (pers. obs.). Instead, the data for Experiment 1 were pooled into 3 min time blocks.

Experiment 2: Effect of meal size on the satiety sequence. The experiment was conducted between 5-11 September 1992. The subjects were 8 juvenile N. sipedon ranging in mass from 21.1-36.9 g (mean=28.1 g). Four of the snakes had been subjects in Experiment 1A. Four snakes were randomly assigned to each of two treatments: (1) a meal consisting of a single small fish, a Longnose dace weighing 10.0-10.4% (mean=10.2%) of snake mass, or (2) a meal consisting of single large fish, a Central stoneroller (Campostoma anomalum: Cyprinidae) weighing 28.0-30.8% (mean=29.3%) of snake mass. Prey were frozen when fresh, then thawed right before each feeding trial. Snakes were fed in their home cages between 1600-1850 h, and were videotaped for approximately 40 min after initiating swallowing. Video records were scored as in Experiment 1.

Experiment 3: Satiation curves. For this experiment, I constructed satiation curves as a quantitative means to establish satiety. The goal was to determine the session duration that would be long enough to insure that the subjects had fed to satiety. Any such time dependent measure would be subject to scaling effects. Based on general principles of scaling (Peters 1983, Schmidt-Nielsen 1984), a large animal should take longer to feed to satiation than a small animal. The time course of meal ingestion was measured in four different sizes of snakes. Three sizes of adult snakes were tested: large adult females (mass=321.4-448.6 g, n=4), small adult females (192.6-258.0 g, n=7), and adult males (67.4-133.7 g, n=5). The adult females were not late term, gravid animals when tested. Five neonate snakes (2.68-5.19 g) from three litters were also tested: two neonates from

each of two Blount Co., TN females, and one from a Morgan Co., TN female.

Adult snakes were maintained for 2-3 months at 26 °C and a 13:11 light cycle prior to testing. Adult females were individually housed in 57 L glass aquaria (62 x 32 x 32 cm) with a clear plastic water dish (37 x 27 x 9 cm) occupying approximately two thirds of the floor area. Adult males were individually housed in clear, plastic cages (38 x 25 x 16 cm) with a clear plastic water dish (31 x 16 x 9 cm). The floor substrate was commercially available, corrugated mat paper designed for animal cages. All cages contained a red brick or large rock in one corner to provide perching substrate and rubbing surfaces for skin shedding. The adults were fed sufficient quantities of bait fishes to maintain their body mass. Females were fed Golden shiners (Notemigonus crysoleucas: Cyprinidae). Males were fed Fathead minnows, a smaller prey species matching the males' smaller size. Most of the adults would feed readily while I watched. The neonates were held in the same temperature and light conditions, but were communally housed by litter and were not fed prior to testing.

The small females and neonates were tested in 1991, the females from 22 July-5 August, the neonates from 5-23 September. The adult males and large females were tested from 5 July-7 August 1993. To ensure that snakes were hungry when tested, adults were fasted for a period of time that was proportional to their size. Thus, males were fasted 7-10 d, while females were fasted 12-20 d. A counterintuitive fasting period was used with neonates. By extension of the logic of scaling, if neonates were treated as scaled-down adults, then I should have fasted them for only a few days. But, since they are born with internal energy reserves from the

resorbed yolk, neonate water snakes essentially already have a large, protein- and lipid-rich meal in the gut. Further, I assumed that the neonates would be naturally wary, especially with no opportunity to habituate to my presence during feedings. Thus, to ensure that their hunger level would overcome any reluctance to feed, I fasted these small snakes for comparatively long periods. The five neonates in Experiment 3 were fasted 13-29 d (mean=22 d). During this time period, they lost an average of 10% of their birth mass. There is no standard time period that neonate water snakes are fasted before naive testing. Burghardt (1968) recorded the tongue flicking responses to prey extracts of 3-4 d old N. sipedon. Dix (1968) held naive N. sipedon and N. fasciata for 7-14 d without food before testing their tongue flick responses to prey extracts. Gove and Burghardt (1975) tested naive N. sipedon at 10 d of age. Dunbar (1979) waited 28 d before offering food to naive N. sipedon. Mushinsky and Lotz (1980) fasted neonate N. erythrogaster and N. fasciata for 28-35 days before testing their tongue flicking responses to prey chemicals.

The ideal length of time to fast neonate water snakes before testing is unknown. Future work to establish an allometric standard for how long to fast snakes of different sizes is clearly warranted. For the purposes of the present work, a minimum value for a fast is suggested by the litter of snakes from Morgan Co. Five of six neonates from this litter did not feed successfully when tested at 13 d of age (personal observation). Three of these did not attack prey, and two captured but later abandoned large prey items. Both circumstances suggest a comparatively low motivation to feed.

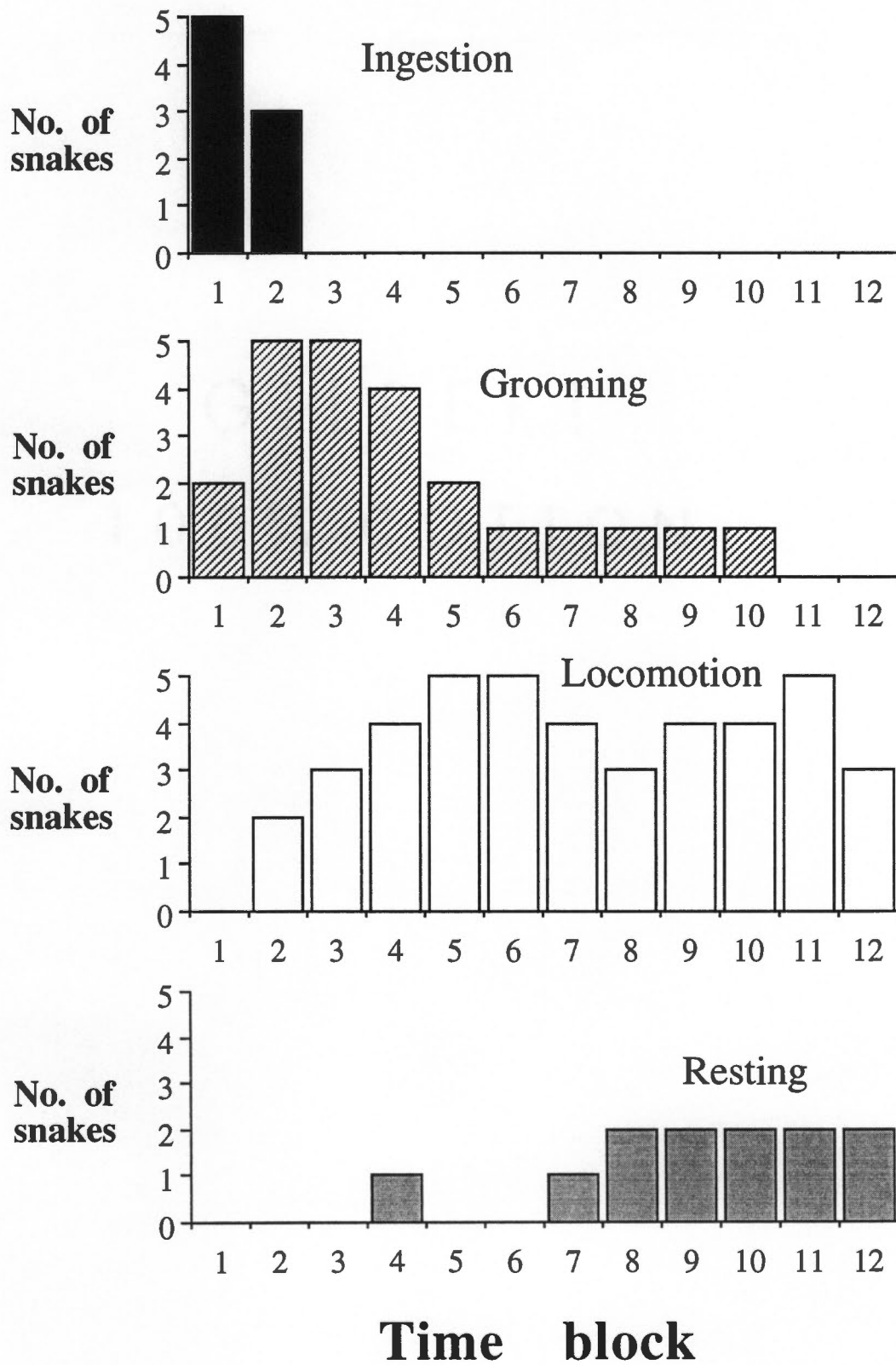
Adult snakes were fed in their home cages by adding to their water dishes a preweighed quantity of live fish (the same prey species as the

maintenance diets of each group). Twenty four hours prior to testing, neonates were removed from group housing and individually placed in clear, round acrylic cages (internal dimensions: 6.3 cm high x 15.1 cm diameter). These cages were filled with 1-2 cm of water, and a piece of rock was placed in each cage to create dry land and anchoring points for the snakes. Testing was conducted between 1500-1830 h. The bait minnows fed to adult snakes were too large for use with neonates. Instead, neonates were fed Mosquitofish (Gambusia affinis: Poeciliidae) collected from a small pond in Knoxville, TN. For snakes of all sizes, prey averaged 3% of snake mass (min-max: 2-5%). The time at which each ingested item was initially grasped was recorded. I continued observations until 1 h had elapsed since the last snake had eaten. Leftover fish were collected and reweighed to determine the number, average size, and cumulative mass of fish eaten. Satiation curves were constructed by plotting the cumulative mass of fish eaten as a function of time since the start of the trial.

2. Results and Discussion of satiety criteria. Each snake's behavior was scored over 12 three min blocks (Fig. II-1). The snakes exhibited a satiety sequence that is virtually the same as that reported for rats (Antin et al. 1975, Kushner and Mook 1984). Following completion of ingestion, a period of grooming ensued, followed still later by locomotion and, finally, immobility.

The similarities of these sequences in animals with such different trophic lifestyles underscores the generality of the satiety sequence. This sequence would seem to be a consequence of the hierarchical organization of motivated behavior, and of a common neural substrate modulating the

Fig. II-1. Satiety sequence of five juvenile Northern water snakes (Experiment 1). Each panel is a frequency histogram of the number of snakes performing a given behavior in each 3 min time block after the start of ingestion. Descriptions and criteria used for the behavior categories are described more fully in the Methods.



responses in diverse vertebrates. In this context, it is instructive to view various behavioral acts as competing for expression at any given time (McFarland 1974). Activities such as feeding, reproduction, and predator detection have, by virtue of their survival value, a high priority of expression. After motivated activities of high priority are performed, lower priority activities are released, or disinhibited. This perspective was discussed by Spruijt et al. (1992) in their review of the neurobiology of grooming. They emphasized the frequency with which grooming, a low priority action, followed the state of stress or arousal associated with performing high priority actions. When feeding to satiety is viewed as such a stressor, the expression of postingestive grooming in a context of neural and hormonal de-arousal (Spruijt et al. 1992) seems likely.

However, it is unclear if the postingestive behavior of snakes, or any animal, would ever differ from the sequence above. Spruijt et al. (1992) also underscored that grooming could be elicited directly by stimuli from the body surface. For many animals, eating a meal (of any size) entails becoming soiled. Therefore, stereotyped components of the satiety sequence such as postingestive grooming may just be responses to stimuli from the skin. Thus, Cunningham (1996) concluded that the progressive increase in head rubbing frequencies of certain garter snakes (Thamnophis melanogaster and T. sirtalis) when fed 5 live earthworms in succession was due to the accumulation of mucus on the snakes' head scales. In terms of seeking satiety indices, it would be instructive to compare the postingestive sequences of animals fed satiating and nonsatiating meals. This was the motivation for Experiment 2.

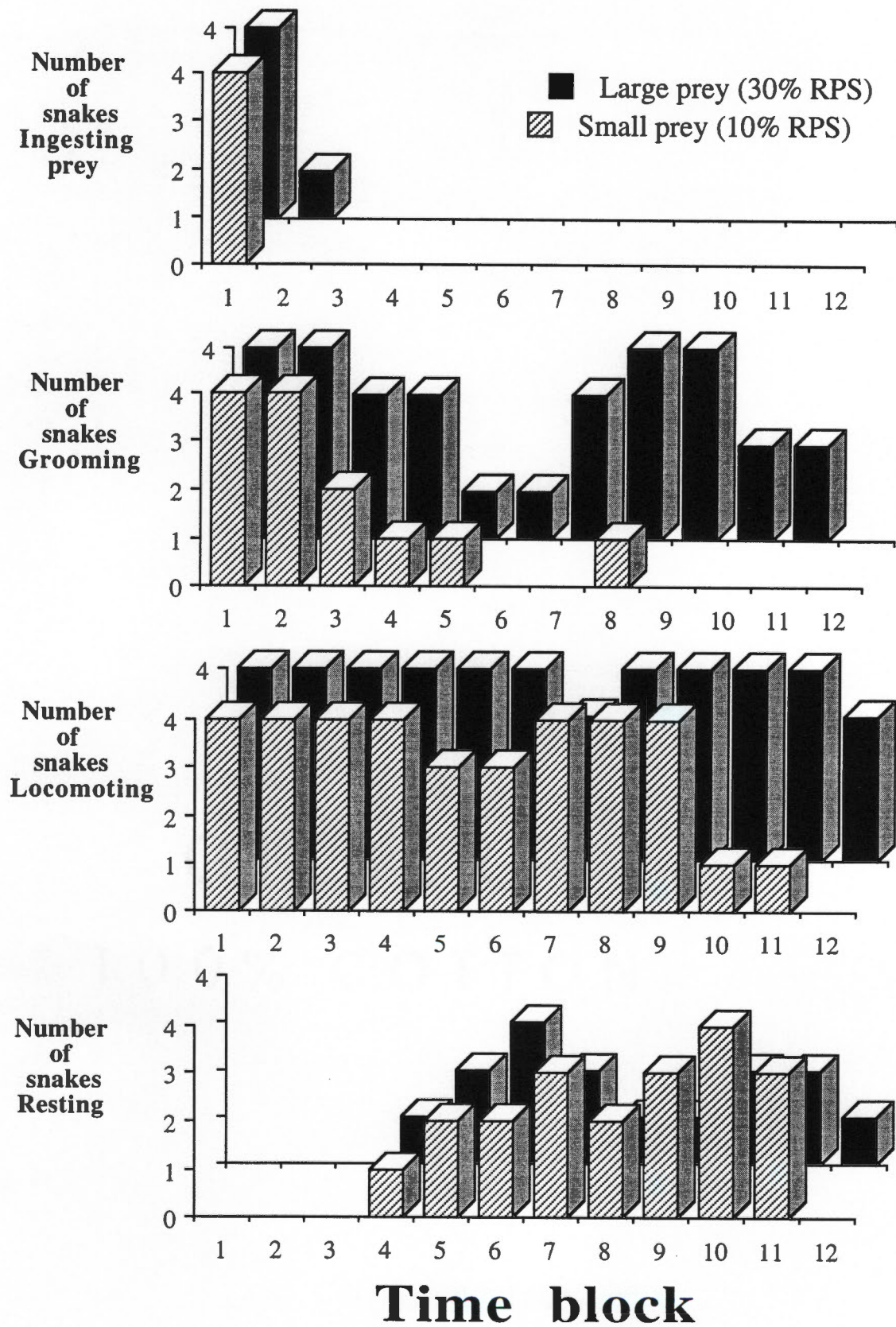
Although the prey sizes in Experiment 2 were considerably different

(10.2% vs. 29.3% of snake mass), each elicited a behavioral sequence that was qualitatively the same. After the completion of ingestion, the snakes groomed, then became active, and eventually came to rest (Fig II-2). Two differences between the treatments are apparent. The snakes that ate large prey had a pronounced, secondary peak (time blocks 7-9) in grooming which was absent in the snakes fed a small item (Fig. II-2). The other major difference was in the timing of the peak of Resting occurred. Snakes which ate large prey came to Rest much earlier than snakes which ate small prey (Fig. II-2, time blocks 6 vs 10).

Given that snakes in one treatment ate a meal three times larger than those in the other, a parsimonious interpretation of the behavioral similarities would be that the qualitative behavioral sequence described here is not an indicator of satiety. This interpretation is also consistent with the extra grooming seen in the large prey treatment group (Fig. II-2). Handling larger fish would leave more mucous on the snakes' scales, thereby eliciting more extensive grooming. Thus, postingestive grooming could be solely a proximate response to stimuli, and not a release of low priority actions after satiation of high priority actions. It may be that these sequences can indeed be used to indicate satiety, but only if they are treated more quantitatively. The snakes that ate large prey came to Rest much sooner than those that ate small prey (Fig. II-2). The postingestive behavior of snakes could be scored after feeding them a range of different prey sizes. If, between one prey size and the next, latency to Rest showed an abrupt change to an earlier onset, it might be possible to identify a quantitative satiety criterion.

However, an intriguing possibility is that the snakes were, indeed,

Fig. II-2. Satiety sequences of Northern water snakes fed large and small prey items (Experiment 2). Four snakes were tested in each treatment group. Large prey were 30% RPS and small prey were 10% RPS. The bars indicate the number of snakes performing each behavior in a given time block. The blocks are three min time periods, beginning with the start of ingestion. For clarity, the bars for each behavior category are not given different symbols (i.e. contra Fig. II-1).



satiated in both the large prey and small prey treatments. It may be that meal size in snakes is not fixed, but, rather, has a threshold value. Any amount greater than that threshold is sufficient to extinguish hunger. Although water snakes can eat single prey that are much larger than 10% of body mass (i.e. 40-55%; see I.C.1), perhaps the ingestion of a single item of 10 or 20% RPS is sufficient to cause the snake to stop hunting and seek a retreat. Although it would be customary in clinical appetite studies to expect meal size to have a target value, are snakes different? Snakes may have a range of satiating meal sizes. Such a range has implications for the evolution of prey size preferences, suggesting some questions for future investigation. How close is the threshold meal size to the typical and maximal prey/meal sizes? Does the threshold change with age/size? How rapidly would a water snake process meals and convert them to body tissue if fed on smaller (e.g. 10-20% RPS) or larger (40-60% RPS) prey, each of which constitutes a satiating meal? Is there an optimum prey/meal size?

This interesting possibility aside, it is difficult to interpret the reality of a qualitative satiety sequence in these snakes. The qualitative "satiety" sequence may be a stimulus-elicited response to any meal, satiating or not. This interpretation is supported by the extra grooming seen in snakes that ate large prey. Alternatively, it may indeed reflect satiety, but the snakes are satiated by a range of different meal sizes. Future work should examine postingestive behavior after small meals ($\leq 5\%$ RPS). Given the difficulties in interpreting a qualitative satiety sequence, the importance of the quantitative criteria from satiation curves was enhanced.

Although they had no prior experience with eating satiating meals in captivity, many of the snakes in Experiment 3 exhibited monotonically

increasing, but decelerating satiation curves (Fig. II-3). In this respect, they resemble laboratory rats (McCleery 1977). For each size class, the longest times (nearest min) needed for meal completion were: large females, 143 min; small females, 42 min; males, 49 min; neonates, 47 min (Fig. II-3). Although the large females took noticeably longer to consume their meals, the other three size classes took about the same time. The logic of scaling relationships would suggest that, all else being equal, small animals should complete meals faster than large animals. From this perspective, the time taken by neonates is comparatively long. Perhaps, however, this result is attributable to the neonates' lack of prey handling experience (cf. Halloy and Burghardt 1990). Given their vulnerability to predators, small snakes may also be under a selective premium to avoid frequent prey handling movements which might attract the attention of a predator (discussed more thoroughly below). Or, it may simply be that snakes need to learn to feed quickly when conditions of superabundant prey are encountered. Based on the meal durations above, I conservatively set the time criteria for meal completion. The inaccuracy in meal size determination would be great if the time allotted were too short. I chose 4 h as the criterion for large females, and 2 h for all of the other size classes.

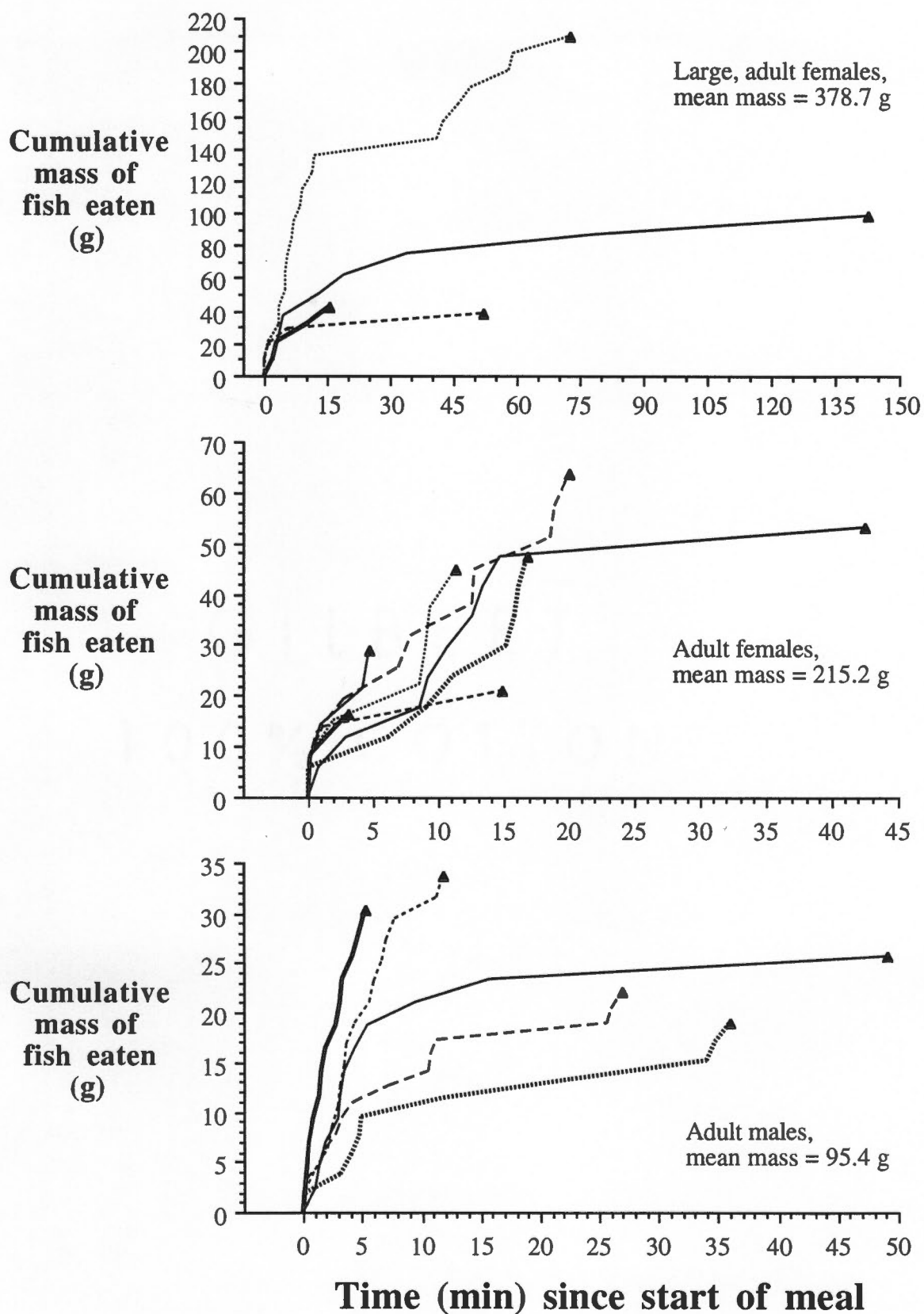
C. The effect of prey size on meal size.

A set of two experiments examined the effect of prey size on meal size in neonate water snakes taking their first meal.

1. Methods.

Experiment 4: Effect of large and small prey on meal size. The subjects were 40 neonates, 10 from each of four litters. Two mothers were

Fig. II-3. Satiation curves for four sizes of Northern water snakes (Experiment 3). The first three panels present data for three size classes of wild caught (i.e. food experienced) snakes: large adult females (n=4), small adult females (n=7) and adult males (n=5). The last panel presents data for neonate snakes (n=5) born in captivity and taking their first meal. The data for each individual within a panel are connected by unique line types. The small triangles denote the end of each snake's meal. The range of the horizontal and the vertical axes is different in each panel. Both groups of females were fed Notemigonus, males were fed Pimephales, and neonates were fed Gambusia.



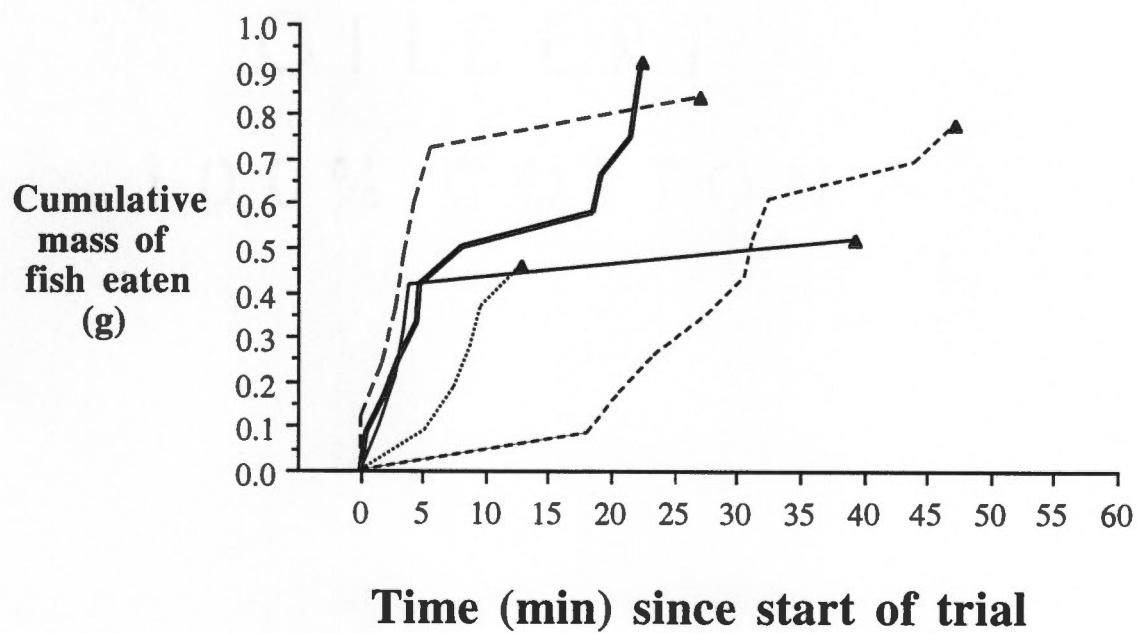


Fig. II-3. (continued)

collected in Little River, Blount County, TN in the summer of 1991. These snakes gave birth on 12 and 17 August 1991. Two mothers were collected in the spring of 1992, one from Boyd's Creek in Sevier Co., TN, and the other from Little River. These two snakes gave birth on 2 and 8 September 1992. Subjects were communally housed by litter at 26 °C and a 13:11 light cycle until testing. Water was provided at all times, but snakes were not fed prior to testing. For the remainder of this dissertation, any mention of naive snakes refers to such ingestionally naive neonates.

Measurements of meal size were made from 27 August-10 September in 1991, and 12-16 September in 1992. Individual subjects were 8-29 d of age when tested (mean = 19 d). During the pretesting deprivation, snakes lost an average of 7% of their birth mass. Snakes from each litter were evenly divided among two treatments. Assignment to treatment was completely random. Snakes in the large prey treatment were each offered a single Pimephales of near maximal size. At the time of these experiments, the largest prey record I had found for N. sipedon was 40% of snake mass (Uhler et al. 1939). Thus, minnows were weighed for size matching to each individual subject, with RPS ranging from 32-55% (mean=45%). Three subjects subdued but were unable to swallow prey of 43, 46, and 52% RPS. These three subjects were retested 1-5 d later, and successfully ingested prey of 41, 32, and 42% RPS, respectively. Snakes in the small prey treatment were offered an excess of small prey. The prey were Gambusia with a mean RPS of 3.1% each (min-max = 2.2-4.5%). Anywhere from 15-28 prey were offered to each snake in the small prey treatment.

Snakes were tested in the same manner as the neonates in Experiment

3 above (i.e. individually housed in clear, round cages). In 1991, testing was conducted between 1500-1830 h. However, many snakes were slow to begin feeding during photophase (pers. obs.). In 1992, testing was conducted between 2245-0200 h. During these night measurements, the testing cages were illuminated with a single, red tinted, incandescent bulb (25 W) suspended 1 m overhead. Under these conditions, snakes initiated feeding much sooner after prey were added (pers. obs.). Regardless of the time of day when tests were started, snakes were given 120 min from the start of the trial to complete their meal. At this point, I assumed that they had fed to satiation (see Satiety Criteria results). The remaining fish were counted and reweighed to determine the mass and number eaten.

Litter means for snake mass were 3.22, 3.70, 4.14, and 4.69 g. These means differed significantly between litters ($F_{3,36}=61.4$, $p<0.0001$). In order to make results more comparable between litters, I analyzed meal size in terms of percentage of snake mass (i.e. total mass eaten/snake mass) $\times 100$). I tested my assumption about the isometry of meal size scaling in a later study (see Experiment 6 below). Meal size data (in %) were analyzed with two way ANOVA. The independent variables were Litter and Prey size, and I chose an α level of 0.05.

Experiment 5: Effect of multiple prey sizes on meal size. The subjects for this study were 39 naive snakes from two litters. One mother captured in Sumter Co., SC in 1992 gave birth on 9 September 1992. This litter ($n=15$ subjects) was tested on 20-21 September 1992. The second mother was captured in Knox Co., TN in May 1993, and gave birth on 31 August. This second litter ($n=24$ subjects) was tested between 11-20 October 1993. Prior to testing, snakes were maintained as described in

Experiment 4 above. Each snake was randomly assigned to a feeding treatment, which consisted of offering the snake an excess of prey of a particular RPS. The assignment of snakes to treatments is outlined in Table II-2. While Experiment 4 compared meal sizes of snakes when fed near-maximal and below-average-size prey, Experiment 5 measured meal sizes at four RPS's within this range: 5, 10, 20, and 40% of snake mass. One difference in testing between 1992 and 1993 was the prey type used. In 1992, snakes in the 20 and 40% RPS treatments were offered Pimephales. The snakes in the smaller prey treatments (5 and 10% RPS) in 1992, and all of the snakes in 1993, were offered Gambusia of the appropriate size (Table II-2). Thus, I am assuming that relatively large Gambusia and similarly sized Pimephales are equally palatable to naive snakes. No one has explicitly measured palatability of different fish species to Nerodia, naive or otherwise. Gove and Burghardt (1975) demonstrated that a litter of naive N. sipedon from Little River had higher Tongue Flick-Attack scores for native fish species than for an exotic species. In the present study, snakes readily attacked and ingested whichever prey type

Table II-2. Protocol for Experiment 5. "Year" indicates the litter.

Year	Treatment = Relative Prey Size (% of snake mass)			
	5%	10%	20%	40%
1992	n=4 neonates fed <u>Gambusia</u>	n=4 neonates fed <u>Gambusia</u>	n=4 neonates fed <u>Pimephales</u>	n=3 snakes fed <u>Pimephales</u>
1993	n=6 neonates fed <u>Gambusia</u>	n=6 neonates fed <u>Gambusia</u>	n=6 neonates fed <u>Gambusia</u>	n=6 neonates fed <u>Gambusia</u>

was offered. All snakes in this experiment were tested at night, as described for the 1992 litter of Experiment 4. Meal size data (in % of snake mass) were analyzed with two way ANOVA as in Experiment 4. The only difference in Experiment 5 was that the Prey size factor had four treatments.

2. Results and Discussion of the effect of prey size. In Experiment 4, there was no significant difference between litters in meal size (see Fig. II-4), although the probability of significance was marginal ($F_{3,32} = 2.42$, $p = 0.084$). Weighting each litter equally, meal sizes of snakes fed small and large prey averaged 21.8% and 44.5% of snake mass, respectively. These means were significantly different ($F_{1,32} = 139.48$, $p < 0.0001$; see Fig. II-4). There were no significant differences in the RPS of the small fishes offered to each of the litters ($F_{3,32} = 0.74$, $p = 0.534$). Thus, the snakes fed small prey were taking much smaller meals than they had "room" for in their gastrointestinal tracts.

This result was confirmed when four different values of RPS were used. In Experiment 5, there was no significant effect of Litter on meal size ($F_{1,31} = 1.40$, $p = 0.25$), but a highly significant effect of Prey size ($F_{3,31} = 6.53$, $p = 0.002$). Weighting each litter equally, the mean meal sizes were, in order of decreasing RPS, 39.2, 27.0, 26.3, and 27.1% of snake mass. There was a marginal trend for a Litter x Prey size interaction, but the evidence was not strong enough to reject the null assumption that the litters showed the same response pattern to Prey size ($F_{3,31} = 1.90$, $p = 0.15$). Post hoc comparisons with Scheffe's test, a very conservative multiple comparison, indicated that meal sizes in the 5, 10, and 20% RPS treatments did not differ from one other ($p > 0.99$ for all). Meal sizes in the 5-20%

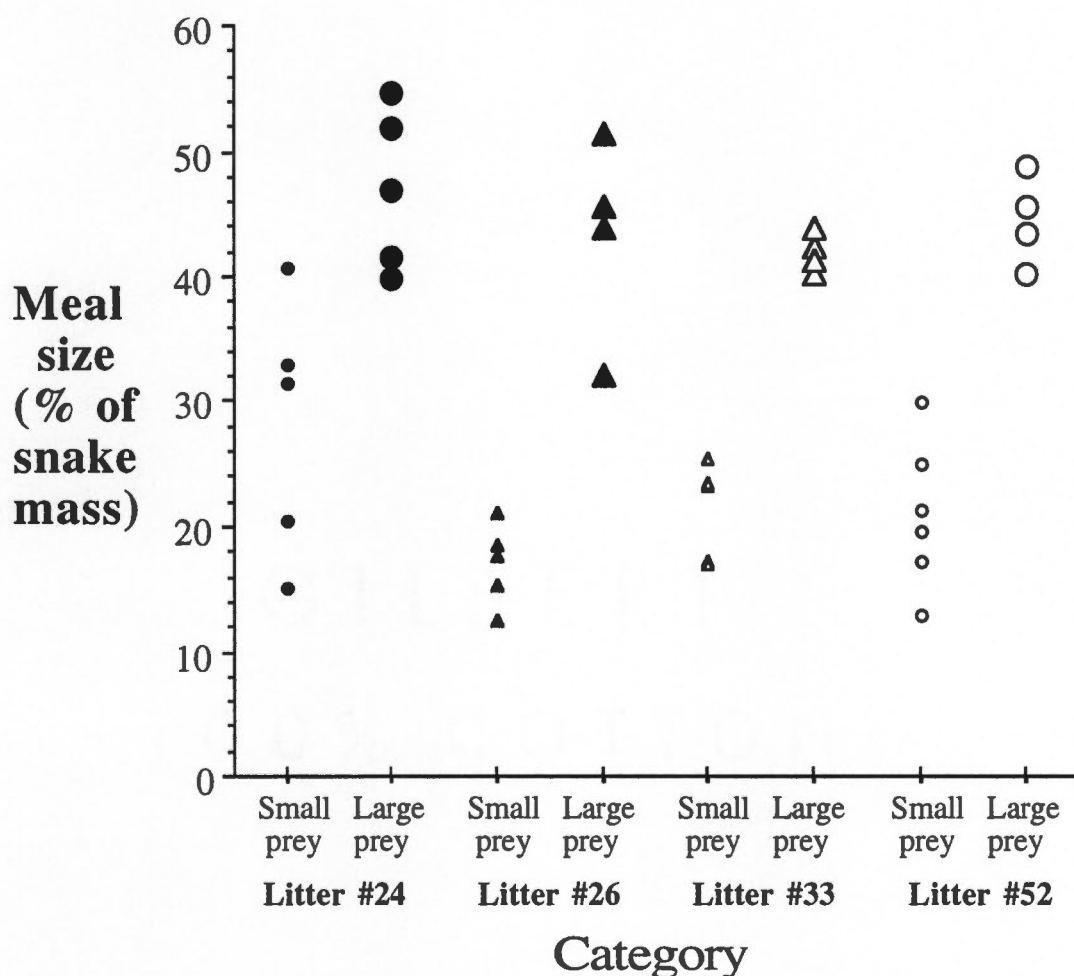


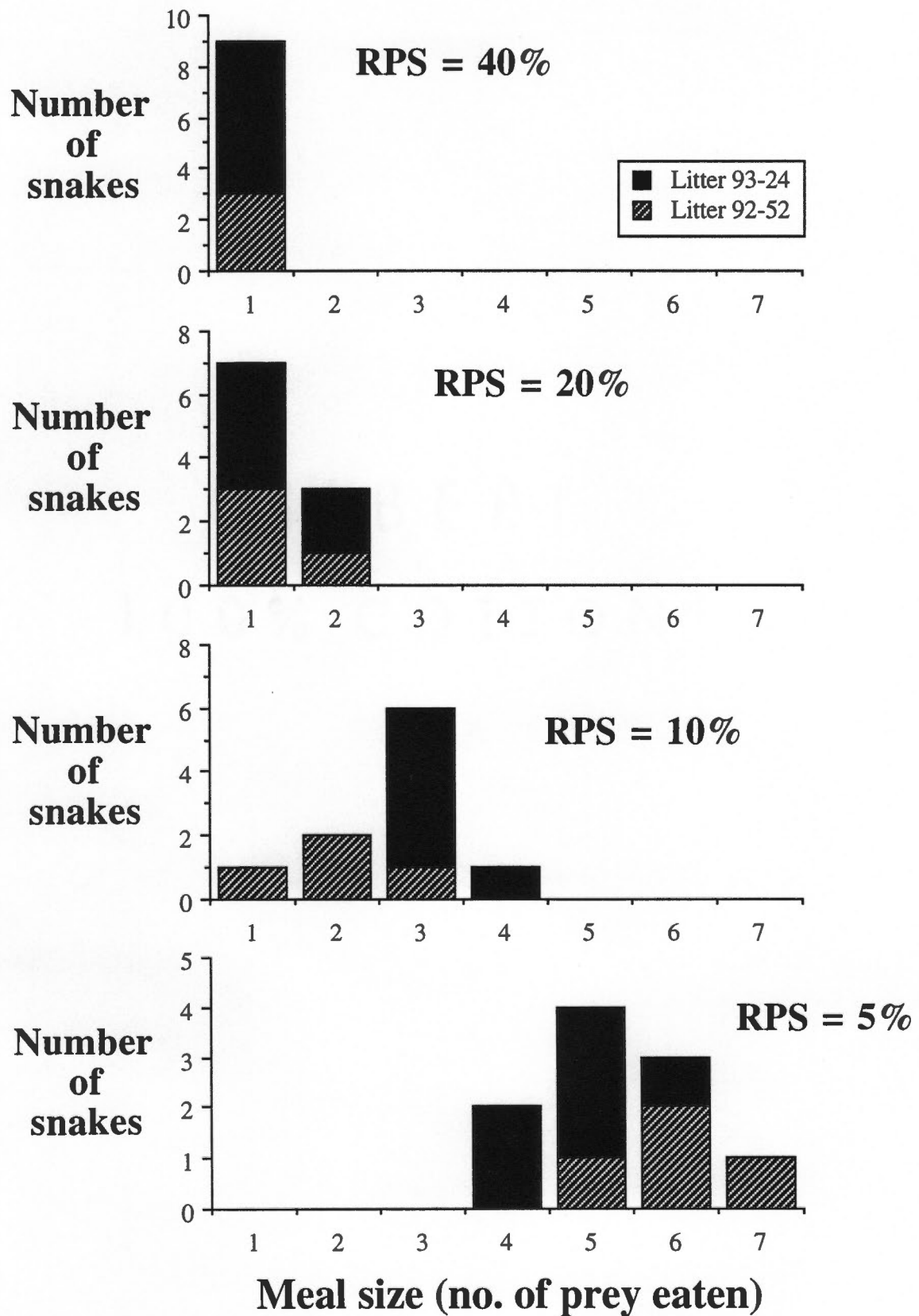
Fig. II-4. Size of the first meal of neonate Northern water snakes offered large or small prey (Experiment 4). Snakes were offered either a single large (ca. 45% RPS) or an excess of small (ca. 3% RPS) fish in a single session feeding. Snakes fed large prey are depicted with large symbols, those fed small prey with small symbols. The different combinations of symbol color and shape distinguish the litters.

RPS treatments each differed from that in the 40% RPS treatment (all p values < 0.01). Thus, in the three smallest RPS treatments, snakes took fewer small prey than the total number needed to sum to 40%. The mean numbers of prey items eaten were, in order of decreasing RPS, 1.0, 1.3, 2.7, and 5.3 (Fig. II-5).

In both Experiments 4 and 5, snakes given any size of prey smaller than the largest took significantly smaller meals. It seems that the satiating influence of individual, small prey does not incrementally sum to the same total meal size as a single, very large prey. This result is reminiscent of oral habituation in rats (Swithers-Mulvey et al. 1991, Swithers-Mulvey and Hall 1992; see discussion in I.B). Based on their study of ingestion in a dicephalous Black rat snake (Elaphe o. obsoleta: Colubridae), Andreadis and Burghardt (1993) speculated that oral stimuli have a satiating influence in snakes. The present results tend to support this assertion for normal snakes in a different colubrid subfamily.

The results of the experiments on the effect of prey size indicate that the meal size of hungry snakes is determined more by the satiating properties of oropharyngeal stimuli than gastrointestinal stimuli. In other words, these snakes are not eating to a particular level of stomach fullness. Given the prodigious ingestive abilities of snakes in general, one might have readily supposed that they would do so. Further, since these studies were conducted on naive snakes, I can exclude the possibility that this effect was learned during previous feeding episodes. These snakes, thus, have an innate reluctance to feed to physical capacity on small prey. This result strengthens the interpretation above (see discussion of behavioral satiety sequences) that these snakes do not have a "target" meal size, but rather

Fig. II-5. Size of the first meal of neonate Northern water snakes offered one of four prey sizes (Experiment 5). Prey were either 5, 10, 20, or 40% RPS. Each panel is a frequency histogram of Meal size (in number of items eaten).



have a range of satiating meal sizes above a minimum threshold. The data in Fig. II-5 suggest that the threshold is a prey item near 20% RPS, as 7 out of 10 snakes in the 20% RPS treatment ate a single item.

Why don't these small snakes always eat to their physical capacity? A physiological explanation could lie in the snakes' abilities to process meals of many small prey versus those composed of few large ones. However, it seems unlikely that a meal of many small prey would be digested less efficiently or more slowly than a single large item would be. For example, a meal of many small prey would have a greater surface area, which would tend to speed digestion. However, each small item would start out with an intact integument, an important barrier to gastric digestion. Thus, the consequences of many small prey versus one large prey for digestion rate are equivocal. As for other physiological interpretations, perhaps snakes follow the predictions of the Eating Paradox (Woods 1991) when they have a choice of meal sizes (i.e. snakes given an excess of small prey). According to the Eating Paradox, small meals would be eaten so as to avoid the major homeostatic perturbation that accompanies a large meal.

Alternatively, the explanations for this effect may be more ecological. There may be a survival cost to gorging on small prey which outweighs the energetic benefits of a bigger meal. One can posit a correlation between the number of prey capture movements a small snake makes and the probability of its being detected by a predator. Pough and Andrews (1985) used such an argument in proposing a "movement minimizer" strategy in lizards. In addition, large meals may reduce the locomotory flight capacity of small snakes (cf. Garland and Arnold 1983,

Ford and Shuttlesworth 1986, Herzog and Bailey 1987). Thus, when small prey are abundant, snakes may eat submaximal meals in order to avoid detection by and/or maintain their ability to escape from predators.

Both the physiological and the ecological explanations suggest fitness consequences for various prey size preferences. In the currency of survival and energy acquisition, one could potentially define an optimal prey size. On the one hand, larger prey yield more energy for growth and reproduction. In addition, concentrating on small prey necessitates more extensive movements that expose the foraging snake to predators. Thus, preference for small prey might be selectively disadvantageous. On the other hand, reduced flight capacity and homeostatic perturbation may select against preference for large prey. In this regard, the comparatively small meals of water snakes when offered small prey suggests that preference for large prey has been selected against. It could be argued that the optimal prey size of Northern water snakes is an item near 20% RPS, i.e. an item at the apparent satiety threshold. Future work should more explicitly treat the fitness consequences outlined here. Studies in the field could further serve to identify constraints on optimality. Thus, how do the availabilities of large and small fish in the field limit the predatory options of foraging water snakes?

Regardless of the ultimate explanation, it is probably the case that the reduced meal sizes at small prey sizes are not unique to neonatal snakes. The meal sizes of experienced water snakes when fed multiple, submaximal prey are approximately the same as those seen in the present study, i.e. about one quarter of body mass (Brown 1958, Tu and Hutchison 1995; see I.C above). This comparison raises the issue of allometric changes in meal

size, which forms the basis of the next section.

D. The effect of predator size on meal size.

Data from several of the experiments described above (Experiments 4 and 5) and below (see Chapter III) were pooled in order to investigate ingestive allometry in water snakes (Experiment 6).

1. Methods. The data for Experiment 6 were, in part, compiled from other experiments in which snakes were fed to satiety on small prey. These data were supplemented with tests of additional subjects to bring the total sample size to 36 juvenile and adult (hereafter, "experienced") snakes. All snakes were from Blount, Knox, and Sevier counties, TN, and were maintained as described above. The pretesting fasts and minimum session durations for each size class of snake followed Experiment 3. Total meal size and snake mass (both in g) were log transformed and regressed against each other. I tested whether meal size scaled isometrically by determining if the 95% confidence interval for the log-log slope encompassed a value of 1.0.

In order to evaluate scaling effects over the largest size range possible, data on meal sizes of 34 neonates were compared to those of adults. The data were taken from the snakes fed small prey in Experiment 4 (n=4 litters), and from the snakes fed prey of 5% RPS in Experiment 5 (n=2 litters). Three neonates from two additional litters were also tested. Regardless of level of experience or prey species used, all snakes in the scaling analysis were fed to satiation on prey of 2-5% RPS. Since the data from littermates may not be statistically independent, meal sizes from one randomly selected neonate per litter were combined with the data for

experienced snakes to generate a pooled regression. Thus, the sample of 44 animals in the pooled regression included 8 neonates.

2. Results and Discussion of the effect of predator size.

The mass range of experienced snakes was 29.2-448.6 g. There was a significant correlation between meal size and snake mass ($r=0.71$, $p < 0.001$). The equation for the least squares regression was: $\text{Log (Meal size, g)} = -0.567 + 0.921 (\text{Log Mass, g})$. The slope is not significantly different from a value of 1.0 (95% confidence interval = 0.62-1.24). The neonate snakes did not span a sufficient size range (2.5-5.2 g) to warrant calculating a separate scaling regression for them. However, meal sizes of neonates fell closely on the extension of the regression line for experienced snakes (Fig. II-6). The regression for the pooled data (i.e. experienced snakes + one neonate per litter) was also highly significant ($r=0.93$, $p < 0.001$). The equation for the pooled regression was: $\text{Log (Meal size, g)} = -0.677 + 0.972 (\text{Log Mass, g})$.

The slope of the pooled regression is very close to a value of 1.0. The most parsimonious explanation is that meal size of hungry water snakes scales isometrically. The meal sizes of snakes of all sizes can thus be compared as a simple percentage of body mass. There was no significant difference between experienced and naive snakes in percentage meal size ($t=0.38$, $p=0.71$). Combining data for all 70 snakes (36 experienced snakes + 34 neonates), meal size averaged 22.4% of snake mass. Frequency histograms of meal size suggest normal distributions for both experienced and neonates, although there was more variability in the experienced snakes (Fig. II-7).

A larger suite of potential predators can prey upon neonates than

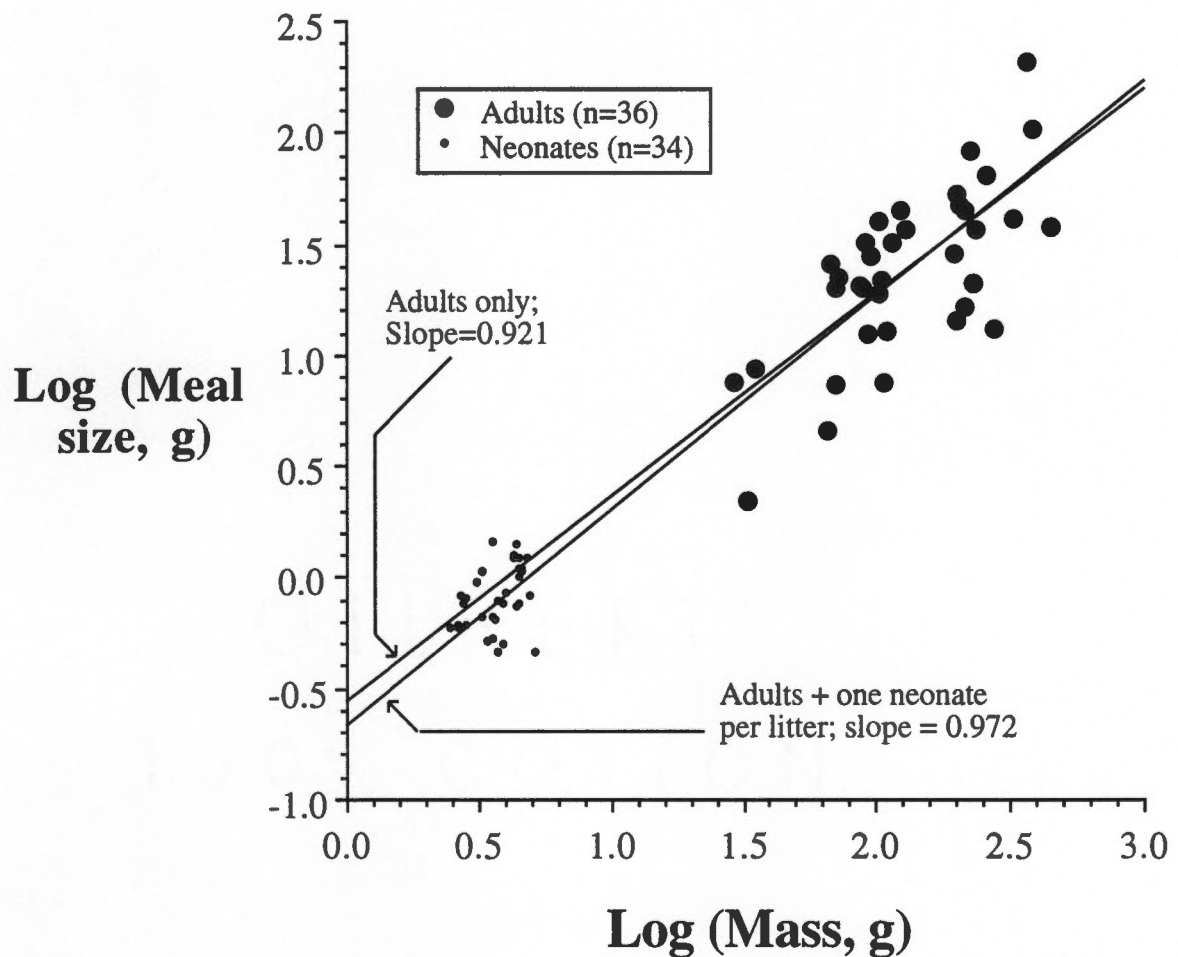


Fig. II-6. Scaling of meal size in Northern water snakes (Experiment 6). Meal sizes of hungry adult and neonate water snakes were $\log_{10}$ transformed and plotted as a function of the log of snake mass. For illustrative purposes, all of the data for neonates are plotted even though they were not used in calculating the regression.

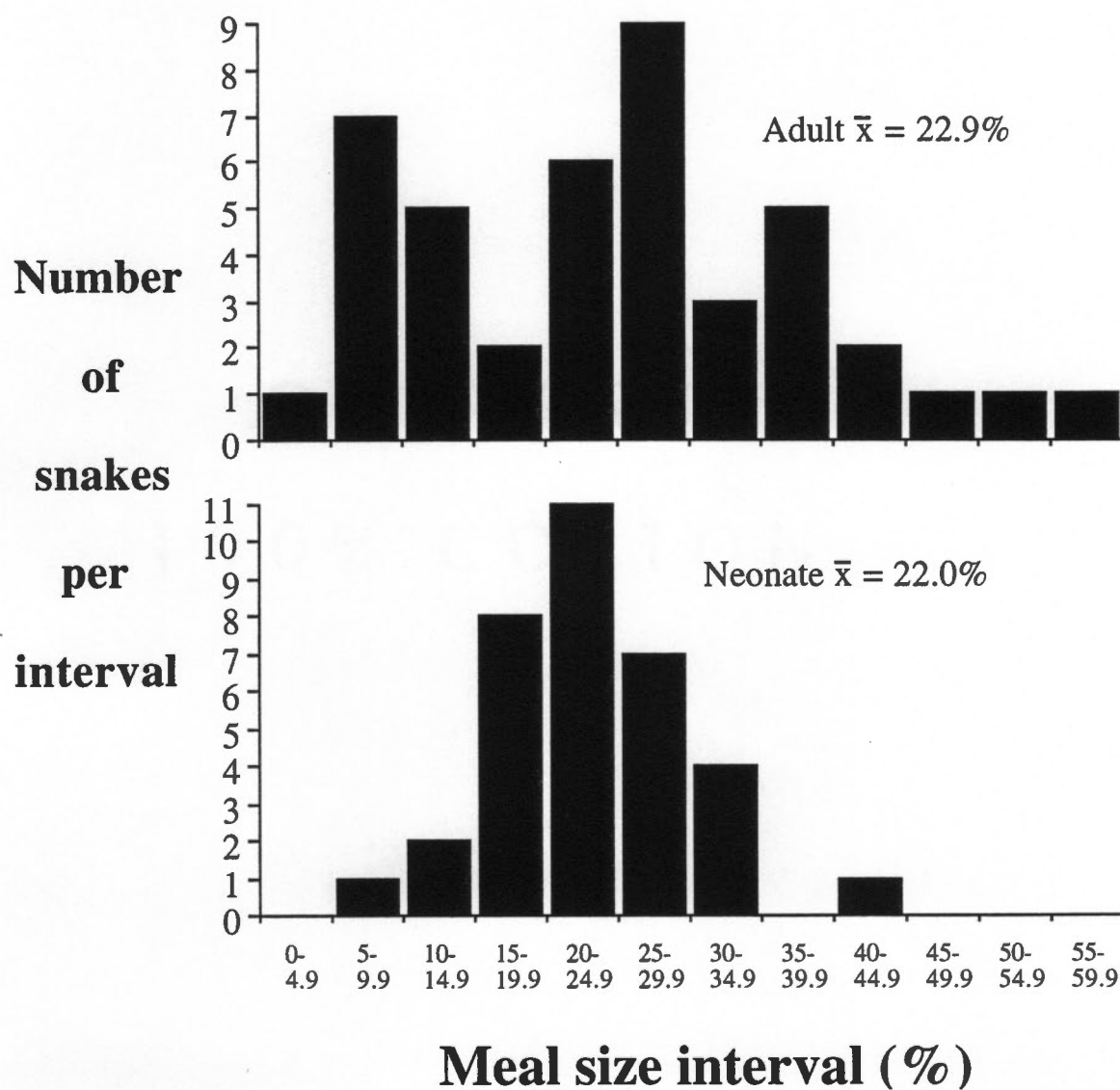


Fig. II-7. Frequency distributions of Meal size (%) of Northern water snakes of various sizes. Experienced snakes are presented in the upper panel, neonates in the lower panel. These data are from the same snakes depicted in Fig. II-6.

adults. Thus, it could be argued that neonates can less afford to be burdened down by carrying a large meal. Under such a scenario, larger snakes could consume relatively larger meals than small snakes. However, the scaling results indicate that hungry snakes of all sizes consume about one quarter of their body mass if they encounter an aggregation of small prey. Because mammals show comparatively little body size variation as adults, intraspecific studies of ingestive allometry as reported here have not been previously described. Further, since naive and experienced snakes take small-prey meals of similar relative size, the parsimonious interpretation would be that the behavior is innate, remaining functional throughout the lifetime of the animal. The greater variation in meal size in adults relative to neonates (Fig. II-7) suggests that other learned, experiential, or maturational factors may also have effects. Overall, these findings and interpretations underscore the utility of ectothermic subjects to generating a comprehensive theory of appetite control.

E. Summary: Individual meals in the session paradigm.

Northern water snakes exhibit a behavioral satiety sequence that closely resembles that in mammals: feeding is followed by grooming, then locomotory activity, and finally, by resting. However, satiety sequences were qualitatively similar after meals of 10 and 30% of snake mass. Because of ambiguity in interpreting this sequence, a temporal criterion derived from satiation curves was used to establish satiety.

Neonate water snakes eat much smaller meals when offered an excess of small prey than when offered a single large prey. At prey sizes $\leq 20\%$ RPS, meal size of neonates was 23.5% of snake mass (average of 6 litter

means). In contrast, neonates can readily ingest single prey of 40% RPS, and sometimes can consume prey as large as 55%. Since snakes exhibited this response in their first feeding, the response is innate.

When RPS is held constant, the meal size of hungry water snakes scales as an isometric function of body mass. Over the mass range of 2.5-449.0 g, meal size averaged 22.4% of body mass ($n=70$). Because snakes are competent foragers over a large range of body sizes, they are ideal models for investigating ingestive allometry.

CHAPTER III

MEAL PATTERNS IN THE FREE FEEDING PARADIGM

A. Introduction.

The free feeding paradigm has become a standard tool in appetite research. When the ad libitum feeding behavior of Norway rats (Rattus norvegicus) was first studied, it was as a model for behavior that occurred in bouts. Richter (1927) sought to identify the factors controlling the initiation and termination of bouts of feeding. The free feeding paradigm also came to be widely used in clinical studies of appetite, particularly following Le Magnen and Tallon's (1966) demonstration of a correlation between meal size and time to the next meal in laboratory rats. Since these early endeavors, the range of taxa sampled has expanded to include other mammals and some birds (Le Magnen 1985; Clifton 1987). However, major taxonomic gaps are apparent. For example, in spite of Rozin's (1964) recommendations that the feeding patterns of nonendothermic species should be examined, ectotherms remain understudied. The closest examples in vertebrates are studies of fishes in aquaculture settings (see Jobling et al.1995). Such work has focused on the end result of fish growth and biomass accumulation for commercial production. The lack of study of ectotherms is unfortunate, as most animals are, of course, ectothermic poikilotherms. The general principles of appetite function obtained to date may thus lack universality within the animal kingdom.

Another dimension of feeding ecology which has not been satisfactorily explored is the spectrum from frequent to intermittent

feeders. Most of the well studied laboratory species can be characterized as nibblers because they take many meals per day. When freely feeding, Guinea pigs (Cavia porcellus) take 20-25 meals per day, Chickens (Gallus gallus) take 30-40, and Norway rats eat 12-15 (Collier and Rovee-Collier 1981). None of the species examined to date can be characterized as having a feast-or-famine feeding pattern. Mammalian carnivores are probably the closest representatives of a feast or famine lifestyle among common laboratory species. However, domestic ferrets (i.e. Polecats, Mustela putorius furo) typically take 10-12 meals per day (Collier and Rovee-Collier 1981), and House cats (Felis catus) take 9-10 meals per day when freely feeding (Kanarek 1975, Kaufman et al. 1980). These carnivores were, of course, fed on commercially prepared foods, so it remains to be seen what the frequencies of meals would be if live prey were offered.

What about animals that feed even less frequently? Among vertebrates, snakes occupy one end of a spectrum of prey size and feeding frequency. The evolutionary history of snakes featured a shift from frequent feeding on small, arthropod prey (Pough 1980, Greene 1982) to taking relatively large, vertebrate prey at infrequent intervals (Greene 1983). Although there is considerable variability among snakes in their feeding ecologies (Greene 1997), all snakes can be considered as having a feast or famine lifestyle relative to other vertebrates. Only one previous study has examined free feeding in a snake. Myer and Kowell (1971; M&K hereafter) offered live mice once per day to four Florida kingsnakes, Lampropeltis getula floridana (Colubridae). On each day that the snakes would feed, they were offered successive prey until satiated. Meals consisted of 1-10 mice, with median meal sizes of three or four mice for

each subject. One of the most interesting findings was that these snakes fed in temporally discrete meals, i.e. that they fed prandially. Intermeal intervals ranged from 1-15 days, with median intermeal intervals of 4-6 days.

Despite this early foray into free feeding by snakes, many questions remain. Do all snakes feed prandially? If so, what are typical meal sizes in both absolute and relative terms (i.e. % of body mass), and how is meal size distributed? In terms of feeding frequencies, M&K technically employed a fixed interval schedule of food access. Thus, by design, snakes could only take one meal per day, raising the question of when snakes would feed under truly *ad libitum* conditions. In addition, more sophisticated methods are now available for separating the pauses between prey within a meal from the intervals between successive meals (e.g. log survivorship analysis; Slater 1974). In his review of the ethology of predation, Curio (1976) emphasized the fact that M&K's subjects generally did not take small meals (e.g. single mice). Such a condition is contrary to the arguments comprising the Eating Paradox (Woods 1991). Because the surge of absorbed nutrients after a meal is potentially harmful deviation from the normal condition of tightly controlled, internal homeostasis, Woods argues that animals ought to take small, frequent meals. Do snakes take relatively small meals when freely feeding, or does their trophic lifestyle both enable and require them to violate the Eating Paradox? Do snakes exhibit similar meal patterns to those reported for other animals (Le Magnen 1985, Clifton 1987)? With regard to this point, M&K did not report any statistical correlations between meal size and intermeal intervals.

I examined free feeding patterns in Northern water snakes. Although they do not embody the extreme feast-or-famine lifestyle of pythons or pit vipers, Northern water snakes can take relatively large meals. Prey items weighing 40-60% of snake mass have been recovered from N. sipedon stomachs (Uhler et al., 1939; Brown, 1979; Andreadis, unpublished data). Since this species simply swallows live prey, muscular fatigue and exhaustion of venom stores do not influence meal size the way they might in constrictors (e.g. L. getula) or venomous species. Water snakes readily feed on commercially available bait fishes, and these prey can not harm the snakes the way that mice can potentially harm rodent eating snakes. Thus, I was able to keep a constant supply of live prey in the snakes' home cages, thereby achieving a true ad libitum availability.

B. Methods

The subjects for this study were four N. sipedon, one each from Knox and Sevier Counties, and two from Blount County, TN. Two male snakes were tested from 22 July-15 September 1993. Two female snakes were tested from 2 September-4 November 1994. All snakes were of similar initial size (see Results). However, N. sipedon exhibits sexual size dimorphism, with adult females averaging much larger than adult males. Given the smallest size at maturity for each sex (Bauman and Metter 1977, Mitchell 1994), the females in the present study were prereproductive, while the males were adults. King (1939) indicated that courtship of N. sipedon could be seen from mid-April through May in Great Smoky Mountains National Park, and Mitchell (1994) observed courtship from 17 April-12 June in Virginia. Thus, none of the subjects would have been

reproductively active during the study period. Snakes were individually housed in cages of clear, acrylic plastic (38 x 26 x 16 cm). The cages were visually isolated from the rest of the laboratory, and from each other. The cage lids were either hardware cloth (3.2 mm mesh) or solid, clear plastic. Aged tap water (24+ h old) was continuously available in a round, glass water bowl (19.5 cm diameter x 6.5 cm high). A red brick (20 x 10 x 3 cm) was provided for the snakes to perch on and to rub against during ecdysis. A stiff, tan colored mat paper with surface corrugations was used for the floor substrate, and was changed whenever darkened by wetting or elimination. Snakes were maintained at 26 °C and a light:dark cycle of 13:11 prior to (2-10 weeks) and throughout the study. The fluorescent ceiling lights were on from 0600 h-1900 h EST. Several red tinted, incandescent bulbs (25 W) remained on at all times. The light of the red bulbs was not significant when room lights were on, but provided sufficient, dim illumination at night for the videocamera to pick up images of the snakes and fish. Night visibility was enhanced by the mat paper's light color, against which the snakes and fish (in glass bottomed bowls) were darkly contrasted.

Snakes were fed exclusively on commercially obtained Fathead minnows (Pimephales promelas: Cyprinidae). The mass of an individual fish averaged 1.90 g (SD = 0.32), which corresponded to 2.6-2.9% of the initial body mass of the snakes. Fish were placed in the water bowl of each snake's home cage. By trial and error, I found that the largest number of fish that could be kept in the bowls without risking overcrowding and suffocation was five or six. Some mortality occurred when fish were transferred directly from their cool (20 °C), well-oxygenated holding tank

straight to the warm, still water in the snakes' bowls. The survival of uneaten fishes was lengthened by acclimating them in a bucket in the snakes' room for 24-48 h prior to using them. The snake cages were checked 2-4 times per day to ensure that live prey were continuously available (but see below). By recording the number of fish remaining, it was possible to determine whether snakes had fed since the last time that they were checked. Whenever the supply of fish in a cage was low or, as occasionally happened, exhausted, a new set was added. The total mass of fish offered in each new provisioning was recorded. Since the individual fishes offered in any one provisioning were of similar size, the mass of fish eaten per feeding bout was based on the number of fish eaten and the average fish mass for that group of prey. The water was changed whenever it became fouled by dead fish or feces.

The snakes were videotaped with a Panasonic time lapse, VHS recorder placed approximately 2 m above their cages. Date and time were recorded on the tapes. The time compression was set to record 48 h of real time on a 2 h VHS cassette. Once every 24 or 48 h, the tapes were removed. If the fish count indicated that snakes had not fed, the tape was immediately rewound and placed back into the recorder for taping over. Since the recorder used in the study was the only unit on which the tapes could be viewed, I had to halt videotaping in order to replay preexisting tapes. Typically, the time required to review an old tape was about 30 min. While reviewing old tapes, I periodically inspected the snakes to see if they had fed.

The time of ingestion of each fish was, where possible, measured to the nearest second. In a few cases, the point at which feeding occurred

could only be narrowed to a certain time window (e.g. 1-60 min). This circumstance occurred when, for example, the snake sat in the water bowl for an extended time, temporarily obscuring the field of view. In such cases, the midpoint of the time window was chosen as the ingestion time. Since the bout criteria which I chose were much longer (ca. 3-6 h; see Results) than this time frame, this level of resolution was sufficient for inclusion in the data set. In very few cases, the time window was lengthy (e.g. many hours) due to camera failures, power outages, improper adjustment of the recorder (causing the tape to run out prematurely), and death of all the prey or their complete consumption by the snake. In such cases, data on interprey intervals were not included. Even in cases where complete data were missing, some useful information could still be obtained. Thus, while the exact timing of a meal might be lost, I could often determine the size of that meal and assign its occurrence to daytime or nighttime categories. As a result, sample sizes for meal sizes, intermeal intervals, prandial correlations, etc. differ slightly from one another for a given snake.

Cumulative mass of food eaten over the course of the study was tabulated in order to examine long term patterns of food intake. These data were combined with the changes in mass of the snakes over the study in order to estimate growth efficiency. Production-ingestion ("PI") ratios were calculated as the increase in body mass over the study divided by the total mass of fish eaten over the same time period (Scudder and Burghardt 1985).

The time intervals between ingestions of individual fish were subjected to a log survivorship analysis (Slater 1974, Clifton 1987). In

brief, cumulative frequency distributions of interprey intervals were constructed in descending order (i.e. number of observations per category declines from left to right). The vertical axis, the number of intervals longer than a given interval, is logarithmic, while the horizontal axis, the length of the time interval, is arithmetic. A behavior that is not organized in discrete bouts appears as a straight line in a log survivorship plot, while a behavior occurring in bouts would have a sharp discontinuity in the distribution (Fig. III-1). The series of short intervals represent the pauses within a bout, with the larger intervals reflecting the lengthier times between bouts. A bout criterion interval ("BCI"), the time interval at which the cumulative frequency distributions show a sharp break, was visually estimated for each snake. This point was used as the time criterion for separating intrameal pauses from intermeal intervals. However, since the two distributions overlapped (as is often the case; see Clifton 1987), no

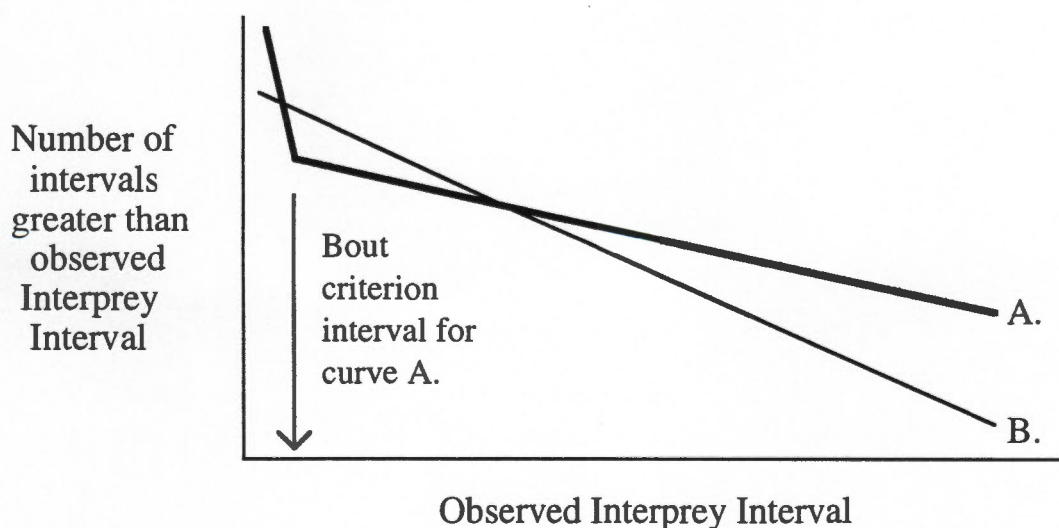


Figure III-1. Theoretical curves from a log survivorship analysis. Curve A is organized in discrete bouts, while curve B is not.

criterion could be a perfect separator, or be chosen with strict objectivity. In choosing BCIs that were the most biologically meaningful, I was guided by the following considerations. Slater (1974) suggested that assignment errors can be minimized by setting the criterion to be the shortest interval that is longer than the most obvious break in the distribution. Extending this logic, I also chose criteria that followed conspicuous gaps in the distributions, and considered each BCI to represent the shortest intermeal pause of each snake.

Once BCI's were chosen, the entire feeding record of each snake was subdivided into meals and intermeal intervals. Frequency distributions, minima and maxima, and measures of central tendency were determined for meal size and intermeal interval. Changes in meal sizes over the course of the study were plotted, as was the temporal relationship of meal taking to periods of ecdysis. I considered the ecdysis period to be the time from when the first detectable opacity of the skin was noted until the old skin was shed. I tested whether feeding activity was distributed randomly over the course of the day with χ^2 a priori tests. The numbers of meals initiated during day and night were tested against the expected ratio of 13:11 set by the photoperiod. Finally, meal patterns were sought in the form of the correlation between sizes of consecutive meals. Other meal patterns that I tested for included the correlation between meal size and the ingestive pause preceeding (the preprandial correlation) and following (the postprandial correlation) the meal. Since meal sizes and intermeal intervals often are not normally distributed (Clifton 1987), I used the Spearman rank correlation statistic to test for the significance of all meal pattern correlations.

C. Results

1. Cumulative food intake and growth. Linear regressions fit to the cumulative food intakes yielded overall ingestion rates of 1.36-3.63 g/d (mean=2.36 g/d) for the four subjects over the course of the study. This 2.7 fold variation is not explained by sex or year of the study, as the two subjects with high ingestion rates (steep trajectories on Fig. III-2) were a male from 1993 and a female from 1994. The cumulative ingestion curves of all four subjects had more of a curvilinear shape than a strictly linear one (Fig. III-2). In general, the snakes fed at a relatively high rate in the early part of the study (approximately the first 16-25 d), then at a lower rate for the remainder.

All snakes increased in mass on the ad libitum ration (Table III-1). In order to avoid overly disturbing the subjects, they were removed for weighing only occasionally. Over periods of time ranging from 36-57 days, the snakes increased in mass by 15-65% (Table III-1). The two snakes with conspicuously high rates of food intake (#93-25 and #94-66) were also the two individuals with the greatest mass increases (cf. Fig. III-2 and Table III-1). Snake lengths were not measured so as to avoid injuring the subjects or having them form negative associations with me or with handling. However, my visual impression was that, though the snakes generally looked more stout, none were conspicuously obese. Indeed, the subject with the smallest percentage increase in mass (15%) was not noticeably longer or stouter to the eye at the end of the experiment. In terms of the efficiency with which snakes converted food into body tissue, PI ratios averaged 0.24 (Table III-1); three snakes were nearly indistinguishable, with one male exhibiting a much lower efficiency.

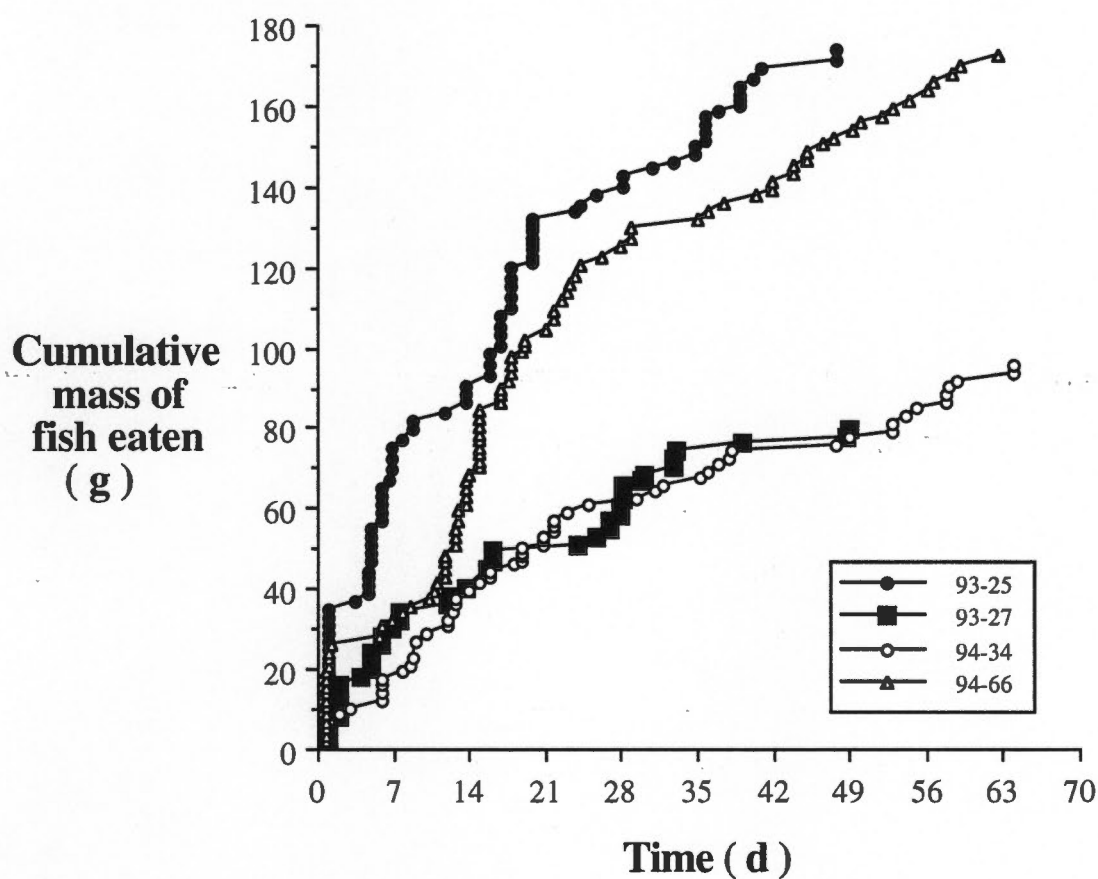


Fig. III-2. Cumulative food intake patterns of four Northern water snakes fed ad libitum. The data for each snake are represented by unique symbols (identified in legend). Long, horizontal portions of these curves reflect extended periods during which the subjects did not feed. For sake of comparison, the curves from both years of the study are set to the same starting point.

Table III-1. Growth increments of four Northern water snakes fed ad libitum. Snakes were not all measured at the same points in the study, so number of days from start of study to last weighing are noted. The mass ratio is the final mass divided by the initial mass. PI ratios are calculated by dividing total mass increase of the snake by the total mass of food consumed over the same time period.

		Start	Initial	Elapsed	Final	Mass	PI
<u>Snake</u>	<u>Sex</u>	<u>date</u>	<u>mass (g)</u>	<u>time (d)</u>	<u>Mass (g)</u>	<u>ratio</u>	<u>ratio</u>
93-25	M	22 July	73.9	36	115.9	1.57	0.268
93-27	M	22 July	69.5	38	80.1	1.15	0.141
94-34	F	2 Sept.	66.0	60	90.6	1.37	0.268
94-66	F	2 Sept.	71.4	62	118.1	1.65	0.271

2. Log Survivorship curves. Cumulative frequency distributions of interprey intervals were constructed for log survivorship analysis (Fig. III-3). In general, these curves approximated the broken-stick shape that is typical of a behavior organized in bouts. However, both males exhibited much sharper breaks between intrameal and intermeal pauses than did the females (Fig. III-3). As a result, the choice of a BCI was somewhat more subjective for the females. The BCI's ranged from 2.98-6.40 h (Table III-2). There was an obvious clustering of intermeal intervals around certain higher values, especially near 24 and 48 h (Fig. III-3; see also "Meal frequency" below).

The BCI of each snake was used to divide its feeding record into a series of meals (n=24-49) and corresponding intermeal intervals. Meal size and meal frequency are described separately in the next two sections.

3. Meal size. The frequency distributions of meal sizes of all four snakes were strongly positively skewed (Fig. III-4). Meal sizes are depicted in terms of number of fish eaten so as to indicate that the modal meal for each snake consisted of a single fish. Forty-four and 51% of the male snakes' meals consisted of one fish, while 70 and 71% of the female snakes' meals were of a single fish. Because of the skew in meal size distributions, medians are reported as an indicator of central tendency. Median meal sizes ranged from 1.70-4.40 g, or 2.7-6.0% of the snakes' initial masses (Table III-3). The maximum meal size ranged from 3.3-10.8 times as large as the median meal size (Table III-3). Minimum meal size was not strictly under the snakes' control, being determined by the size of the smallest fish that I provided. Since it was not clear what the true minimum meal size of the snakes would be, this parameter is reported as

Figure III-3. Log survivorship curves of the interprey intervals of four Northern water snakes fed ad libitum. The number of interprey intervals longer than a given time interval is plotted as a function of the length of the time interval. The scale of the Y axis is logarithmic, the X axis arithmetic. The bout criterion intervals were fitted by eye to separate the numerous interprey intervals of very brief duration (i. e. intrameal pauses) from the longer time intervals between the last prey item of one meal and the first item of the next meal (i. e. intermeal intervals). The ranges of the X axes are different for each panel.

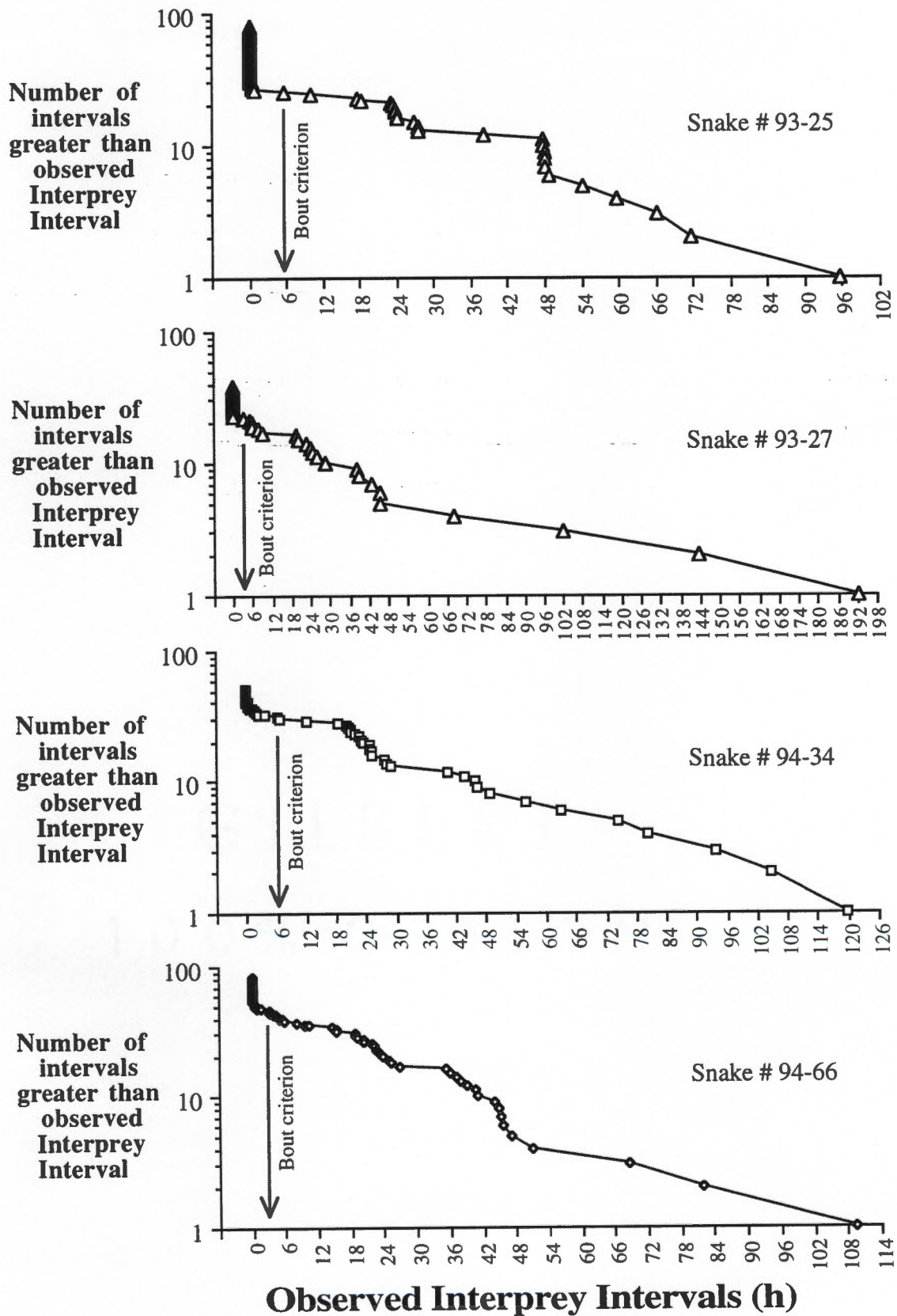
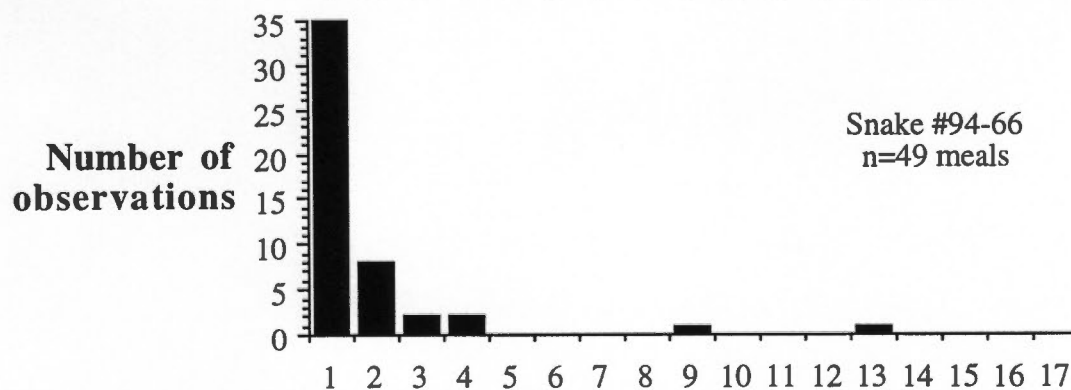
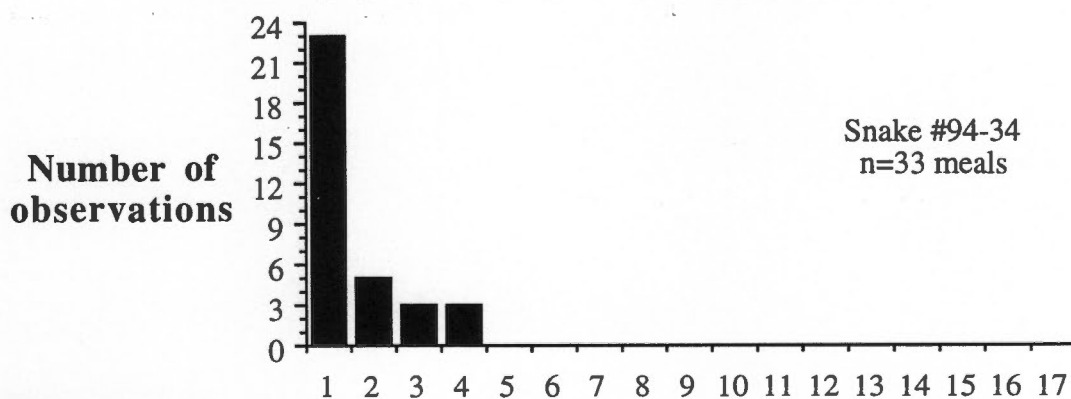
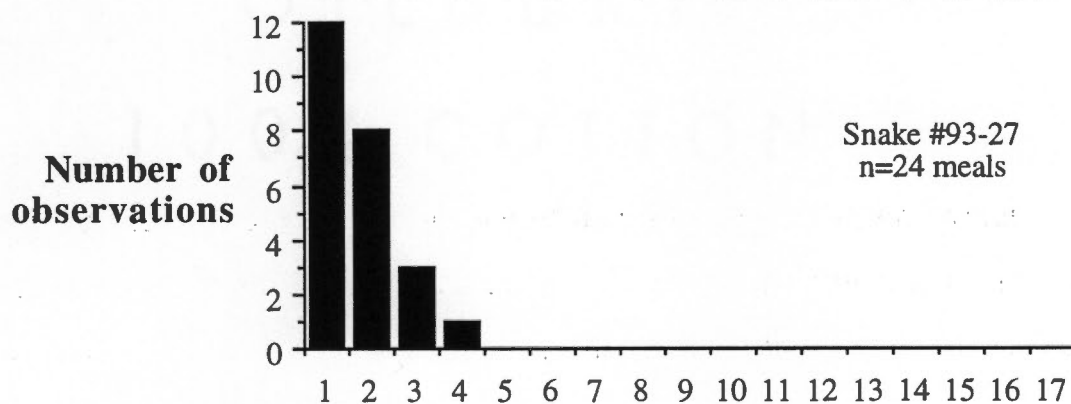
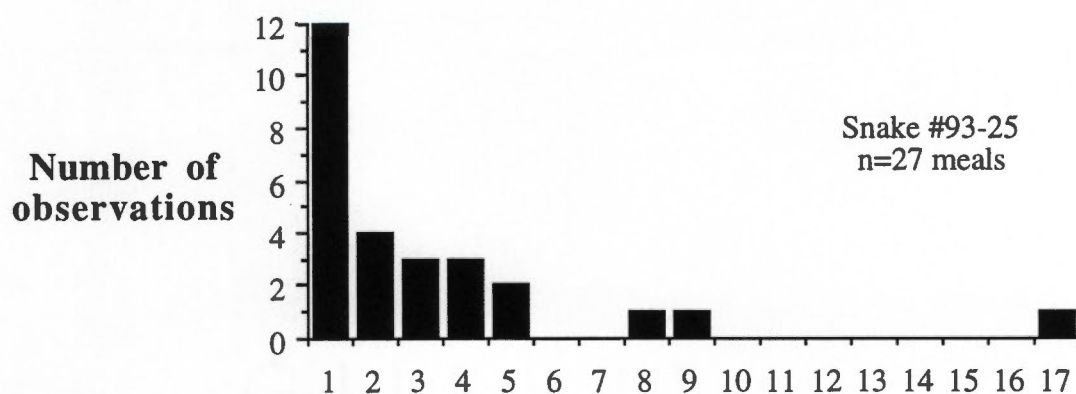


Table III-2. Meal parameters of four Northern water snakes fed ad libitum. Bout criterion intervals were determined by log survivorship analysis of interprey intervals, and represent the shortest intermeal interval of each subject. Meal sizes were calculated by multiplying the number of fish eaten in a meal by the average fish mass in that provisioning. Because meal sizes and intermeal intervals were both strongly skewed, medians are reported as measures of central tendency.

		Initial	Bout	Total	Median	Median
<u>Snake</u>	<u>Sex</u>	<u>Mass (g)</u>	<u>Criterion</u>	<u>no. of</u>	<u>Meal</u>	<u>Intermeal</u>
			<u>Interval (h)</u>	<u>Meals</u>	<u>size (g)</u>	<u>Interval (h)</u>
93-25	M	73.9	5.57	27	4.40	32.79
93-27	M	69.5	2.98	24	2.45	26.12
94-34	F	66.0	6.40	34	1.75	26.38
94-66	F	71.4	2.98	49	2.10	22.65

Fig. III-4 Frequency distributions of meal sizes of four Northern water snakes fed ad libitum. Meal sizes are reported as number of fish eaten. Most meals consisted of a single prey item.



Meal size (no. of fish eaten)

Table III-3. Meal size parameters of four Northern water snakes fed ad libitum. Meal size entries are reported three ways: absolute mass in grams, percentage of initial snake mass, and number of fish eaten. "Minimum meal size" is actually an average of all meals consisting of a single fish.

<u>Snake</u>	<u>Minimum meal size</u>	<u>Median meal size</u>	<u>Maximum meal size</u>	<u>Ratio of Median to Max.</u>
93-25	2.05 g 2.8 % 1 fish	4.40 g 6.0 % 2 fish	34.47 g 46.6 % 17 fish	0.13
93-27	1.89 g 2.7 % 1 fish	2.45 g 3.5 % 1.5 fish	8.04 g 11.6 % 4 fish	0.31
93-34	1.70 g 2.6 % 1 fish	1.75 g 2.7 % 1 fish	7.32 g 11.1 % 4 fish	0.28
93-66	1.97 g 2.8 % 1 fish	2.10 g 2.9 % 1 fish	22.62 g 31.7 % 13 fish	0.09

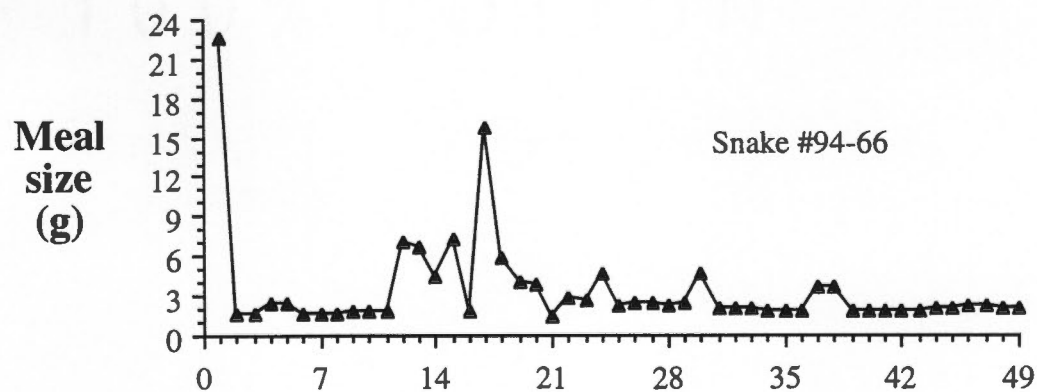
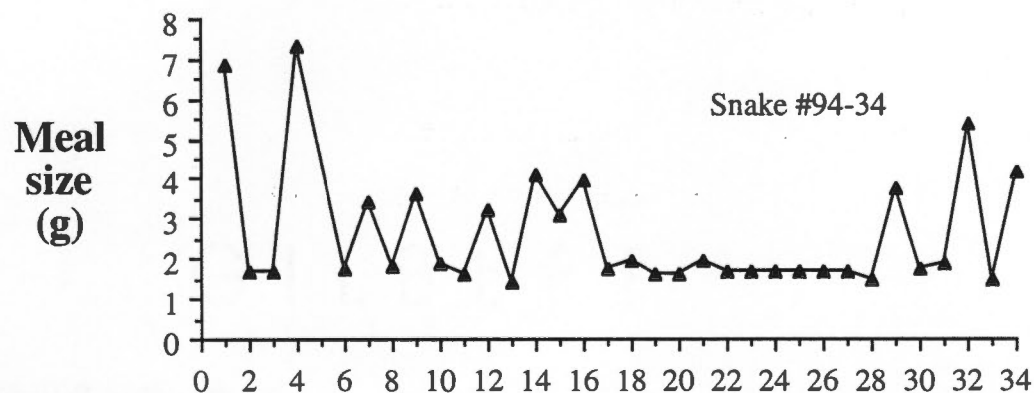
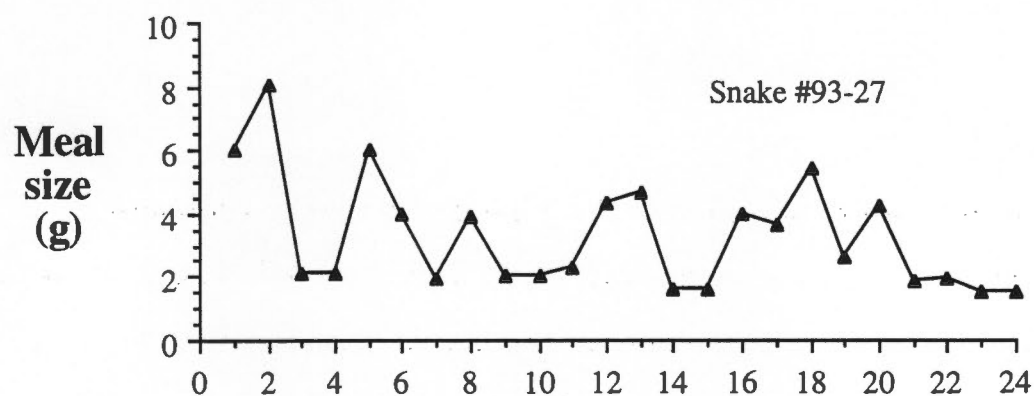
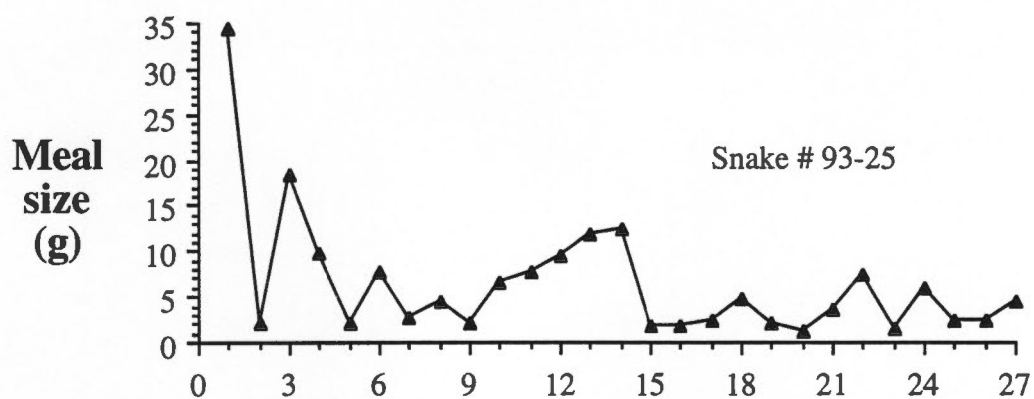
the average of all meals consisting of a single fish. Maximum meal sizes were 4.3-16.8 times as large as the minima (Table III-3).

Snakes typically took much smaller meals than they were capable of ingesting (Fig. III-4, Table III-3). In general, the snakes ingested their largest meals early in the study. The maxima were the first, second, fourth, and first meals of the respective subjects (Fig. III-5). It should be noted that, before the ad libitum study, snakes had been fed a maintenance ration that allowed them to keep their capture weight, but not to grow.

4. Meal frequency. The frequency distributions of intermeal intervals showed distinct peaks (Fig. III-6). Two of the snakes had large numbers of observations in the shortest intermeal interval category (0-5.9 h). These snakes both had short BCI's (both 2.98 h). The comparatively lengthy BCI's of the other two snakes (5.57 and 6.40 h) ensured that there would be few observations in the 0-5.9 h intermeal interval category. Over the entire frequency distribution of intermeal intervals, the modal category for three of the four snakes was the 18-23.9 h category. The modal category for the fourth was the 24-29.9 h category. Continuing to longer intermeal intervals, the snakes exhibited secondary peaks in the 36-41.9 h category (one snake) and 42-47.9 h category (three snakes).

5. Effect of ecdysis. All four snakes shed at least once during the study; one snake initiated a second shed cycle near the end of its experimental run (Fig. III-7). Some of the data suggested a reduction in feeding rate during these times (e.g. #93-27), but all four subjects fed during their shedding cycles. Three of the four snakes exhibited a tendency for meal size to increase from about the middle of the shed cycle till shortly after the old skin was cast off. Overall, however, there was no

Fig. III-5. Line plot of the sequence of meals of four Northern water snakes fed ad libitum. Meal sizes are indicated on the vertical axis, and meals are arranged from left to right in the order in which they occurred during the study. The range of the horizontal axis in each panel reflects the differences in the number of meals taken by each subject. It should be noted that the spacing between these meals was highly variable (see Fig. III-6). Further, because of missing data (see Methods), these plots are not strict chronologies of all consecutive meals. Rather, they serve to illustrate the general tendency for the largest meals to occur early in the study.



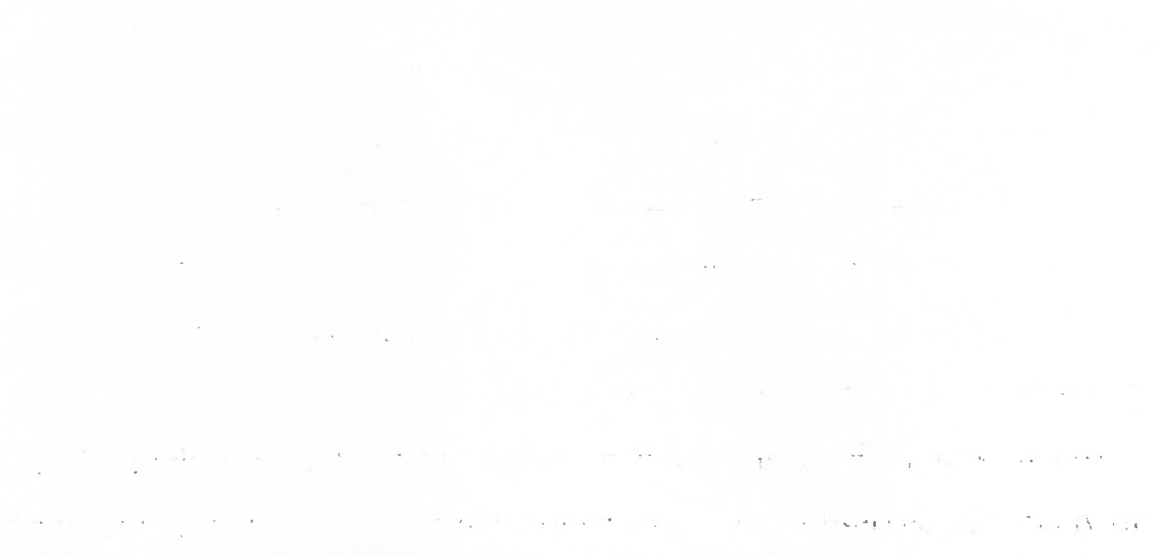


Fig. III-6 Frequency distributions of intermeal intervals of four Northern water snakes fed ad libitum. Intermeal intervals are the time periods from the end of one meal to the start of the next. Although these plots are frequency histograms, they are represented as line plots to better display how the distributions peak near 24 and 48 h.

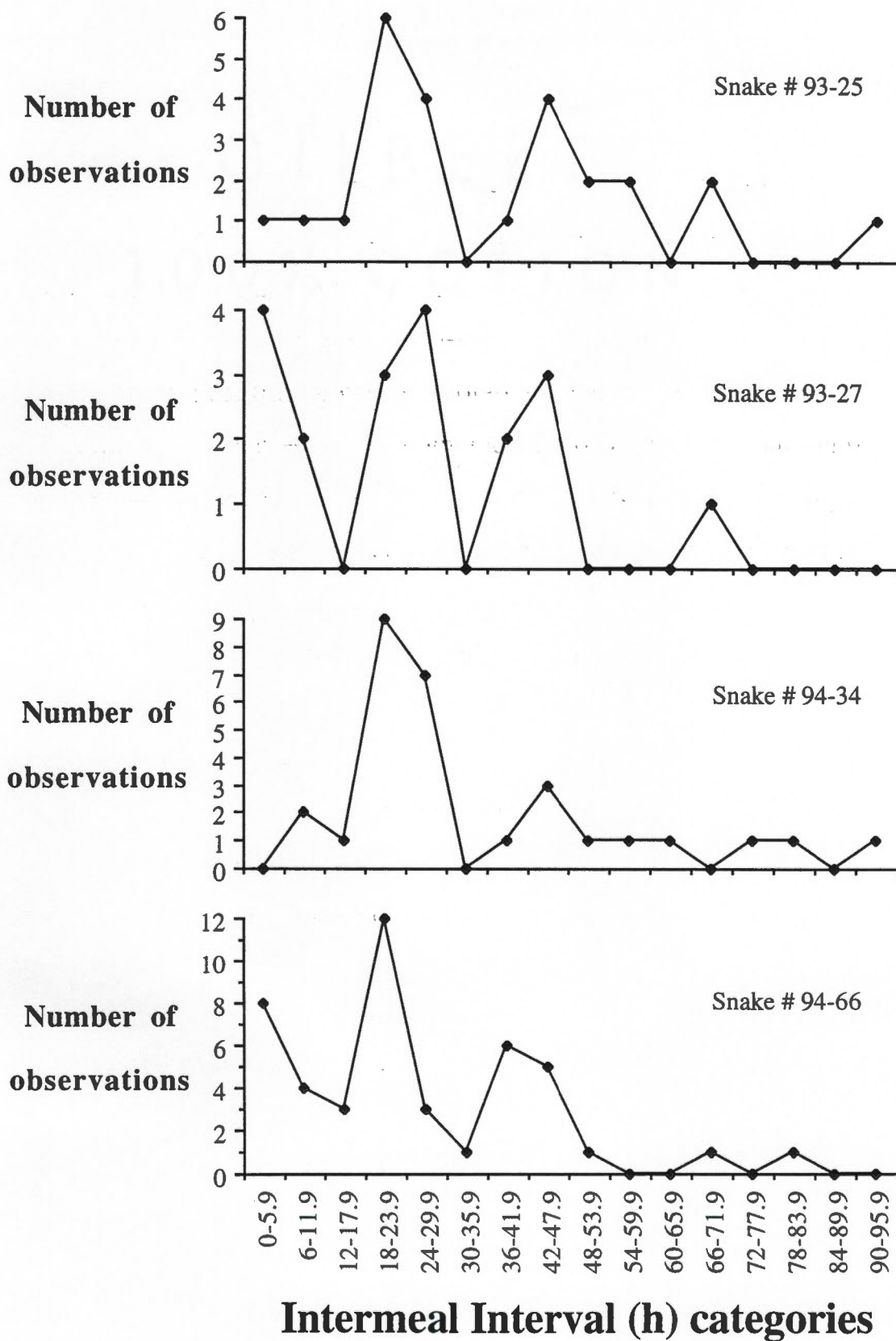
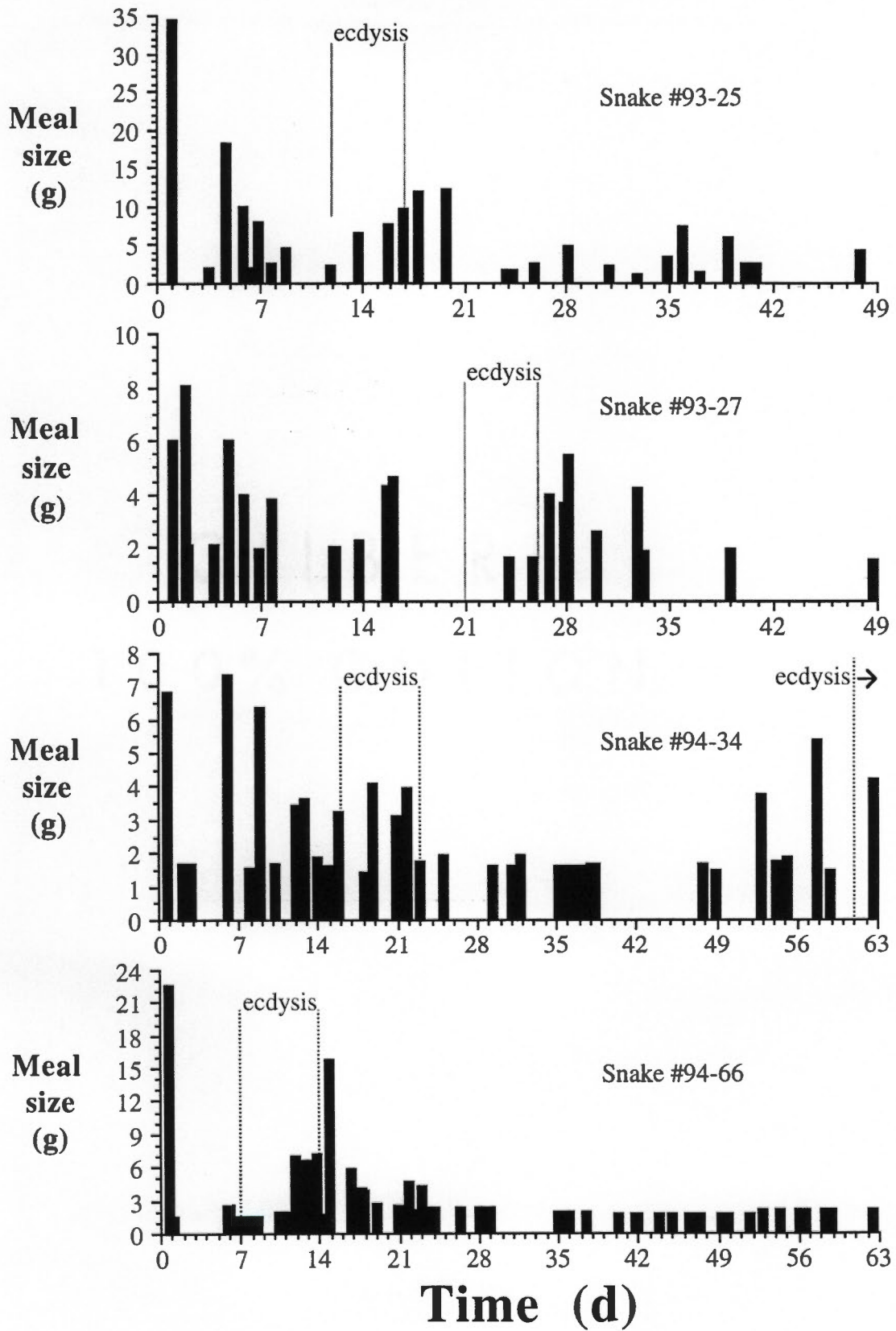


Fig. III-7. Relationship of meal taking to shedding cycle in four Northern water snakes fed ad libitum. Each solid vertical bar represents a single meal. The time periods labeled "ecdysis" denote the time from when the snake was first observed to be opaque until it shed. Snake #94-34 did not complete it's second shedding cycle before to the end of the experiment. Experiments were run for different lengths of time in the two years of the study, so the range of the horizontal axes varies between panels.

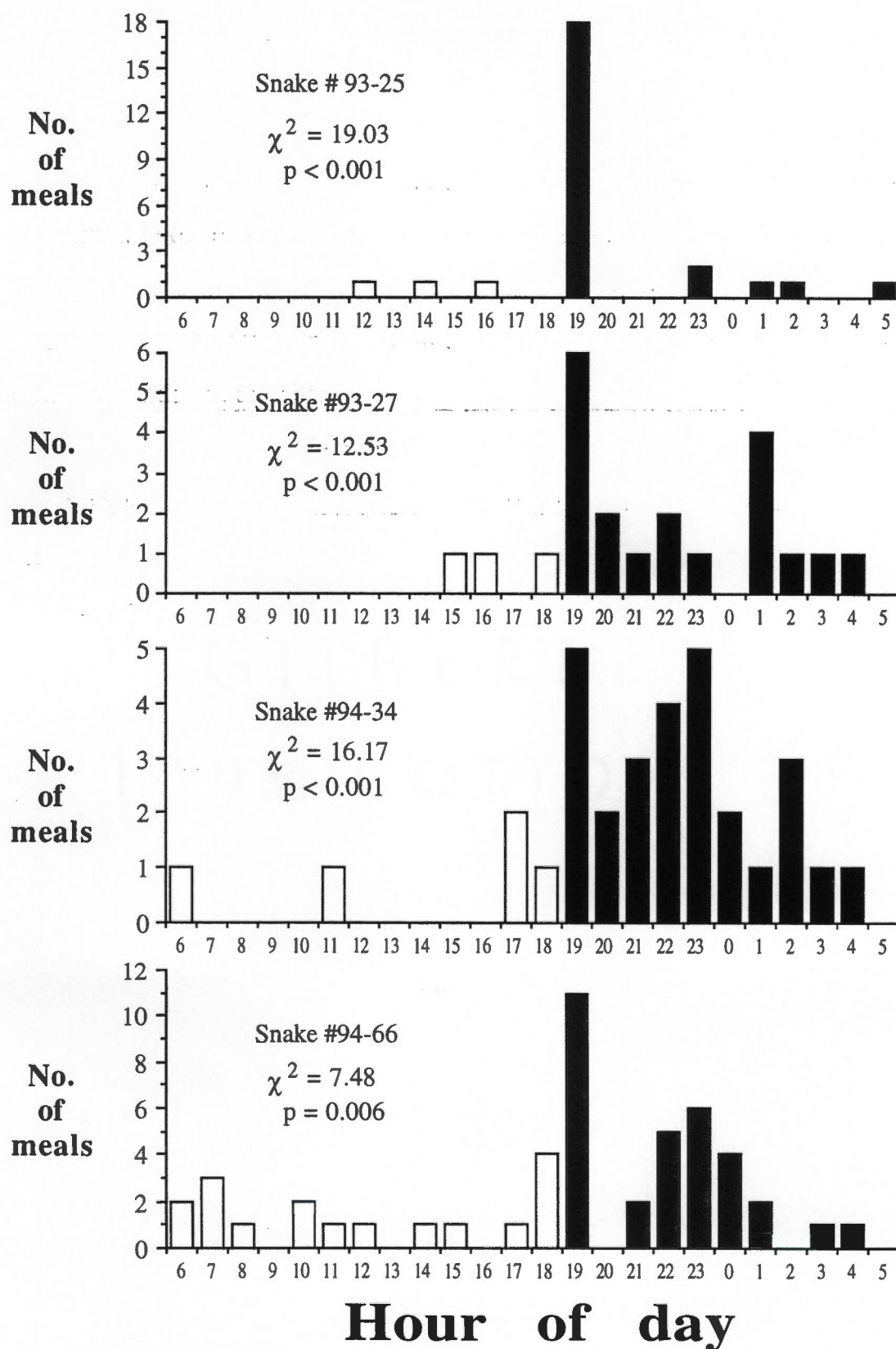


consistent association between feeding rate and the timing of ecdysis.

6. Diel cycles. Meals were not distributed randomly over the day. All four subjects initiated significantly more meals during the night than during the day (Fig. III-8). More specifically, the snakes exhibited a distinct crepuscular pattern, with 78, 32, 19, and 34% of the respective snake's nighttime meals beginning in the first hour of darkness. Only 9% of the meals (i.e. 1/11) would be expected to occur during the first hour of an 11 h night if meal timing was due solely to chance. Even this analysis underestimates the degree of diel coincidence, for I observed that many of these crepuscular feedings took place within the first 10 min after lights-out! I could not test for crepuscularity in each snake. The expected χ^2 values for a one hour category out of an eleven hour night would be too small (Siegel and Castellan 1988) given the number of meals that each snake took. A contingency table analysis indicated that the complete data set of nighttime meals could not be lumped either (null hypothesis of equal distributions among snakes rejected, $p=0.001$). This result is due mainly to snake #93-25, whose meal initiations were more tightly clustered in the first hour of the night than were those of the other snakes (Fig. III-8). The distributions of meals over the night were not different among the other three snakes ($p=0.375$). Combining the data for these three snakes, 22 meals were taken during the first hour after darkness, and 56 were taken over the remaining 10 h of the night. This distribution is significantly different from the expected ratio of 1:10 ($\chi^2=46.22$, $df=1$, $p<0.0001$).

Although crepuscular feeding was apparent in each snake, the distributions of meal initiation times also suggested a secondary feeding peak. Three of the four snakes exhibited a secondary peak between 2300-

FIG. III-8. Diel cycle in meal initiation of four Northern water snakes fed ad libitum. The frequency histograms indicate the number of meals that were initiated during each hour of the day. Lights were on from 0600-1900 h. The χ^2 tests assessed whether meal initiation times of each snake were distributed equally between day and night (expected ratio 13:11). All subjects were significantly nocturnal.



0100 h (Fig. III-8).

7. Meal patterns. Virtually none of the various meal pattern correlations were significant (Table III-4). The snake with the largest sample size of meals and intermeal intervals (#94-66) exhibited a significant positive correlation between the sizes of consecutive meals ($r_s=0.325$, $p=0.03$). A positive correlation for this meal pattern would indicate a tendency to feed in runs, and such a result is reflected in this snake's meal sequence (Fig. III-5). Snake #93-27 exhibited a weak trend for a positive correlation in this meal pattern as well ($r_s=0.309$, $p=0.15$). Most of its small (i.e. single fish) meals occurred in runs of 2-4 consecutive meals (Fig. III-5). Snake #94-34 exhibited a weak trend for a negative correlation between the sizes of consecutive meals ($r_s=-0.235$, $p=0.18$). Such a result, if real, would indicate significant alternation in meals sizes between consecutive meals (Fig. III-5). None of the prandial correlations between meal size and intermeal intervals suggested even weak trends (Table III-4).

D. Discussion

One motivation for the present work was to apply some standard methods from appetite research to a comparatively unstudied species. Where appropriate, I compare my results for N. sipedon to those from studies of laboratory mammals. I also compare and contrast certain results for N. sipedon with those for L. getula reported by M&K.

1. Feeding rate and growth efficiency. The most likely explanation for the deceleration of the cumulative food intake curves (Fig. III-2) is that the snakes were initially both filling storage depots as well as

Table III-4. Summary of meal pattern correlations for four Northern water snakes fed ad libitum. Each entry is a Spearman rank correlation, with the associated probability in parentheses beneath each coefficient. Sample sizes are indicated below each snake's identification number. The sample sizes are slightly smaller than the number of meals recorded above for each snake because of missing data on intermeal intervals. The "Meal_{n-1} to Meal_n" correlation is the correlation between the size of a meal and the size of the preceeding meal. The preprandial correlation is the correlation between the size of a meal and the time since the last meal; the postprandial correlation is that between meal size and time to the next meal.

Snake ID & <u>sample size</u>	Meal _{n-1} to Meal _n correlation <u>(probability)</u>	Preprandial correlation <u>(probability)</u>	Postprandial correlation <u>(probability)</u>
93-25 (n=26)	$r_s = 0.011$ (p = 0.96)	$r_s = -0.216$ (p = 0.28)	$r_s = -0.010$ (p = 0.96)
93-27 (n=23)	$r_s = 0.309$ (p = 0.15)	$r_s = -0.206$ (p = 0.33)	$r_s = -0.109$ (p = 0.61)
94-34 (n=32)	$r_s = -0.235$ (p = 0.18)	$r_s = 0.066$ (p = 0.71)	$r_s = 0.091$ (p = 0.62)
94-66 (n=48)	$r_s = 0.325$ (p = 0.03)	$r_s = 0.049$ (p = 0.74)	$r_s = -0.046$ (p = 0.76)

supplying energy for maintenance and growth. Under this interpretation, once fat body stores were replete, the rate of ingestion decreased. Prior to the free feeding study, the snakes had been fed only a maintenance ration. I wanted the snakes to start out the study quite hungry in order to see how typical meal sizes would compare to maximal ones (see below). Despite the curvilinearity of cumulative food intake, linear approximations were adequate ($r \geq 0.91$ for all four snakes) for broad comparative purposes.

The average feeding rate of 2.36 g wet mass/d compares favorably to predictions from scaling relationships. Peters (1983) used the data set compiled by Farlow (1976) to construct a relationship between body mass and rate of food intake. A 70.2 g carnivorous poikilotherm would be expected to ingest 1.1 g wet mass per day. Peters assumed that Farlow's data were generally taken from studies done near room temperature (approximately 20 °C). Hence, this expected rate can be corrected for the higher temperature (26 °C) used in the present study. Assuming a Q_{10} value of 2.25 (based on Lillywhite 1987) yields an estimated ingestion rate of 1.64 g/d; this expected value is 31% lower than the rate of 2.36 g/d observed in the present study. The agreement is close given that some (most?) of the values in Farlow's data set were taken from captive animals that were not being fed ad libitum. It would be interesting to see how the food intake of more frequently feeding poikilotherms such as lizards compares to that of snakes and to scaling predictions.

The PI ratios in the present study were similar to literature values for rat snakes, Elaphe, and water snakes (Table III-5). Although Scudder and Burghardt (1985) demonstrated effects of feeding frequency on length increase, mass accumulation was much less obviously affected. What is

Table III-5. Growth efficiencies of well fed colubrid snakes in captivity. PI ratios are calculated on the basis of body mass gained per unit mass of food consumed. In sources 3-6, snakes were fed to satiation in each meal; sources 1 and 2 did not note this qualification. The PI ratios from source 4 were visually estimated from graphical data. Sample size (n) refers to the number of individual snakes.

<u>Species</u>	<u>Feeding</u>		<u>n</u>	<u>Source</u>
	<u>interval</u>	<u>PI ratio</u>		
<u>Elaphe guttata</u>	7 d	0.34	10	1
<u>Elaphe obsoleta</u>	7 d	0.27	17	2
<u>Elaphe obsoleta</u>	5 d	0.27	1	3
<u>Nerodia fasciata</u>	2 d	~0.25	6	4
<u>Nerodia fasciata</u>	3.5 d	~0.20	5	4
<u>Nerodia fasciata</u>	7 d	~0.24	7	4
<u>Nerodia sipedon</u>	2.5-5.1 d	0.27	11	5
<u>Nerodia sipedon</u>	ad libitum	0.24	4	6

Sources: 1-Barnard et al. 1979.

2-Ford 1974.

3-Andreadis and Burghardt 1993.

4-Scudder and Burghardt 1985.

5-Brown 1958.

6-present study.

noteworthy about the similar PI ratios in Table III-5 is that, with the exception of the present work, all of the studies used feeding frequencies which were less than ad libitum. It would seem that Elaphe and Nerodia fed at any ration adequate or better for growth will convert about one quarter of ingested food mass into their own tissues. As mentioned above, it would be interesting to directly compare growth of snakes to that of animals such as lizards which typically feed more often. I would hypothesize that snakes preserve their growth efficiencies over a wider range of feeding frequencies than would more frequently feeding species.

2. Meal criteria. The results of the log survivorship analysis indicate that Nerodia sipedon feeds prandially, i.e. in temporally discrete meals, as M&K concluded for Lampropeltis getula. Short pauses on the order of minutes were apparent within feeding bouts (left tails of distributions in Fig. III-3). Longer intervals of, especially, one or two days between feedings were also typical (Fig. III-5). However, feeding intervals of intermediate duration, i.e. 3-8 h, were also apparent (Fig. III-3). Given that most feeding bouts were initiated at night (Fig. III-8), the intermediate length intervals might indicate a tendency for the snakes to take multiple, distinct meals per night. Such a finding is consistent with the secondary peak in feeding activity seen from 2300-0100 h (Fig. III-8). Alternatively, the presence of intermediate length interprey intervals might indicate that the BCI's which I chose were biologically inappropriate, i.e. too short. These snakes may actually take meals of particularly long duration. It might be that a typical "meal" is, in fact, a bout of feeding that begins at sunset (Fig. III-8)) and extends over much of the night. Although the data are relatively few, the log survivorship curves suggest (especially

for the females) the possibility of three classes of interprey intervals rather than the more familiar condition of two (i.e. an intrabout-interbout dichotomy).

3. Meal size. A major distinction between snakes and many other vertebrates in their feeding behavior is the amount of food that they can consume in one feeding bout. Based on trophic lifestyles, I would predict that (1) typical meal sizes of freely feeding snakes would be a larger fraction of the animal's body mass than those of laboratory mammals, and that (2) typical meal sizes of freely feeding snakes would be larger in relation to their maximal meals than those of laboratory mammals. In the present study, median meal sizes averaged 3.8% of the snakes' initial body masses and 20.3% of their respective maximal meals (Table III-3). However, minimum meal sizes were not under the snakes' control, being set by the size of the individual fish offered (average=2.7% of snake mass). This fact complicates meal size comparisons, since mammals can mechanically reduce their food items to as small a particle as desired. Regarding prediction 2 above, a single fish was the modal meal size for the water snakes (Fig. III-4), so the true ratio of typical meal size to maximum would be overestimated.

In addition to floor effects on meal size in the present study, the quality of the food differs from that of most studies of laboratory mammals. Captive mammals are often fed dry, pelleted diets, which, no doubt, contributes to the well established phenomenon of postprandial drinking. For example, Kanarek (1975) reported a close temporal proximity of drinking and eating in freely fed cats offered ground chow. Thus, the "true" mass of a meal in laboratory mammals may be the sum of

the food and water masses taken in during a given bout of ingestion. In this regard, free feeding studies of cats fed whole prey would be instructive. Snakes consuming whole vertebrate prey receive the considerable body water of an ingested item. M&K reported that, in contrast to the kingsnakes' episodic feeding, they drank at a relatively constant rate. To illustrate the difficulties in comparing "wet" and "dry" meals, I graphically estimated rat meal size from de Castro (1988). The average meal size of freely feeding rats of approximately 290 g body mass was about 2.5 g of dry pelleted diet, or 0.87% of body mass. Comparison of this value to that which I recorded for water snakes (3.8%; Table III-3) would tend to support prediction 1 above. However, any water intake concomitant with the rats' feeding bouts would increase meal mass and reduce the disparity in relative meal sizes. Kanarek (1975) commented on water intake in her study of free feeding in cats. Two cats with average body mass of approximately 2200 g ate an average of 5.6 g of ground cat chow per meal. The cats also drank about 1.6 ml water/g food, yielding an estimated meal mass of about 14.6 g, or 0.65% of body mass. Interestingly, this amount seems roughly comparable to the mass of a single small rodent or bird. Thus, limited evidence from ad libitum feeding studies suggests that snakes do eat relatively larger meals than mammals, though similarity of diets would facilitate comparisons. Various piscivorous mammals or birds (e.g. certain otters, seals, sea lions, herons, kingfishers) could be more directly compared to piscivorous snakes, as could cats and ferrets to rodent eating snakes if the former were fed live mice.

Woods (1991) coined the Eating Paradox to indicate that, despite its

necessity in animals, eating has short term consequences which are decidedly nonhomeostatic. Diseases like diabetes underscore that the postingestive surge in absorbed nutrients can indeed be detrimental, especially if chronically endured. Another example is evident in domestic cats, which are prone to kidney stones and kidney infections. These conditions are thought to be caused by large postingestive changes in blood pH which adversely affect urine pH. Finke and Litzenberger (1992) have recommended that cats be fed small, more frequent meals to dampen the deleterious swings in urine pH. Thus, even mammalian carnivores appear to abide by the Eating Paradox. Interestingly, M&K's study of king snakes gave little indication of a reduction in meal size or intermeal interval. The feeding records of two snakes, the only detailed data presented by M&K, indicate a fairly lengthy spacing of consistently large (i.e. multiple prey) meals. In contrast, water snakes seem to follow the Eating Paradox prediction of small, frequent meals. The snakes in the present study typically took much smaller meals (i.e. one fish) than their maxima (= 4-17 fish; Table III-3, Fig. III-5). The most typical pattern was for the water snakes to take one prey item per day. Why one snake species should follow the predictions of the Eating Paradox and one should not is worthy of future investigations. Some possible factors include experimental differences in prey digestibility, testing temperature, body size, and prey handling costs (the latter two factors are discussed below). Interspecific differences in prey availabilities are another possible cause.

Although the preceeding discussion of meal size considered interspecific differences, i.e. N. sipedon versus L. getula, the present study also provided an opportunity to explore intraspecific differences. Sex may

be an important source of variation in meal size. The two male water snakes took more multiple-prey meals (=49% and 66% of their respective meals) than did the females (29% and 30%; see Fig. III-4). Given the small sample of animals, this observation alone is only weak evidence for sex differences. Interestingly, however, the feeding histories of the male snakes were also more easily subdivided into meals. In other words, the feeding behavior of the males was more cleanly divisible into bouts than was that of the females (see Fig. III-3). These two pieces of evidence suggest the possibility that male water snakes tend feed more like intermittent gorgers, while females feed more like continuous nibblers.

4. Meal timing. As for factors that affect feeding frequency over the long term, the general consensus of the older herpetological literature is that snakes curtail feeding during molt cycles. M&K confirmed this for L. getula fed ad libitum, as long ingestive pauses preceded shedding. However, there was no obvious reduction in feeding during ecdysis in the present study (Fig. III-7). Intrinsic species differences may be involved. It may be that, in water snakes, ecdysis curtails activity but not appetite. In other words, water snakes with opaque eyecaps might become reclusive in the wild, but would feed if food presented itself at close range. Although water snakes use a diversity of active and passive foraging tactics (Balent and Andreadis, In press), perhaps they are more effective sit and wait predators than king snakes, i.e. better able to select a retreat that is also an appropriate ambush site.

One conspicuous difference between M&K's report and the present study is the frequency with which the snakes fed. While median intermeal intervals of the king snakes were 4-6 d, the median intermeal intervals of

water snakes were 0.9-1.4 d (Table III-2). Part of the discrepancy is undoubtedly attributable to body size differences. In general, larger snakes should have longer intermeal intervals. While M&K did not report the mass of each subject, the two snakes for which extensive data were provided were approximately 320 and 360 g. In contrast, the water snakes I studied averaged 70 g body mass. To address the role of scaling, I combined the data for L. getula (n=2) and N. sipedon (n=4). A log-log plot of intermeal interval versus body mass yields a regression equation with a slope of 0.948. This value is much higher than would be expected under the assumption of standard scaling principles. Farlow (1976) reported that ingestion rates (mass/d) of poikilotherms scaled to the +0.82 power of mass. The number of days over which a unit of mass was eaten should, therefore, scale as the inverse, or the -0.82 power. Most physiological volumes and masses (e.g. lung volume, heart mass) scale isometrically with mass (Schmidt-Nielsen 1984, Peters 1983). If the mass per meal also scales to the +1.0 power, its inverse, the number of meals over which a unit of ingested mass would be distributed, scales to the -1.0 power. Meal frequency would thus be proportional to:

$$\frac{\text{No. of days per unit mass eaten}}{\text{No. of meals per unit of mass eaten}}, \text{ or } \frac{\text{Mass}^{-0.82}}{\text{Mass}^{-1.00}}$$

The expected scaling exponent for the time interval between meals is thus $-0.82 - (-1.0) = +0.18$. The observed exponent from the combined data set (0.948) is much too large for allometry to explain the interspecific difference in meal frequency. To put this argument in more tangible terms, small animals can be "scaled up" to match the size of larger ones.

Using the expected scaling exponent of 0.18, and assuming that meal size scales isometrically, a hypothetical 340 g water snake (= the same mass as M&K's king snakes) would have an expected intermeal interval of 1.5 d. With observed meal frequencies of 4-6 d, the king snakes of M&K's study were feeding much less frequently than would water snakes of comparable size.

Part of the disparity in meal frequencies between these two studies may lie in the prey used. M&K's king snakes were fed domestic House mice (Mus musculus). Evacuation of mice from the king snakes' stomach may have been slowed by the indigestible hair of the mammalian integument. Such a delay in gastrointestinal processing might translate into longer intermeal intervals. My observations of the stomach contents of water snakes (Nerodia) and rat snakes (Elaphe) indicate that the skin of teleost fishes is much less of a barrier to digestion than is mammal skin. Other differences in fish and mammal prey (e.g. body shape, adiposity, water content, tonicity of tissues) could also contribute to differences in digestion rate.

Perhaps the most influential factor affecting intermeal intervals in the two studies is meal size. The king snakes were taking much larger meals relative to their body size than were the water snakes. M&K do not report typical meal masses of individuals, but with the ranges provided, the range of possible values can be bracketed. Median meal sizes of the freely feeding king snakes ranged from 62-113 g. The smallest snake whose mass was explicitly mentioned weighed 319 g at the start of the study, while the largest mentioned was 751 g. Possible values for relative meal size thus range from 8-35% of snake mass. Assuming the more likely case that the

extremes of meal size correspond to the snakes with the extremes in body mass, the range is 15-19% of snake mass. The king snakes in M&K's study thus took meals that were somewhere between two and nine times as large as those taken by the water snakes (3-6%, Table III-2) in the present study, with a 4-5 fold difference most likely. The relatively larger meal size would therefore extend the ingestive pauses between meals. It should be noted that relative prey size in M&K's study was probably greater than in my study. In addition, the need for the king snakes to subdue their live prey by constriction would add procurement costs. Such costs can have major consequences for meal frequency and size (Collier and Rovee-Collier 1981, Collier 1985; see discussion below).

The strongest influence on water snake feeding which I found was one which I had not initially sought to study, namely biological rhythms. Under conditions of constant food availability, *N. sipedon* fed primarily at night (Fig. III-8). Although the older herpetological literature suggested that water snakes were diurnal, that conclusion was based mainly on the times of day when researchers went looking for, and found, basking snakes. More recent summaries of snake natural history generally recognize the nocturnal feeding of *Nerodia*; Ernst and Barbour (1989a) state that most foraging by *N. sipedon* takes place between 1800-0000 h.

The nocturnal meal taking was predominantly confined to the first hour of darkness (Fig. III-8). One subject (#93-25) had such a regular pattern of crepuscular meal taking (Fig. III-8) that it could practically be considered a clock! I have made numerous observations in the field to confirm a pronounced peak in snake activity in the early evening. The crepuscular time window may be a period of vulnerability of prey fishes to

snake predators. Neither strongly diurnal nor nocturnal fishes see well at twilight, and the activity and foraging success of predatory fishes increases greatly at this time (Helfman 1986). At twilight, fish may be less effective at visually detecting the approach of foraging snakes. Since water snakes rely heavily on tactile and chemical cues for guiding predatory behavior (Drummond 1979, 1983), they themselves are unhampered by difficult viewing conditions. Varying over the day, prey vulnerability may, thus, be a strong selective force for crepuscular feeding in N. sipedon.

The presence of a strong diel cycle in feeding may explain the general lack of significant meal pattern correlations (Table III-4). Laboratory mammals generally do not display similar constraints on intermeal intervals. While laboratory rats are significantly biased toward nocturnal meal taking, they still take several meals in both the day and the night (Le Magnen 1985). Thus, intermeal interval is more free to vary. The intermeal intervals of N. sipedon appear to be more externally driven than internally set, although endogenous clocks might be an important, internal control mechanism. It was perhaps simply chance that the relative prey size which I chose (~2-3% of snake mass) was appropriate for these snakes to take at 24 or 48 h intervals to achieve an ad libitum food intake. Thus, the interaction of a relatively fixed intermeal interval with a given prey size resulted in little variation in meal frequency or size. Significant meal patterns might yet be found by repeating this study with prey of different sizes, especially smaller prey. This procedure would also help address the problem of a floor effect on meal size discussed above. Alternatively, snakes of different sizes could be tested. Very small snakes could potentially take more meals per day, as do laboratory rats. Much

larger snakes could also be tested, since sufficient variation in intermeal intervals (e.g. various multiples of 24 h) might exist.

5. Constraints and recommendations. Studies of free feeding in snakes entail certain constraints relative to studies of typical laboratory animals. Since snakes are obligate carnivores, a study in free feeding becomes, by necessity, an exercise in husbandry of the prey. The choice of the right snake species can, to an extent, ameliorate such difficulties. Piscivorous snakes offer several advantages over, especially, rodent-eating snakes. Both fish and rodent prey are commercially available. However, bait minnows like those that I used are less expensive than mice, can be kept in large numbers more easily, and, as ectotherms, have lower energetic requirements for maintenance. Furthermore, soft-finned bait fishes generally can not harm the snake, and can be easily confined in an environment that maintains the prey but is accessible to the predator. Colubrid genera whose diets offer similar advantages include certain egg eaters (e.g. Dasypeltis, or perhaps Elaphe), worm eaters (Carphophis, Cyclophiops, Tropidoclonion, certain Diadophis populations and Thamnophis species), and slug eaters (Contia, Storeria).

One constraint of free feeding studies of snakes which is inevitable and, indeed, even expected, is the small sample sizes of meals taken. While a freely feeding rat might accrue a sample of 50 meals in three or four days, in the present study only one snake out of four approached this large a sample in two months! Certain feeding parameters such as prandial correlations, which are highly significant in rats with samples of hundreds of meals per individual (e.g. Le Magnen 1985), may not be detectable with such small samples. In order to compensate, (1) a metaanalysis could be

conducted on larger samples of snakes, (2) smaller snakes could be used, or (3) snakes could be kept at warmer temperatures. My choice of subjects for the present study was guided by the fact that a larger sample of snakes would have entailed a prohibitive time cost. In addition, my decision to study individuals of the sizes that I used was prompted by M&K's study. Two king snakes for which they showed data had body masses of about 320 and 360 g; these subjects took, respectively, 12 and 19 meals over a four month period.

A final constraint of studying predators that feed on live prey is that posed by the time and effort of prey capture. Collier and colleagues have amply demonstrated that adding costs to meal procurement causes most animals to take fewer, larger meals. Compared to laboratory rodents feeding on pelleted diets, there would be a measurable time and energy cost to predators for capture, handling, and ingestion of live prey. While it might seem that there would be minimal capture cost for the snakes in the present study, a few observations raise questions. On some occasions, I saw snakes feed at atypical times (e.g. middle of the day) after a fish jumped out of the water bowl and was flopping around. Although they were confined in a relatively small space, fish in the water bowl could temporarily evade the snakes by protean flight. The escape capacity of a fish out of water is obviously reduced. Thus, future work with predators freely feeding on live prey must not ignore the possibility that fish in a barrel must still be caught. One way to approach this problem is to see if the density of prey offered (e.g. the number of fish maintained per food bowl) affected meal size or meal frequency. Elaborating on this point, I can speculate on part of the explanation for the particularly large and

infrequent meals of M&K's king snakes relative to the present study. Although it is not explicitly stated, M&K apparently fed their snakes live mice. Since king snakes are constrictors, there were undoubtedly appreciable costs in time and muscular effort for ingesting each meal. Applying Collier's arguments about the effects of meal costs, constricting snakes fed live prey should take larger, less frequent meals than if they were fed "easier" prey.

An alternative interpretation to fish out of water having lower procurement costs is that such prey are perceived as qualitatively different by the snake. I have observed that the mechanical stimulus of a flopping fish is a potent releaser of Nerodia attacks. I have kept many water snakes that could be induced to launch an attack at my hand by irregularly drumming my fingers on the cage. It may be that the differences between fish in and out of water are more akin to differences in palatability of different prey types. To my knowledge, no one has investigated palatability in snake ingestion. The large database on tongue flicking responses to prey chemicals (e.g. Burghardt 1970) offers a starting point to search for candidate predator species. Initially, one could suppose that fish and amphibians with such antipredator defenses as thick scales, fin spines, or skin toxins would be less palatable to water snakes than undefended prey. Taking a broad perspective, it should be noted that palatability might simply be the proximate means by which the ultimate selective advantage of reducing prey procurement costs is realized. Toward the practical goal of keeping all prey in a free feeding study equivalent in palatability, a lip around the top of the water bowls would probably have precluded fish escape.

E. Summary: Meal patterns in the free feeding paradigm

A feeding study was conducted with four Northern water snakes (mean mass=70.2 g) offered live minnows (mean mass=1.9 g) ad libitum. All feeding events were recorded with time lapse video. Snakes converted 14-27% of ingested mass into body tissue. Snakes fed prandially, with bout criteria ranging from 3.0-6.4 h. Median meal sizes were 1.8-4.4 g (2.7-6.0% of initial snake mass). Snakes typically took much smaller meals (44-71% of meals consisting of one fish) than their maxima (4-17 fish). Median intermeal intervals were 22.7-32.8 h, and the shedding cycle did not appear to affect the timing of meal taking. Intermeal intervals of approximately one and two days were prevalent, with the likely cause being a strong diel cyclicity. Subjects fed significantly nocturnally, with crepuscular feeding predominating (19-78% of meals initiated during first hour of darkness). Most meal pattern correlations were not significant.

CHAPTER IV

FEEDING FREQUENCY IN THE WILD

A. Introduction.

Early in their evolutionary history, snakes underwent a shift in trophic ecology. While most lizards feed relatively frequently on small arthropods (Greene 1982), snakes adopted a strategy of feeding infrequently on large, vertebrate prey (Greene 1983). This feast-or-famine pattern has consequences for all aspects of ophidian biology, and was linked with the adoption of macrophagous habits. The ability of snakes to ingest extremely large prey has received much popular and scientific attention, especially regarding the unique adaptations of the skull for engulfing large prey (Cundall 1987). The infrequency with which snakes feed in the wild is similarly extreme. This parameter, though often invoked, remains largely unquantified.

Since the early part of the century, ichthyologists have used various methods to estimate feeding frequency in natural populations of fishes (Gerking 1994). A technique which would also be well suited for use with snakes is the gastric evacuation method (Bromley 1994). This method requires knowledge of (1) the time course of digestion of typical prey under naturalistic conditions, and (2) the fraction of the study population that contains food. One gastric evacuation model whose assumptions can be reasonably met in studies of snakes is that of Diana (1979). Diana estimated the interval between feedings for the Northern pike (Esox lucius: Esocidae), a piscivorous top consumer. The model assumes that (1) the

predator typically contains a small number of items at any one time, (2) digestion time is typically shorter than the interprey interval, (3) digestion time under the conditions of measurement (e.g. lab, field enclosure) is similar to that in the field, and (4) that the population, as a whole, feeds asynchronously. The equation is:

$$\text{Feeding interval} = t_{\text{GE}} / (1 - E)$$

The quantity " t_{GE} " is the total gastric emptying time for an average sized prey item, and E is the fraction of the predators sampled that have empty stomachs.

Godley (1980) used a variation of this method to estimate feeding frequency in the Striped crayfish snake (Regina alleni), a small, aquatic colubrid that feeds on hard shelled crayfish. Instead of gastric evacuation, Godley used clearance time (i.e. total gut throughput time; Martinez de Rio et al. 1994). On average, adult R. alleni (45 g) consumed prey equalling 7.5% of body mass every 3.0 days. The extent to which this interval is unusual can not be evaluated until a variety of snakes of different sizes and trophic ecologies have been similarly studied.

In the present study, I used Diana's (1979) method to estimate feeding rates of adult female Northern water snakes. This snake is a nonvenomous, semiaquatic colubrid that feeds on fishes and amphibians (Ernst and Barbour 1989a). Brown (1958) reported that 88% of 207 field collected N. sipedon with food had a single item in the stomach. This observation suggests that assumptions 1 and 2 of Diana's model are valid. The scaling equation of King (1993) predicts the prey size of a 300 g N. sipedon to be 6.4% of body mass. In the laboratory, I measured gastric evacuation of single prey averaging 5.0% of snake mass (limits: 4.5-5.5%).

I then estimated the fraction of the population in the field that contained food to generate an estimate of the average feeding interval.

B. Methods

I chose to use adult females because of their large size. I felt that I would be better able to sample individuals engaged in a diversity of activities. While actively foraging snakes are relatively conspicuous, reclusive individuals often revealed themselves only by a brief emergence of the head from the water to take a breath. I reasoned that large, reclusive individuals would be more detectable than small, reclusive ones. Thus, focusing on the largest size class would yield less bias against recently satiated and less active snakes.

The laboratory subjects were eight adult female N. sipedon with an average mass of 294 g (limits: 234-364 g). Prior to data collection, snakes were fed 1-3 Golden shiners every 5-8 d so as to maintain body mass. Snakes were acclimated to a 13:11 L:D cycle and a room temperature of 26 °C for 2-4 months prior to and during the study. I chose 26 °C as a compromise between minimum nighttime temperatures and maximal daytime (i.e. basking) temperatures. During the period in which field stomach contents were collected (dates in Results), nighttime water temperatures were in the range of 16-22 °C (Andreadis, unpubl. data). Preferred temperatures of N. sipedon in thermal gradients are in the range of 28-32 °C (Kitchell 1969, Justy and Mallory 1985). I chose 26 °C as a reasonable estimate of the average temperature experienced by N. sipedon in the field. Given the thermal dependence of digestion rate (Skoczytas 1970, Naulleau 1983, Stevenson et al. 1985), gastric emptying should have

proceeded at a comparable rate to that in the field (assumption 3 of Diana's model). Godley (1980) made a similar assumption, keeping his largely aquatic snakes at 23 °C. Regarding assumption 4, although I do have some evidence for a pronounced crepuscular peak in feeding (Chapter III), there is no evidence to suggest that the entire population feeds on the same days.

Four of the females were gravid, but four had been collected in the spring prior to mating. At the time of the gastric evacuation measurements (6-8 and 14-15 August 1994), all eight snakes were feeding regularly. The dates of parturition were the tenth, thirteenth, fourteenth, and twenty first of September 1994, which were 35, 30, 39, and 46 d after gastric evacuation measurements, respectively.

At 2200 h, each snake was fed one Golden shiner in its home cage, and checked after one hour to determine if it had fed. After a randomly assigned period of time for digestion (6-40 h), stomach contents were manually recovered with the palpation method of Fitch (1987). I gauged the completeness of stomach content removal based on diminishing returns from repeated palpations. Most snakes had to be palpated 3-4 times. Wet mass of remains was weighed to the nearest 0.01 g, and gastric evacuation rate was determined by plotting the percentage of initial wet mass remaining as a function of digestion time.

In order to measure the proportion of snakes with food, I collected N. sipedon in streams and rivers in three contiguous counties (Blount, Knox and Sevier) in eastern Tennessee over four field seasons. Data from all adult female snakes collected from 24 April to 6 July and within the mass range of 200-425 g were included. A snake was scored as having food if it (1) had solid matter in the stomach (i.e. not just liquid chyme), or

(2) was seen handling a prey that was ultimately swallowed. I manually recovered stomach contents of field caught snakes as above.

C. Results.

Gastric evacuation proceeded in an essentially linear fashion (Fig. IV-1). Linear and curvilinear evacuation curves have been reported for lizards (Windell and Sarokon 1976, Avery 1973). Secor and Diamond (1995) reported that gastric evacuation of rodent prey (25% RPS) was curvilinear in Burmese pythons (Python molurus). However, the evacuation of all but the last 10% of the meal was essentially linear, the slowly evacuating remainder consisting solely of the indigestible hair from rodents. Both linear and curvilinear evacuation have been reported in fishes, but Jobling (1987) suggested that linear evacuation is the most appropriate function to use in studies of piscivorous fish (i.e. predator is fed whole, vertebrate prey). Bromley (1994) speculated that a linear model might be best used in studies of fishes with large stomach capacities that eat large prey at infrequent intervals. Since the last description seems to best fit the trophic ecology of snakes, I assumed that a linear model was an adequate descriptor here. Fitting a linear regression by the least squares method, I estimated the time to 100% evacuation (i.e. the X intercept) to be 49 h. Regarding the adequacy of the linear model, the coefficient of determination was 0.875. I then used the regression statistics for inverse prediction (Seber 1977). This procedure yields a discrimination interval for the independent variable. The 95% discrimination interval for time to 100% evacuation of stomach contents was 37-64 h.

The proportion of field caught snakes with food was 18/34, or

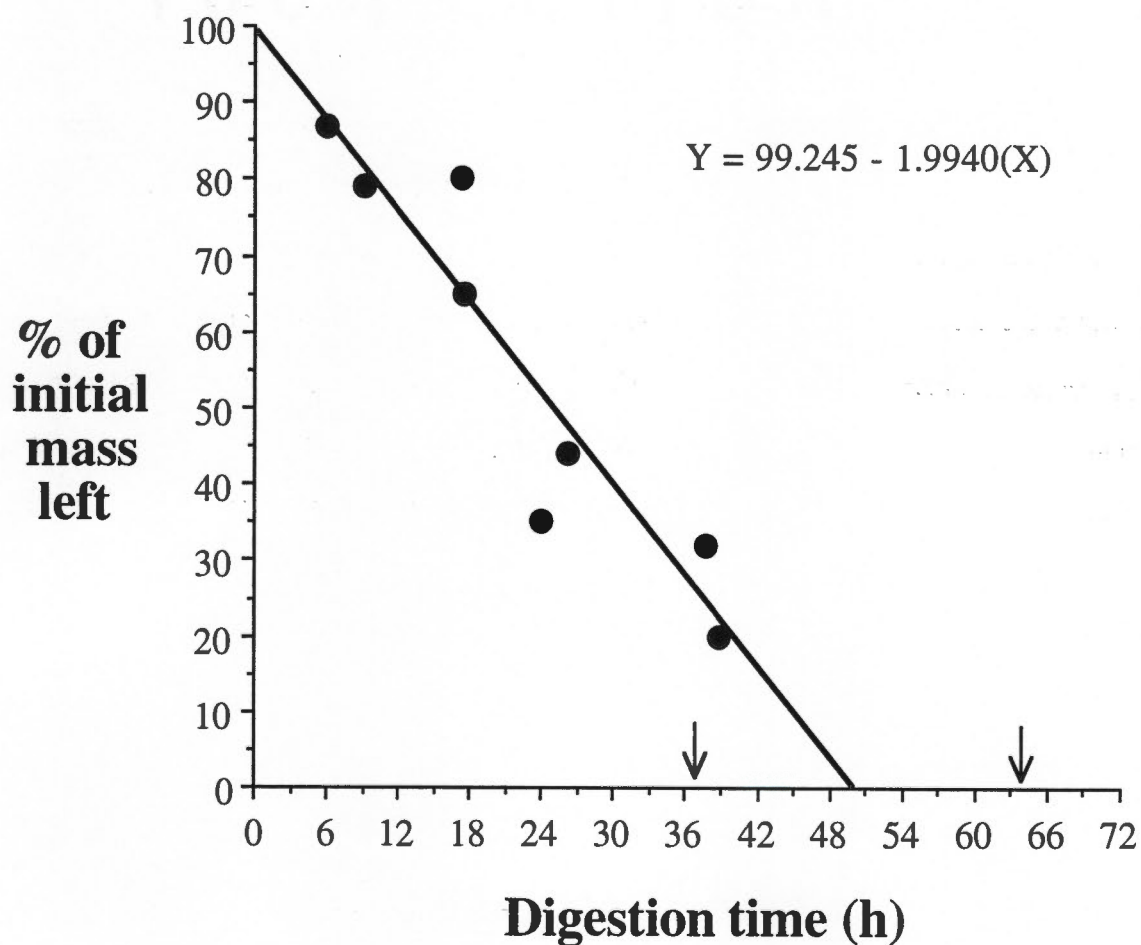


Fig. IV-1. Gastric evacuation of wet mass in adult female Northern water snakes. Snakes were fed one prey item averaging 5% of snake mass. Snakes were held at 26 °C during the evacuation testing. Each point below represents a single individual. The portion of the X axis between the small arrows is the 95% discrimination interval for digestion time.

52.9% (Table IV-1). The estimated time interval between feedings on average prey is thus $(49 \text{ h} / 0.529) = 93.5 \text{ h}$, or 3.9 d. Using the 95% discrimination interval for total gastric emptying time yields a range of values from 2.9 - 5.0 d.

D. Discussion.

I estimate that, on average, an adult female Northern water snake in Little River feeds on a typical prey item once every four days. It is prudent to consider potential sources of error which would lead to over- or underestimates. For example, digestion rate is dependent on ingestion rate, and not the reverse, as is often assumed. Thus, Side blotched lizards (*Uta stansburiana*) given satiation feedings twice daily had passage times that averaged 1.8 d faster than lizards fed more restricted rations (Waldschmidt et al. 1986). The effect of feeding rate on gastric evacuation rate has not been quantified in reptiles, but Talbot et al. (1984) found that fasting both before and after a test delayed the evacuation of test meals in salmon. The implication of these studies is that snakes fed more often would process food faster. Since the estimated feeding interval in the wild (4 d) is nearly half of the feeding interval that snakes were fed in the laboratory (up to 8 d), it begs the question of how much faster digestion would have proceeded if I had fed them at a higher frequency.

Another potential source of error is my choice of temperature. It may be that 26 °C is not an accurate simulation of the temperature experienced by water snakes in the spring and early summer. I excluded data from most of July and August because of high environmental temperatures; I have measured water temperatures in Little River as high

Table IV-1. Food records for adult female Northern water snakes. Records are arranged in calendar order. The time of capture is in Eastern Daylight Savings Time. Collection sites are indicated by abbreviations. Little River sites: 411=U.S. 411 Bridge, CB=Coulter Bridge, PM=Peery's Mill, WB=Walland Bridge, PIC=Picnic pulloff on U.S. 321; other bodies of water: LC= Love Creek, Knox Co.; 2C=Second Creek, Knox Co.; LP= Route 416 Bridge, Little Pigeon River, Sevier Co. Snake snout-vent length is in mm and mass is in g. Blank spaces indicate missing data. Food was found in 52.9% of the snakes.

Date	Time	Site	SVL	Mass	Food?	NOTES
24 April 93	2100	PM			No	Adult female, ~ 250g
25 April 93	2150	411	870	390.6	Yes	Fresh <u>Erimystax</u> ; chyme, vertebrae
25 April 94	2300	CB			Yes	Adult fem.; chyme, caudal fin rays
25 April 94	0004	CB	763		No	Empty
28 April 93	2130	PM	775	420.5	No	Empty
28 April 93	2210	PM	700	213.9	Yes	Some chyme and vertebrae
28 April 93	2250	PM	740	256.9	No	Empty
28 April 94		PM	704	206.3	Yes	Fresh <u>Cottus</u> ; older cyprinid
29 April 93	1500	2C	685	229.5	Yes	Fresh <u>Campostoma</u> ; older darter
5 May 93	2245	LC	705	332.1	No	Empty
6 May 93	0000	LC		352.3	Yes	Saw it catch a <u>Campostoma</u>
11 May 93	2130	PM	775	344.0	No	Trace of chyme
11 May 94	0045	PM	745	202.2	Yes	Fresh lamprey
11 May 94	0145	PM	800	322.4	Yes	Small, folded lamprey
11 May 94	0300	PM			Yes	Adult fem. eating <u>Campostoma</u>
16 May 94		PIC	702	216.8	No	Empty

Table IV-1 (continued)

Date	Time	Site	SVL	Mass	Food?	NOTES
17 May 92	2300	PM	785	356.0	Yes	2 fresh <u>Cottus</u>
21 May 92	2230	411	712	212.0	No	Empty
31 May 94	0200	WB	765	240.2	No	Empty
2 June 94	2250	CB	773	298.0	Yes	Half digested darter
2 June 94	2345	CB	770	359.5	Yes	Fresh centrarchid
7 June 93	2315	LC	745	370.1	Yes	Fresh <u>Campostoma</u>
7 June 95	2330	PM	693	255.7	No	Empty
10 June 93	2240	PM	840	340.4	No	Empty
10 June 93	0205	PM	735	278.5	Yes	unID'd, partial fish carcass
20 June 93	2200	TO	690	205.2	Yes	Fish flesh, vertebrae, and tail
24 June 95	2230	PIC	767	405.6	No	Empty
24 June 95	2310	PIC	691	217.3	No	Empty
24 June 95	0000	PIC	693	258.9	No	Empty
27 June 95	0115	WB	688	227.1	Yes	Crayfish; fresh minnow; chyme
30 June 95	2305	PM	726	216.2	Yes	Fish flesh and bone
1 July 94	2150	LP	660	237.0	No	Empty
1 July 94	2300	LP	729	274.7	No	Empty
6 July 94	2300	LP	727	314.4	Yes	Fresh <u>Cottus</u>

as 27 °C in August. I have also collected snakes in Little River in April at water temperatures as cool as 14 °C. I think that it is unlikely that the average body temperature is greatly different from 26 °C. Nonetheless, even if 26 °C is a good estimate of their average temperature, the snakes' physiology may function at rates that correspond to the highest temperatures achieved during the day. Goodman (1971) measured metabolic rates of Nerodia taxispilota acclimated to various, constant temperatures, and to temperatures that varied between 20 and 30 °C. He found that the metabolic rate of snakes kept at a temperature varying between 20-30 °C was closest to the rate of snakes kept at a constant 30 °C. If this phenomenon is generally true, it may be that the best, constant temperature at which to measure gastric evacuation would be one near the snakes' preferred temperature. If true, then time to gastric evacuation and feeding interval were underestimated in the present study.

Some errors also may be present in my estimate of the fraction of the population with food in the stomach. The majority of my collecting was done at night (Table IV-1). I have observed that snakes are much less able to detect my presence at night, thus facilitating captures. However, the ad libitum feeding data suggest that these snakes feed preferentially at night (Chapter III). It could be argued that my sample is biased toward hungry individuals, i.e. those with little/no food in the stomach. However, I also noted in the ad libitum study that snakes would routinely enter the water at lights-out, even if they ultimately did not feed that evening (unpublished observations). Osgood (1970) noted that Nerodia fasciata in outdoor enclosures usually entered the water after sunset, when the air temperature dropped to the water temperature. Similarly, Goodman (1971) mentioned

that Nerodia taxispilota invariably spent the night in the water. It may be that Nerodia enter the water at night, whether or not they have recently fed. What is surprising is that, if my sample was biased toward hungry animals, then adult water snakes actually feed more frequently than once every 4 d.

Assuming that the present estimate of feeding frequency is accurate, limited comparisons to other taxa can be made. My estimate of feeding interval is about one-third longer than Godley's (1980) estimate for Regina alleni. Given that my subjects were about 6.5 times the mass of Godley's, the similarity of estimates is perhaps surprising. This comparison underscores the need for an allometric perspective in comparative studies (see below). However, with the exceptions of Godley's (1980) study and the present work, feeding intervals have not been explicitly considered in snakes. Some approximations can be derived from studies of long term rates of food intake. The approximate feeding intervals of Coachwhips (Masticophis flagellum; mean mass = 170 g) and Sidewinders (Crotalus cerastes; mean mass = 130 g) in the Mojave Desert are, respectively, once per week and once per month (Secor and Nagy 1994; S. M. Secor, pers. comm.). Diller and Johnson (1988) studied the rate of food intake in Western rattlesnakes (Crotalus viridis; mean mass = 410 g) and Gopher snakes (Pituophis melanoleucus; mean mass = 220 g) in outdoor enclosures in southwest Idaho. It is unclear how the rate of provisioning corresponded to typical prey availabilities in the snakes' semiarid habitat. Diller and Johnson's data indicate an approximate feeding interval of once every 16.5 d. The feeding intervals of the two semiaquatic snakes (3-4 d) are conspicuously shorter than the rough estimates from other taxa (7-30

d). The considerable variation among these various taxa suggests that habitat (e.g. high productivity freshwater vs. low productivity desert), latitude (California vs. Idaho), foraging mode (active vs. ambush) and body size (R. alleni vs. N. sipedon) are important influences.

Assuming that the measurement of feeding interval described here is accurate, it is informative to use scaling relationships to make predictions for animals of other sizes. If the proportion of the population that contains food does not change greatly with changing body mass (a potentially incorrect, but testable, inference), then changes in feeding interval scale similarly to gastric evacuation time. Measurements of gastric evacuation time in fishes usually indicate a scaling exponent of approximately 0.40 (Jobling 1981). The curve in Fig. IV-2 was generated using a mass of 294 g, a feeding interval of 3.9 d, and scaling exponent of 0.40. Some interesting implications are found by combining this information with the strong tendency for nocturnal-crepuscular feeding (Chapter III). Snakes weighing approximately 10 g are predicted to feed, on average, about once every 24 h. If these snakes are as strongly crepuscular as larger snakes (Chapter III), then it would imply that they would have to be successful each dusk in order to average one feeding per day. Although hunting success is very difficult to quantify in any animal, if we conservatively assume that they capture prey on half or fewer of their foraging bouts, then small snakes could not be strictly crepuscular. The typical size of neonate N. sipedon is 3-5 g, and snakes are born from August-October (Mitchell 1994, Palmer and Braswell 1995, personal observation). Thus, these snakes probably do not reach a sufficient mass to be strictly nocturnal/crepuscular until sometime in their first full, active season. The

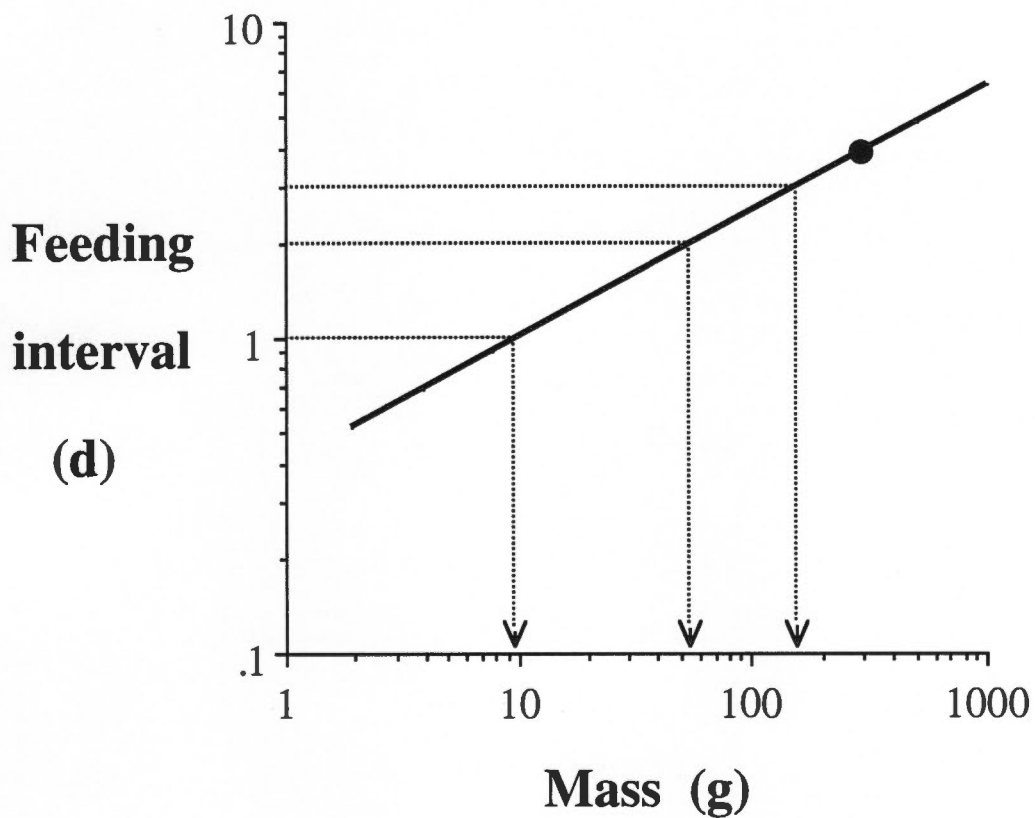


Figure IV-2. Theoretical relation for scaling of feeding interval. The axes are logarithmic, and the point is the estimate of feeding interval for adult, female Northern water snakes. The line assumes that feeding interval, like gastric evacuation, scales with an exponent of 0.40. The approximate masses of snakes with feeding intervals of 1, 2, and 3 d are indicated by the dotted arrows.

possibility that yearling snakes shift from round-the-clock feeding to a more restricted, daily schedule is worthy of future research.

At the other extreme of size, large snakes can probably be quite choosy about times to hunt. A large female water snake in Little River would have a mass of about 500 g (pers. obs.), and a predicted feeding interval of 4.8 d (Fig. IV-2). Such a snake could afford to hunt only at particularly productive or safe times. Thus, larger snakes could probably easily achieve an average intake by only hunting crepuscularly. Further, such large snakes could afford to suspend hunting for prolonged periods of unfavorable conditions, e.g. high water from flooding. One factor which may affect the timing of water snake foraging is the lunar cycle (see Chapter V). If it was successful on half of its hunts, a 500 g snake could maintain an average feeding rate by completely suspending hunting for all but a 12 d period out of the 29.5 d lunar month.

The indeterminate growth of an ectotherm can, via the allometric influences on meal timing, have major implications for the control of appetite. The speculations above should be validated with studies of feeding interval in snakes of many different sizes.

CHAPTER V

BIOLOGICAL RHYTHMS: LUNAR CYCLE IN FORAGING

A. Introduction.

The ad libitum feeding study above underscored the importance of the diel cycle in controlling water snake appetite. Various ultradian (shorter than 24 h) and infradian (longer than 24 h) rhythms have also been found to be important in other biological systems. Among the latter, lunar cycles may be particularly important for organizing the foraging activities of nocturnal animals. The lunar cycle lasts approximately 29.5 d and is traditionally divided into four phases: new moon (dark), first quarter (waxing half moon), full moon (completely lit), and last quarter (waning half moon). From new to full moon, the brightness of the cloudless sky varies by orders of magnitude (0.009-0.2150 lux; Austin et al. 1976). Moonlight-dependent effects on nocturnal animals are often reported in the context of visually mediated predator-prey interactions (Lima and Dill 1990). Thus, the activity of various heteromyid and murid rodents in desert habitats is influenced by risks of predation which vary with lunar illumination (Kotler et al. 1988, Wolfe and Summerlin 1989, Daly et al. 1992, Bowers and Dooley 1993, Hughes et al. 1994, Vasquez 1994, Bouskila 1995).

I examined the effect of the lunar cycle on the nocturnal foraging activity of Northern water snakes, Nerodia sipedon. Despite suggestions from some early, influential herpetologists that moonlight affected nocturnal snake collecting (Klauber 1939, Kauffeld 1957, 1969), the

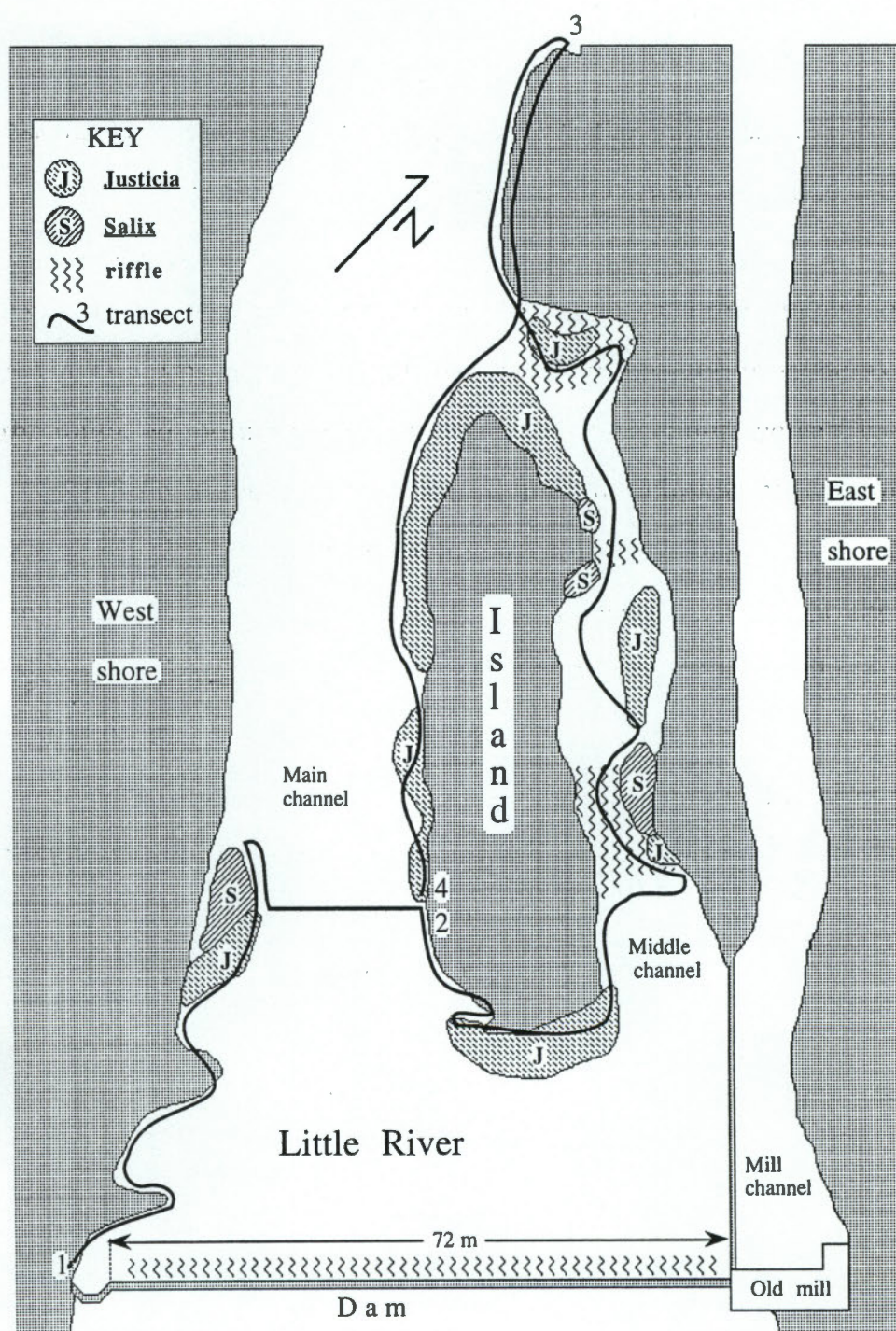
possible influence of the lunar cycle was long overlooked by herpetologists (see Discussion). In general, with the exception of daily cycles in behavioral thermoregulation, biological rhythms have rarely been studied in nonavian reptiles (Rusak 1981). Given the importance of diel cycles in appetite that I found in the laboratory (Chapter III), I wanted to examine biological rhythms which would influence the expression of appetite in the field. Since water snakes are much more difficult to catch and observe during the day (personal observations), daily cycles in foraging would be logistically difficult to address in the field. In contrast, rhythms which might influence foraging behavior from one night to another are not similarly constrained. In addition to a desire to explore lunar effects, part of my motivation for the present study was born of personal frustration. Having searched for N. sipedon on many seemingly ideal summer nights, I have been puzzled as to why I have seen many snakes on some nights, but only very few on others.

B. Methods

The study was conducted on the Little River in Blount Co., TN, at the eastern edge of the Ridge and Valley physiographic province. With headwaters in the Great Smoky Mountains, the Little River has not, like most rivers in eastern Tennessee, been impacted by large scale impoundment and still supports a diverse fish fauna (Etnier and Starnes 1993). The study site is near rivermile 22, elevation 275 m, immediately below the dam at Peery's Mill (Fig. V-1). The principal woody, riparian vegetation is alder (Alnus glutinosa), silky cornel (Cornus amomum), and black willow (Salix nigra); waterwillow (Justicia americana) dominates the



Fig. V-1. The study site at Peery's Mill on the Little River, Blount Co., TN. The census transect began near the west end of the dam at the point labeled "1", and followed the path depicted by the dark line. It took approximately 15 min to walk from point 1-2, 20 min from point 2-3, and 10 min from point 3-4.



emergent vegetation. The water is clear (when not flooding, Secchi readings near 3.0 m; Heacock 1995) and fast flowing over a gravel and cobble substrate. Northern water snakes are abundant at the site.

I established a transect that began at the base of the dam, paralleled the west shore 50 m in a downstream direction, crossed the main channel, circumnavigated two thirds of an elliptical (80 x 20 m) island, followed a gravel bank below the island for 30 m, then doubled back and completed the perimeter of the island (Fig. V-1).

Censuses of water snake foraging activity were conducted from 1995-1998, between the months of May and October (Table V-1). The site was censused by walking the transect beginning 65-164 min (mean=100) after sunset. Censuses took an average of 46 min (limits=35-54 min), with some of the variation due to seasonal changes in water level and height of emergent vegetation (see Table V-1). I slowly walked along in ankle to knee deep water, visually scanning for snakes with a portable, 12 V spotlight (approximately 20,000 candlepower). I have found N. sipedon to be quite conspicuous in the river at night; when a snake's head emerges from the water, the light colored chin is readily lit by spotlight. Any nonneonate snake (see below) observed in the water was counted as a foraging animal. Snakes that were on the shore or perched in vegetation and that were obviously wet were also counted as foragers. When a snake was noted, I continued on without disturbing it. On the parts of the transect that involved doubling back (Fig. V-1), I only counted snakes that were of a different size class than those seen on the first pass through that area. Censuses from mid August to October overlapped the parturition season. Newborn snakes (readily distinguished based on size) were not

Table V-1. Census dates for evaluation of lunar cycles. Each row, denoted by a unique ID code, contains the data for a given set of four moon phases (i.e. a single lunar month). The arabic numeral in the ID code indicates the year. Each tabular entry denoted as a mean is the average of the four censuses for that lunar month. Mean time since sunset is with respect to census starting times. River flow rates were taken at the Maryville gauging station of the Tennessee Valley Authority.

ID code	Dates	Mean				
		Mean census duration (min)	time (min) since sunset	Mean air temp. (°C)	Mean water temp. (° C)	Mean flow rate (m ³ /s)
95-JJ	7 Jun.-26 Jun.	40	85	18.8	20.4	7.19
95-JA	14 Jul.-4 Aug.	45	100	23.7	25.7	2.78
95-AS	17 Aug.-9 Sep.	49	137	22.5	24.9	2.94
96-AS	14 Aug.-5 Sep.	44	93	21.7	22.1	7.50
97-JA	20 Jul.-11 Aug.	39	92	24.1	23.6	6.03
97-AS	18 Aug.-10 Sep.	43	96	21.9	22.8	3.54
97-SO	16 Sep.-9 Oct.	44	100	19.4	19.9	2.63
98-MJ	12 May-2 Jun.	45	97	20.3	20.2	13.62
98-JJ	16 Jun.-9 Jul.	49	97	21.9	23.2	9.77
98-JA	15 Jul.-6 Aug.	50	98	22.8	24.2	5.15
98-AS	13 Aug.-4 Sep.	54	101	23.4	25.4	2.38

counted in order to avoid attributing the appearance of many, small snakes to the lunar cycle when it might be due to a chance timing of birth. Upon completion of each census, air and water temperatures were measured to the nearest 0.2 °C with a rapid reading, mercury thermometer, and recorded along with census duration, number and location of snakes seen, and weather conditions.

I censused all four moon phases in each of 11 different lunar months (Table V-1). The time of a given census was set to be ± 60 h of the exact time of the intended moon phase; in practice, all but a single census were actually within 36 h of the desired phase. This time window allowed me to census near a particular moon phase while avoiding any inclement weather on a given day. The time between consecutive censuses within one lunar cycle ranged from 5-12 d (mean=7.4). Data on timing of lunar phases were obtained online from the U. S. Naval Observatory, Astronomical Applications Department (Internet URL= <http://aa.usno.navy.mil/AA/>).

Temperature could vary considerably between censuses. Since temperature strongly affects all aspects of snake biology and performance (Lillywhite 1987), I had to account for thermal changes in order to assess lunar effects. I regressed number of snakes seen per census against temperature, then used the residuals about this regression as a temperature-independent measure of snake foraging activity. I performed a Friedman's Two Way ANOVA on relative number of snakes seen (i.e. the number above/below that predicted by temperature) to test the null hypothesis of equality between moon phases. A repeated test was used because of the possibility of seasonal effects (e.g. daylength, water level, thickness of emergent vegetation) that would make censuses within a given lunar cycle

more similar to each other than to those in other cycles (see Table V-1). I chose a nonparametric test because the relatively small data set (i.e. 4 data points per month) would have precluded a confident assessment of normality. Some conspicuous outliers in the data (see Results below) suggest that this decision was warranted. The alpha level for acceptance was set at $p=0.05$.

C. Results.

The numbers of snakes seen per census ranged from 0-26 (mean=8.2). There was a strong, positive relationship between numbers of snakes seen and water temperature (Fig. V-2). However, the function was curvilinear. A logarithmic transformation of number of snakes seen was regressed against temperature, yielding a significant linear regression ($r=0.57$, $p=0.001$). Relative number of snakes seen ranged from +16.2 to -5.7, and varied in a "V" shaped pattern over the lunar cycle (Fig. V-3). A Friedman's ANOVA rejected the null hypothesis of equal medians between moon phases. In general, snake foraging activity was high during the new moon and last quarter phases, and low during the full moon and first quarter phases. Although not all lunar months showed the same pattern (Fig. V-4), some consistencies produced the overall trend. In 8 of 11 months, the phase with the highest activity was either the new moon or last quarter. In 9 of the 11 months, the phase with the lowest activity was either the full moon or last quarter. The pattern of activity was appreciably different during two of the lunar months (Fig. V-4, lower panel), with the first quarter actually exhibiting the highest level of snake foraging activity.

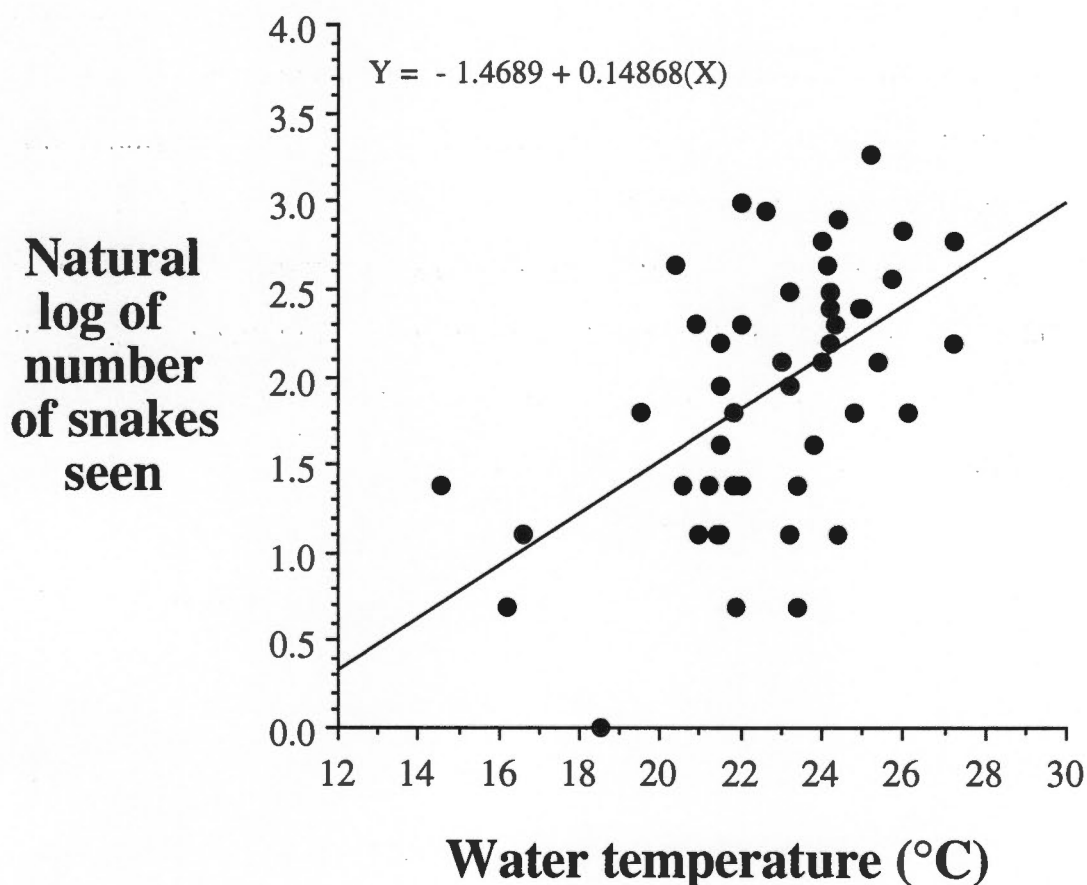


Fig. V-2. The number of Northern water snakes seen per census as a function of water temperature (n=50 censuses). Data are included from six censuses that were not part of the lunar cycle study, but which were conducted in an identical manner.

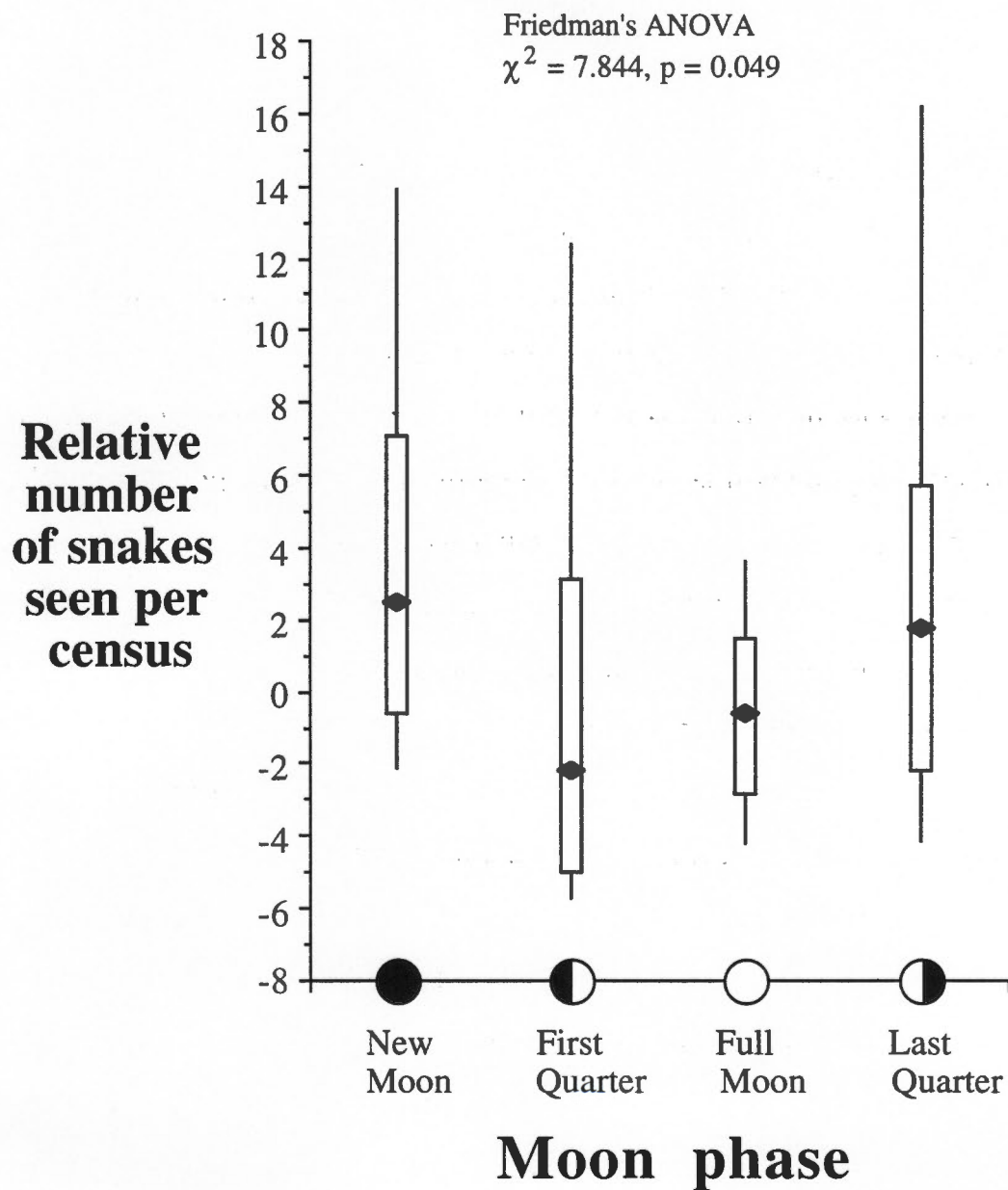
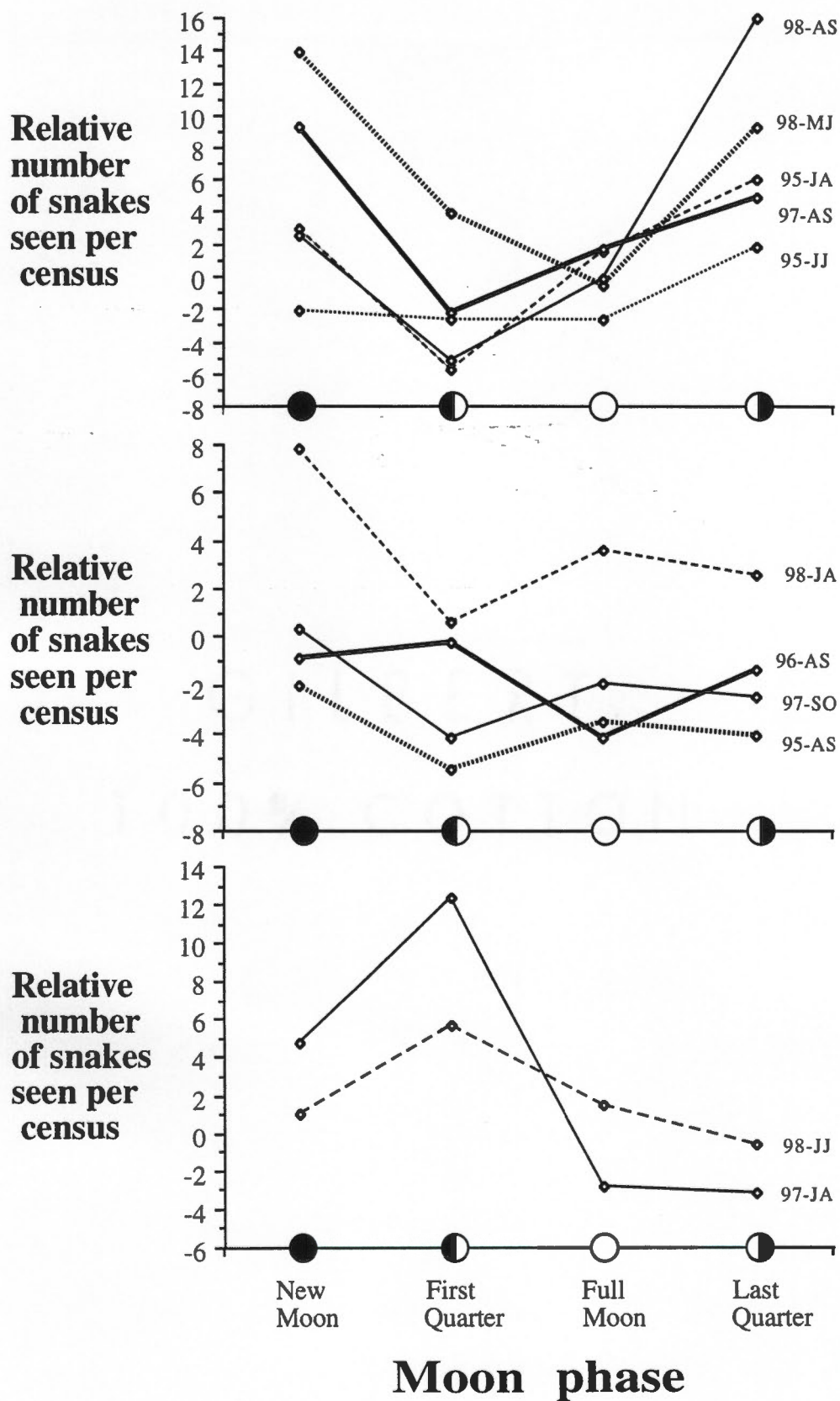


Fig. V-3. Relative number of Northern water snakes seen as a function of lunar phase. The four phases were sampled in each of eleven lunar months between May 1995 and September 1998. The dark symbols are medians, the clear boxes are interquartile ranges, and the vertical lines are overall ranges.



Fig. V-4. Line plots of relative number of Northern water snakes seen as a function of lunar phase. Each line symbol connects the points within a given lunar month. Each of the three panels in the figure groups months with similar patterns. The code for the lunar months, at the right hand side of each panel, is summarized in Table V-1.



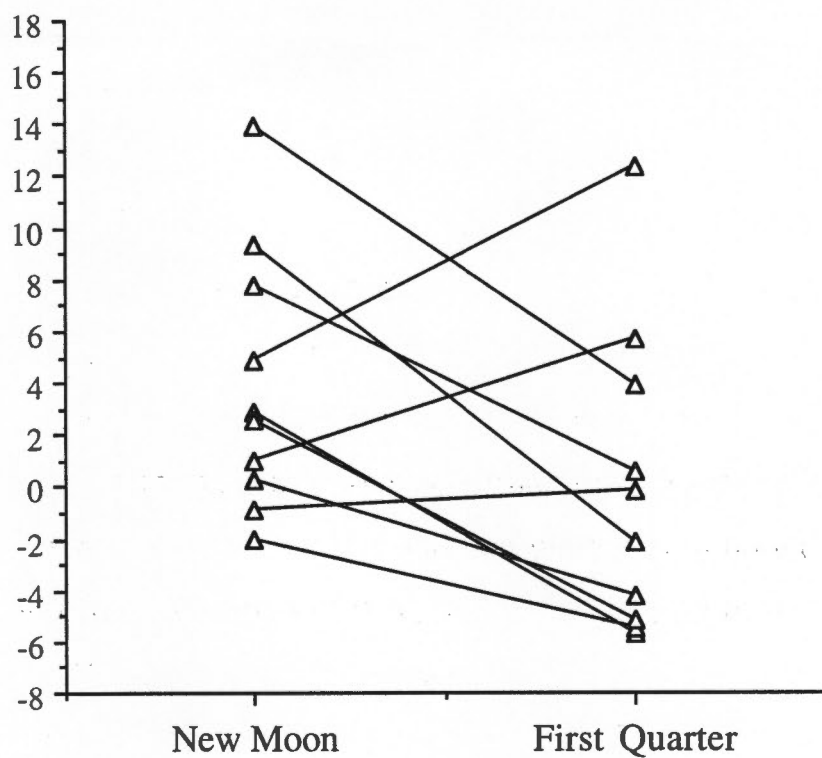
Inspection of these trends and a consideration of the astronomical events of the lunar cycle suggested two post hoc comparisons. A design which preserved the repeated nature of the initial analysis was to compare consecutive "dark" moons and "bright" moons. New and first quarter moons were both considered dark moons because, though the first quarter moon is half illuminated, it does not rise until approximately midnight (see Discussion below). Thus, during both of these phases, the sky is dark for the first few hours after sunset. Full and first quarter moons were collectively considered bright moons. In the post hoc analyses, the data were recast into dark-bright pairs that were consecutive (Fig. V-5). Ten "new moon-first quarter" pairs and 10 "full moon-last quarter" pairs resulted. A Wilcoxon signed rank test indicated a significant increase ($T^+=52$, $p=0.005$) in median foraging activity between full moons and the last quarter moons which immediately followed them (Fig. V-5, upper panel). The drop in median snake activity in going from new moons to first quarter moons (Fig. V-5, lower panel) was only marginally significant ($T^+=44$, $p=0.053$). The magnitude of the difference between full moons and last quarters was generally smaller than that between new moons and first quarters, but difference in the former was more consistent. Considering all such paired comparisons, on average I saw 4 more snakes during dark moon censuses than during the bright moon censuses which immediately preceded or followed.

D. Discussion.

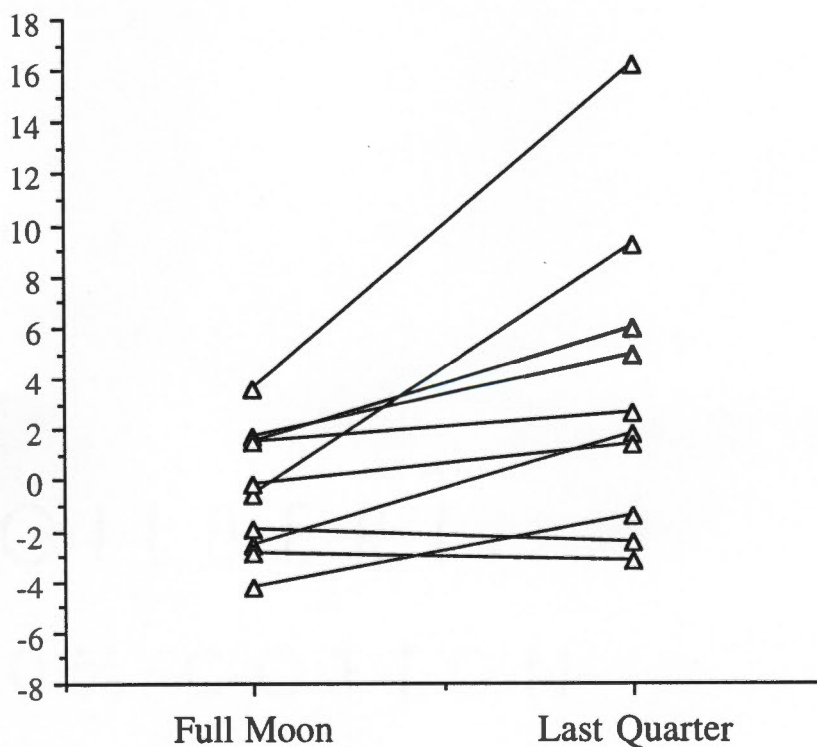
Both temperature and moon phase were significantly correlated with water snake foraging activity. Mechanistically, a temperature correlation

Fig. V-5. Post hoc comparisons of adjacent dark and bright moon phases. The lines plots compare either adjacent new moons and first quarters (upper panel) or adjacent full moons and last quarters (lower panel). Ten pairs of consecutive phases were assembled in each comparison.

**Number
of snakes
more/less
than
expected
for temp.**



**Number
of snakes
more/less
than
expected
for temp.**



Moon phase

would undoubtedly be attributable to the thermal dependencies of snake physiology (Lillywhite 1987). Warmer snakes have higher rates of metabolism, need more food, and were closest to their preferred body temperature (approximately 28 °C; Lillywhite 1987) at the warmest water temperatures seen in this study. A strong association between moon phase and snake foraging activity has previously been underappreciated. Before discussing this relationship, I should address the nature of the change in snake activity. It is unlikely that most of the water snake population goes without eating for two week periods during bright moons. Water snakes appear to feed much more frequently than this, e.g. adult female snakes average one prey item every four days (see Chapter IV). The measure of snake activity that I used reflects the proportion of the population that is actively hunting at the time of the census. Thus, I interpret the moon phase as affecting the probability that a snake will be hunting at a given time. One way such an effect might be manifested is by a change in the frequency of foraging. Hypothetically, for example, a one third reduction in number of snakes seen would occur if snakes foraged every night during a dark moon period, but every third night during bright nights. Alternatively, a shift in activity time could produce similar results. For example, most snakes may forage every night, but a one third reduction would result if two thirds of the snakes waited to forage until after the time period corresponding to my censuses. There is a regular relationship between moon phase and moon rise/set times that could make predictions about such hypothetical shifts in timing of nightly activity (see below).

Earlier comments on the possible effects of moonlight on snake collecting (Klauber 1939, Kauffeld 1957, 1969) did not immediately lead

to increased scrutiny of the issue. In the last 15 years, however, the importance of lunar phenomena has been described in both freshwater and desert snakes (Table V-2). Lunar cyclicity has now been reported for three genera of nocturnal, piscivorous snakes from two families on three continents. These results suggest that lunar cycles are a ubiquitous mediator of predator-prey interactions of aquatic snakes. However, it is not clear whether the ultimate determinant of the rhythm is the role of these snakes as predators or as prey.

In general, although vision can play a part, tactile sensation and chemoreception are the most important modalities guiding predatory behavior of Northern water snakes (Brown 1958, Drummond 1979, 1983). Thus, any differences in snake foraging success are probably not attributable to changes in the ability of snakes to see their prey (see also Skutelsky 1996). Instead, light levels may act indirectly by affecting the ability of prey fishes to detect predators. Although examples of nontidal, lunar rhythms in fishes are few (Gibson 1978), the migratory activity of eels (Anguilla) in rivers is highest during dark moon phases (Tesch 1977, Gibson 1978). In reviewing daily activity patterns of fishes, Helfman (1986) characterized a number of fish families as being solely diurnal. The demands of night and day vision are somewhat incompatible in fish visual systems (Helfman 1986); strictly diurnal fishes have good day vision at the expense of night vision. Having generally poor night vision, diurnal fishes may be even more vulnerable to snakes on nights with less light (i.e. dark moons). Of the important groups of prey fishes reported for N. sipedon (Brown 1958, Ernst and Barbour 1989a), many minnows (Cyprinidae) and darters (Percidae) are considered diurnal (Helfman 1986, Craig 1987).

Table V-2. Correlations between moon phase/illumination and snake activity in the field and enclosures.

Species (Family)	Habitat	Correlate of dark moon	Source
<u>Lycodonomorphus bicolor</u> (Colubridae)	Freshwater lake	Higher % of snakes with food	1
<u>Acrochordus arafurae</u> (Acrochordidae)	Freshwater lagoon	More snakes active	2
<u>Nerodia sipedon</u> (Colubridae)	Freshwater river	More snakes active	3
<u>Crotalus cerastes</u> (Viperidae)	Desert	More prey captures recorded	4
<u>Trimeresurus flavoviridis</u> (Viperidae)	Enclosure	Emerge at dim illumination	5
<u>Crotalus viridis</u> (Viperidae)	Enclosure	More extensive moves; use open area more	6

Sources: 1-Madsen and Osterkamp 1982.

2-Houston and Shine 1994.

3-present study

4-Bouskila 1995.

5-Yamagishi 1974.

6-Clarke et al. 1996.

Since they rely on nonvisual senses when they hunt, more snakes may forage on dark nights because of predictably higher chances of success.

An effect of the lunar cycle on the vulnerability of snakes to their own predators should also be considered. It may be the case that more snakes restrict their activity on bright nights because of greater predation risk from visual predators. During night field work, I have observed a number of vertebrates that I consider to be potential predators of water snakes (Table V-3). From this suite, four nocturnally active predators that may rely heavily on vision to detect prey and that have been reported to eat snakes include: bullfrogs (Wright and Wright 1949), snapping turtles (Ernst and Barbour 1989b), night herons (Bent 1963), and screech owls (Bent 1961). To the extent that most of a snake population consists of younger individuals, population level changes in activity will be most conspicuous when they preferentially involve small animals. During most nighttime visits to the study site, I saw large bullfrogs hunting in the shallow water. Many of the smaller N. sipedon that I have observed were also in shallow water, so large frogs could be important predators of small snakes. The greater susceptibility of small snakes to predators should not suggest, however, that large snakes would not be influenced by the moonlight. Large snakes do not need to eat as frequently as small snakes, and larger animals can better tolerate lengthy food deprivations. Thus, large snakes can afford to curtail hunting activity during unfavorable time periods. In Chapter IV, I estimated that a 500 g N. sipedon might be able to maintain an adequate rate of food intake by only foraging for about 12 d per month. Even slight selection pressures from predation during bright moons could dictate that foraging activity of large snakes vary over the

Table V-3. Potential water snake predators seen during night field work in streams of eastern Tennessee.

Common name	Scientific name
Longnose Gar	<u>Lepisosteus osseus</u>
Largemouth Bass	<u>Micropterus salmoides</u>
Bullfrog	<u>Rana catesbeiana</u>
Mink	<u>Mustela vison</u>
River Otter	<u>Lutra canadensis</u>
Raccoon	<u>Procyon lotor</u>
Snapping Turtle	<u>Chelydra serpentina</u>
Spiny Softshell Turtle	<u>Apalone spinifera</u>
Black Crowned Night Heron	<u>Nycticorax nycticorax</u>
Screech Owl	<u>Otus asio</u>

lunar cycle. As a general point, it should be noted that predatory success of and predator avoidance by snakes may not be mutually exclusive. Both selection pressures may have simultaneously influenced the evolution of increased activity during dark moons.

In terms of the proximal causation of behavioral rhythms, it is a core tenet of ethology that internal and external stimuli interact to produce behavior. Biological rhythms, including those with daily, lunar, and annual cycles, are exemplary phenomena. For many biological rhythms, endogenous biological clocks with a variety of periods keep time quite precisely, even in environments where external cues are held constant (reviews in Brady 1979, Aschoff 1981). However, because of a slight mismatch between internal and external periods, such rhythms need to be entrained by recurrent, reinforcing cues from the environment. Endogenous circadian clocks are well known in reptiles (Jones 1974; Underwood 1992), but no studies have mechanistically investigated lunar clocks in reptiles. The results of the present study offer little to distinguish between a truly endogenous clock and a system that is driven solely by extrinsic, environmental cues. One census conducted during a first quarter moon (a phase that generally displays low snake activity) recorded a low number of snakes despite there being a continuous cloud cover. This single observation offers weak evidence for an endogenous clock.

If external cues, either directly or indirectly (i.e. as entraining cues for endogenous rhythms), are the primary stimuli driving lunar cyclicity, which types are involved? Lunar brightness at night varies by orders of magnitude over the lunar cycle (Austin et al. 1976). If lunar brightness is the relevant cue, it would be interesting to determine which sense organ

transduces the stimulus. In many vertebrates, the pineal gland (and, when present, the associated parietal eye) is the most important organ mediating diel rhythmicity. While this generalization applies to most reptiles, the pineal gland of snakes is exceptional in lacking photoreceptor-like cells (Underwood 1992). Thus, the eyes may be the primary receptors that transduce lunar brightness and transmit that information to the central nervous system. The possibility that nonvisual cues are the relevant stimuli could also be considered. For example, water snakes may be reacting to the lunar cycle indirectly if they are simply tracking the behavior of their prey. Field studies of lunar cyclicity in the prey fishes themselves would help to establish whether prey behavior was actually the relevant cue.

Although first and last quarters have similar brightness levels, the present results suggest that all half moon phases are not alike. There were noticeably more snakes foraging during the last quarter than during the first quarter (Fig. V-2). The first quarter was the phase with the lowest snake activity in 7 of 11 lunar months; the last quarter was the phase with the highest snake activity in 3 of 11 censuses, and had the single, highest value for the entire study (16.2 more snakes than predicted from temperature). The specific moon phase in which freshwater eels (Anguilla) show a pronounced peak in migratory activity is the last quarter (Tesch 1977, Gibson 1978). Regarding snakes, Madsen and Osterkamp (1982) suggested that snake foraging activity decreased from new moon to full moon. However, inspection of the data (their Fig. 2) indicates that, in fact, the last quarter was the peak in proportion of snakes containing food, and that the first quarter was the trough. Collectively, these observations suggest that the illumination level per se of a moon phase is not the only

relevant factor. This distinction is worthy of consideration, as previous studies in enclosures have examined mainly the effect of light level (Yamagishi 1974, Clarke et al. 1996). Another important factor is the daily timing of lunar ascent and descent.

A regular relationship exists between the phase of the moon and the time of day when the moon is above the horizon. This relationship is illustrated with data from the four lunar phases of April 1997 (Fig. V-6). During the new moon, the entire night is dark. During the last quarter, though, there is a period of darkness in the first half of the night, before the half moon rises. The censuses in the present study began 65-164 min after sunset. High snake activity during last quarter censuses may be caused by a concentrating an entire night of activity into a short, moonless period in early evening. During their active season, water snakes show a pronounced tendency for crepuscular/early evening feeding, even when held in the laboratory under ad libitum food conditions (III.C.). As discussed above, there is a period of vulnerability of fishes to predators that occurs during early evening (Helfman 1986). In such a case, the full moon phase can potentially be more productive for a predatory water snake than the dimmer first quarter. Since the full moon rises approximately at sunset (Fig. V-6), it may not ascend to the relevant (i.e. activity suppressing) height before the evening feeding peak. However, the first quarter moon is at its zenith approximately at sundown, remaining high in the sky in the early evening. In this context, it is noteworthy that the moon is dimmer at the horizon than at zenith due to atmospheric attenuation (Austin et al. 1976), and that the moon's light is often blocked by topography or vegetation when near the horizon. Such a phenomenon

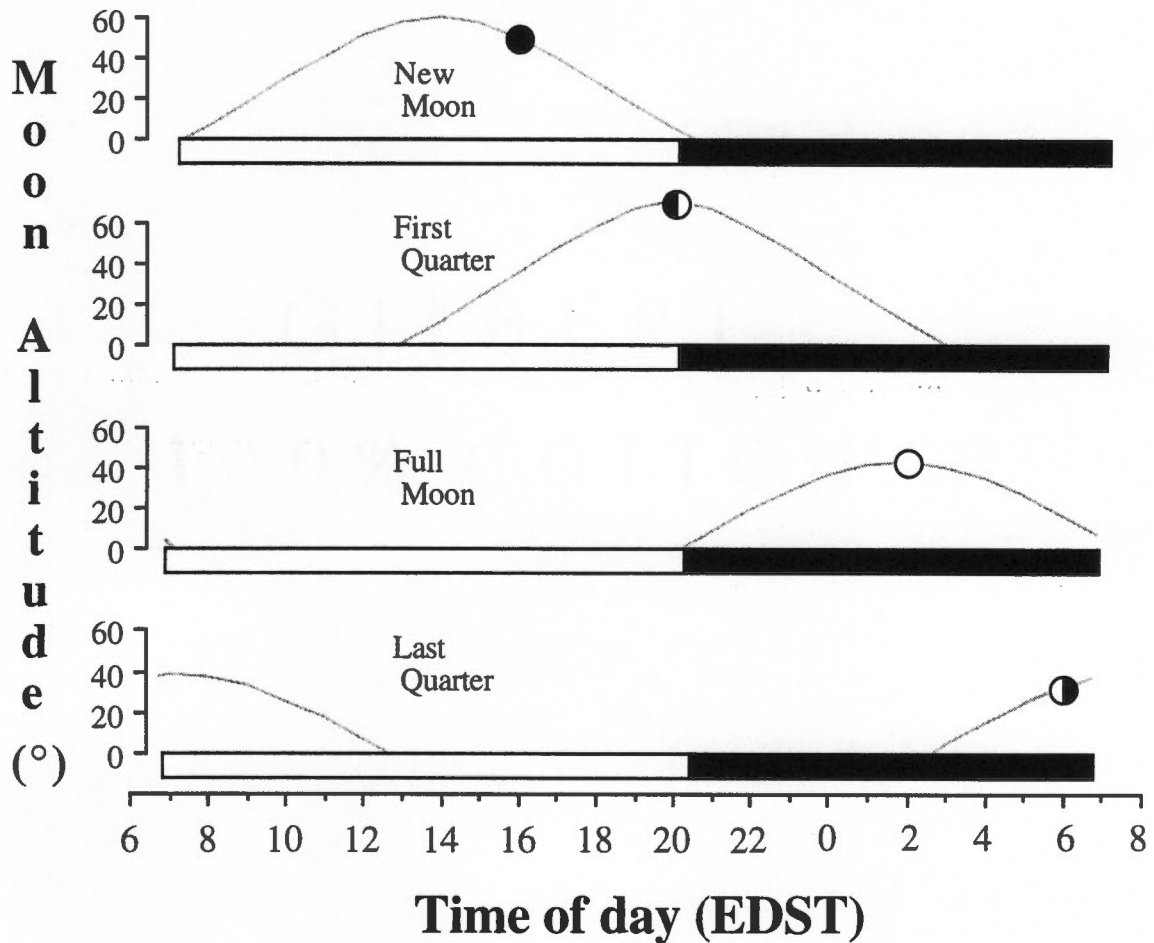


Fig. V-6. The trajectory of the moon across the sky on the days of the four lunar phases in April 1997. Moon altitude is in degrees above the horizon. The bars at the bottom of each panel indicate the lengths of day (white) and night (black). The data for Maryville, Blount Co., TN, plotted here were obtained online from the Astronomical Applications Department of the U. S. Naval Observatory (see Methods).

could explain why snake activity during the full moon phase can be higher than during the first quarter (Madsen and Osterkamp 1982, this study). Thus, in addition to endogenous lunar cyclicity, another mechanism can potentially produce a lunar rhythm: a circadian rhythm interacting with moonrise/set times that vary around the lunar cycle (see Neumann 1981).

Although lunar rhythms have historically been studied mainly in reference to the tidal responses of marine organisms (Gibson 1978, Neumann 1981), increasing scrutiny in nonmarine habitats has revealed lunar effects in a variety of animals. It seems likely that the phenomenon exists for many nocturnal taxa in habitats where vision mediates predator-prey interaction (Lima and Dill 1990). In the context of acting as visual predators, and on the practical side, I would encourage snake researchers to investigate lunar cyclicity in the course of their field collecting of nocturnal taxa.

E. Summary: Lunar cycle in foraging

There is greater water snake foraging activity at higher water temperatures. Water snake foraging activity is also significantly higher during dark moon periods than bright moon periods. Predation both by and upon the snakes may be relevant to understanding the origin and maintenance of this phenomenon. Changes between moon phases in the timing of lunar ascent/descent may be an important part of lunar rhythms in addition to changes in illumination. Lunar rhythms probably await discovery in many taxa of predators and prey in aquatic systems. Attention to lunar cycles may help the researcher in scheduling field collecting times.

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VITA

Paul Timothy Andreadis was born 13 June 1962 in Cincinnati, OH. The second oldest of 9 children, Paul was a shy introvert and a seemingly instinctive herpetologist. One of his earliest memories was coming face to face with "Big Al", a lifesize Allosaurus replica that leaned down with parted jaws to greet visitors at the Cincinnati Museum of Natural History. Through his early years, Paul spent his indoor time devouring books on reptiles, especially Carr's The Reptiles, absorbing every nature show on television, and building models. He spent his outdoor time playing in the dirt, climbing trees, and seeking critters. Strongly influenced by several outstanding, summer courses on natural history, Paul wrote an essay in 9th grade about how he planned to obtain his Ph.D. studying reptiles. Paul was proud of the diversity of his accomplishments, earning varsity letters in wrestling, maintaining perfect attendance, and graduating 11th in his class at Anderson Senior High School. Paul then attended the Ohio State University in Columbus, OH. The two most significant things that happened there were that (1) he decided to forego shyness, making a concerted effort to become an extrovert, and (2) he met his future wife, Debra Karen Williams. Paul graduated with a B. S. in Zoology with Honors in the Liberal Arts in 1984. He then fulfilled a lifelong dream by attending the mecca of herpetology, the University of Florida. He received his M.S. in Zoology in 1988, having spent many happy nights knee deep in cypress swamps. He and Debra were married in 1988, and they moved to Knoxville, TN in 1989 to attend the University of Tennessee. Their greatest accomplishment was the birth of their daughter, Kassandra Lynne, in 1993. Paul received his Ph.D. in 1998.