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I am submitting herewith a dissertation written by Barbara Ann Conner Savitzky entitled "Aquatic Foraging in Two Independently Evolved Species of Aquatic Snake: *Nerodia rhombifera* (Colubridae) and *Agkistrodon piscivorus* (Viperidae)." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Life Sciences.

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AQUATIC FORAGING IN TWO INDEPENDENTLY EVOLVED SPECIES OF SNAKE: *NERODIA RHOMBIFERA* (COLUBRIDAE) AND *AGKISTRODON PISCIVORUS* (VIPERIDAE)

A Dissertation

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Degree

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Barbara Ann Conner Savitzky

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To Christopher and Heather

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ABSTRACT

This study compares piscivory in two species of sympatric snakes, the highly aquatic natricine, the diamond back water snake, *Nerodia rhombifera* (Colubridae), and the generalist crotaline, the cottonmouth, *Agkistrodon piscivorus* (Viperidae) in terms of the relationship among foraging behavior, ontogeny and the habitat. Current issues of interest in snake foraging are discussed, focusing on the role of ectothermy and problems peculiar to piscivory.

Piscivory was studied in the laboratory in a large naturalistic pool, and in the field at Reelfoot Lake, Tennessee. Ontogenetic changes in the foraging of both species were studied in the laboratory. Each study examined water depth, the use of cover and open water, the amount of time spent above and below the water, and specific types of emergent and submergent behaviors. Prey variables included live versus dead fish and relative size. Predatory behaviors were divided into attacking, capturing and handling prey, and the ingestion of prey.

The two species exhibited very different foraging tactics. The negatively buoyant *Nerodia rhombifera* attacked mainly live fish from the water. Fish were handled and ingested where captured, including underwater. Size and sex differences were found. The positively buoyant *Agkistrodon piscivorus* foraged from the water's edge, selecting mainly dead fish. Fish were handled and ingested largely out of water, and always above water. There was very little overlap in habitat use between the two species.

Ontogenetic changes were found in both species. *Nerodia rhombifera* neonates initially used sit-and-wait attacks at the surface, and later attacked more underwater and used more types of attacks. The open-mouthed foraging considered typical of the

species developed over time. Field work on *N. rhombifera* corroborated laboratory work, including size and sex differences. Neonate *Agkistrodon piscivorus* initially attacked live prey from the edge and later attacked from below the surface as well. Although juveniles employed more methods of attack, they still attacked only from the edge. Dead fish were taken more frequently by larger snakes, although the juveniles tested still preferred live fish. Predation on fish was similar to predation on rodents in terms of prey handling techniques, including the use of envenomation.

This study clarified the relationship between foraging behavior and habitat in *Nerodia rhombifera* and *Agkistrodon piscivorus*. Additionally, ontogenetic changes in foraging in these precocial species were documented, with open-mouthed searching and other underwater behaviors developing after birth. The generalist-specialist continuum of snake piscivory was more clearly defined as a result of this study. Open-mouthed searching was found to be an efficient tactic for both generalist and specialist piscivores.

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CHAPTER I

INTRODUCTION

1. STATEMENT OF THE PROBLEM

The ecology of snakes: morphology and habitat use. While the characteristic elongate, limbless *bauplan* and highly derived jaw mechanism of snakes influence all aspects of their ecology (Greene, 1983), it is generally agreed that dietary demands have been especially important in the evolution and radiation of snakes (Arnold, 1972; Gans, 1961, 1975, 1983; Greene, 1983; Pough, 1983b; Pough and Groves, 1983; Savitzky, 1980; Toft, 1985). Understanding foraging, then, would seem to be crucial to understanding the ecology of snakes.

Habitat use, of course, is also an important aspect of snake ecology (Kephart, 1982; Reynolds and Scott, 1982; Toft, 1985). Since diet and habitat use are usually the two most important determinants of niche, the relationship of foraging behaviors to the environment not only is the proximate determinant of diet, but also in large measure defines the niche. The value of studying foraging in relationship to the environment was demonstrated in MacArthur's (1958) classic study of New England warblers.

Methodological problems in studying snakes. Snakes are secretive and feed infrequently. Consequently, even intensive field studies have offered little information about how snakes find and capture prey in their habitat as observations

information about how snakes find and capture prey in their habitat as observations of feeding are rare (Cook, 1983; Fitch, 1960; Mushinsky and Hebrard, 1977a; Wharton, 1958). Although some extensive observations of natural foraging exist (Drummond, 1980, 1983; Mushinsky and Hebrard, 1977a; Mushinsky 1987; Jayne et al., 1988; Patterson and Davies, 1982; Hailey and Davies, 1986a,b,c), many published accounts of snakes feeding in the wild are the result of serendipitous observations (Batts, 1961; Bothner, 1974; Evans, 1942; Gillingham and Rush, 1974; Leavitt, 1956; Richmond, 1944; Stoner, 1941; Tevis, 1943; Trapido, 1943; Yerger, 1953). The publication of these unplanned and usually incomplete accounts of snake feeding attest to their significance (see comments by Fitch, 1987).

Thus, while field methods are important sources of information, laboratory methods are needed to deal with the problems of secretiveness and infrequent feeding by snakes. Approaching snake ecology from an ethological perspective, I examined foraging and its relationship to the habitat in a naturalistic, but controlled laboratory setting. Because snakes are so specialized, I chose to look at a particular foraging specialty, piscivory.

The ecology of snakes: phylogeny and sex. Prey specialization has suggested that diet and evolution are especially closely linked in snakes. Therefore, the role of phylogeny in snake ecology was also examined in this study. A review of the literature made it clear that size and sex also needed to be considered as diet has proved to be size and sex specific in some species of snakes, including piscivores (Mushinsky, 1987). Therefore, this study also addresses these issues.

Details on the reasoning and methodology of this study are discussed later in this chapter. These sections are preceded by a review of snake ecology emphasizing issues of special importance for this study, and a discussion of piscivory as a foraging problem. The chapter ends with a discussion of the ecology of the species studied.

2. BACKGROUND ON SNAKE FORAGING

Habitat Use and Prey Availability

The question of habitat use. In most field studies, dietary information about snakes is obtained by capturing snakes in traps or by hand and then examining gut contents. It is generally assumed that the snake's prey was captured near the site of capture. The validity of this assumption has not been determined and is quite suspect when snakes are captured along drift fences. But this assumption is also suspect even when the snakes are caught by hand, however, because snakes often alter activity patterns after feeding, becoming inactive and maintaining a higher body temperature to aid digestion (Greenwald and Kanter, 1979; Kitchell, 1969; Naulleau, 1983; Regal, 1966).

Post-feeding snakes thus have needs similar to, but of shorter duration than, those of gravid snakes. Post-feeding snakes, like gravid snakes, also experience reduced locomotor ability (Garland and Arnold, 1983; Seigel et al., 1987), and would similarly be expected to avoid activity. Habitat use in gravid snakes of at least some species differs from that of nongravid snakes (Duvall et al., 1985; Keenlyne, 1972; Reinert, 1984; see discussion in Gibbons and Semlitsch, 1987; and Gillingham, 1987).

This differential habitat use has been related to the need for gravid females to maintain higher body temperatures for the developing embryos, and to the fasting of heavily gravid females in some species (Gregory and Stewart, 1975; Prestt, 1971 in Gregory and Stewart, 1975). There is good reason, then, to suspect that habitat use in foraging snakes differs from habitat use in the post-feeding snakes frequently sampled.

The problem of local dietary specialization. Population differences in diet, or local specialization (Fox and Morrow, 1981), are a fairly widespread phenomenon in snakes. Kephart (1982) even found that microgeographic differences in diet were more pronounced than interspecific differences among the species of garter snakes he studied. Thus, whereas snakes are generally prey specialists (Arnold, 1972; Schoener, 1977; Shine, 1977; Toft, 1985), the total prey list for a species is sometimes remarkably long. The proximal causes of local specialization, in snakes, have been shown to be primarily (a) intraspecific genetically controlled prey preferences (Arnold, 1981; Burghardt, 1970, 1975; Dix, 1968; Drummond and Burghardt, 1983; Gove and Burghardt, 1975; Henderson et al., 1983), and (b) local prey availability within a habitat (Kephart, 1982; Kephart and Arnold, 1982; Lagler and Salyer, 1945; White and Kolb, 1974; see Mushinsky, 1987; see also Greenwell et al., 1984). Even when prey availability is the same for different populations (*e.g.*, artificial ponds stocked with the same types of fish), differences of habitat structure such as vegetation density and incline of the bank of a body of water appear to play a role in the diet of semi-aquatic snakes (Bowers, 1966; Plummer and Goy, 1984; Reynolds

and Scott, 1982; Hebrard and Mushinsky, 1978; Mushinsky and Hebrard, 1977a; Mushinsky, 1987).

Niche overlap and resource partitioning in snakes. Finally, knowing the precise relationship of habitat use to foraging is an important issue in snake ecology as there is often remarkable niche overlap among snakes (Gregory, 1978, 1984; Hebrard and Mushinsky, 1978; Kofron, 1978; Mushinsky and Hebrard, 1977a,b; Mushinsky et. al., 1980; Reinert, 1984; Reynolds and Scott, 1982; Shine, 1977; Toft, 1985; White and Kolb, 1974). Yet, competitive interactions have been difficult to document (Gregory, 1978, 1984; Reichenbach and Dalrymple, 1980), appear unlikely (Kephart, 1982; Reichenbach and Dalrymple, 1986), have been documented only in areas of unusually severe prey limitations (Shine, 1977), or appear to be limited by the role of abiotic factors (Brown and Parker, 1982; Drummond and Macias Garcia, 1989).

What are the most important resource dimensions for snakes? After reviewing hundreds of studies on reptiles and amphibians, Toft (1985) concluded that snakes were an exception in resource partitioning: for snakes, the most important resource dimension is food. This, of course, coincides well with the generalization that snakes are prey specialists. Toft (*op. cit.*), however, also found that habitat use was quite important. Habitat structure, where studied, has been found to be critical to understanding snake resource partitioning (see Mushinsky, 1987), especially where food overlap is high. It has been found, for example, that two species may capture the same types of prey in the same area, but that the species differ in their preferences

for amount and type of cover (Carpenter, 1952; Hebrard and Mushinsky, 1978; Reinert, 1984; Reynolds and Scott, 1982).

Additionally, prey availability and habitat differences are related in complex ways as described in the preceding paragraph. Structural differences are important in part, then, because of the foraging abilities or limitations of species (Drummond and Macias Garcia, 1987). As Gregory notes (1984, p. 2020) in regard to aquatic foraging by garter snakes, "Prey abundance and prey availability are two different matters...".

3. SNAKES AND FORAGING THEORY

Snakes as Specialized Ectotherms

Snakes as elongate ectotherms. While foraging theory has progressed rapidly in recent years, no theory has been tested using snakes. Given the low-energy-flow, ectothermic lifestyle of reptiles (Pough, 1980, 1983a), different foraging rules probably apply to snakes than those applied to high-energy-flow endothermic vertebrates (Gans and Pough, 1982; Greene, 1986b; Pough, 1980, 1983a; Toft, 1985).

For example, the elongate body of snakes, with its high surface-to-volume ratio, results in a rate of heat loss untenable for endotherms (Pough, 1980, 1983a; Gans, 1983). While other terrestrial ectotherms have elongate bodies, elongation certainly is most extreme in snakes and is, in fact, characteristic of snakes. While elongation may have been selected for as an adaptation to fossorial life (Gans, 1961, 1975, 1983), its continued hypertrophied expression in non-fossorial species suggests that it is beneficial or at least not selected against. Just as this shape allows rapid

Matching energy expenditure to energy input. Like other ectotherms, adult snakes deprived of food for long periods (*e.g.*, 6 weeks) suffer little weight loss. Snakes do not defend body weight either. Adult snakes, at least in one study, did not regain weight lost during forced deprivation in the laboratory (Myer and Kowell, 1971). Other studies also indicate related, unique patterns of weight control. In the rattlesnake, *Crotalus viridis*, females appear not to feed for the year while gravid. Yet, in one study, post-parturition females divided into high and low food groups regained weight at the same rate, in spite of a twofold difference in food intake between the groups (Charland and Gregory, in press). The snakes appeared to have adjusted energy expenditures through manipulating metabolic rates by the only way available to them in the experimental enclosures: behavioral thermoregulation. Some species maintain an extraorinarily low metabolic rate and, predictably enough, extremely sluggish behavior (Shine, 1986a).

Energy output can also be manipulated by altering reproductive output. In a multi-year study of five populations of four species of snakes, Seigel and Fitch (1985) found that clutch size was correlated with autumn rainfall to such an extent that within-population clutch sizes differed significantly among years in most populations. Additionally, intrapopulation clutch sizes differed more than interpopulation clutch sizes.

Juvenile snakes can modify growth to match food supply (Myer and Kowell, 1973; Scudder and Burghardt, 1985), and can survive without eating for considerable periods (Wharton, 1958). Ectotherms, as adults and juveniles, thus appear to modify energy expenditures to match food supply (Lillywhite et al., 1973; Myer and Kowell,

1973; Pough, 1980, 1983a). This sets them apart from endotherms which are committed to set energy needs, and, as juveniles, to set growth rates (Pond, 1977).

The consumption of large, infrequent meals. The highly kinetic skull of most snakes (Gans, 1961; Pough, 1983a,b; Pough and Groves, 1983; Schmidt, 1950) and the venomous oral secretions of certain species (Savitzky, 1980), are unique specializations for the capture, ingestion, and digestion of relatively large prey. The standard snake feeding regime is the consumption of large, infrequent meals (Pough and Groves, 1983; Savitzky, 1980; Thomas and Pough, 1979), although some species of higher snakes have secondarily adopted a pattern of smaller, more frequent meals (Greene, 1983). Snakes in general appear to eat less frequently than the closely related lizards (Mushinsky, 1987).

Because of the large meals and small energy requirements, some temperate snakes only eat 6-8 times a year (Fitch, 1960, 1982; Greene, 1986b). Fitch (1982) estimates that cruising foragers such as *Nerodia sipedon* need to consume only about 300% of their body weight each year. Pough and Groves (1983) calculated that a standard viper meal was sufficient to sustain the snake for 285 days. Greene (1986b) reported that 6 meals like the one consumed by a bushmaster after 24 days of continuous monitoring were adequate to sustain the snake for a year at tropical temperatures. As Greene (1986b) suggests, search and handling times, and whatever decision rules snakes make, are in time frames orders of magnitude longer than those of endotherms.

Efficiency of nutrient extraction. From these large, infrequent meals, snakes, like all ectotherms, can extract far more of the nutrients, around 74-90%, than can endotherms (Burghardt, 1977; Greenwald and Kanter, 1979; Naulleau, 1983; Pough, 1980, 1983a; Reichenbach and Dalrymple, 1986). For snakes, costs of obtaining prey are low relative to the energy intake, even for active foragers which engage in vigorous activity to subdue their prey (Feder and Arnold, 1982; Pough and Andrews, 1985).

Physiological limitations. On the negative side of ectothermy, the sustained activity involved in capturing, subduing, and ingesting large prey may result in pronounced oxygen debt, the repayment of which may take hours and limits the anaerobic scope of the animal until repaid (Feder and Arnold, 1982; Gratz and Hutchison, 1977). Juveniles appear to be more hampered than adults in this regard (Pough, 1977, 1978). Snakes, like all ectotherms, are at the mercy of temperature, which affects digestion (Naulleau, 1983; Skoczylas, 1970; Stevenson et al., 1985), locomotion, including swimming (Stevenson et al., 1985; Lillywhite, 1987), foraging tactics (Hailey et al., 1982), tongue flicking (Burghardt and Pruitt, 1975; Lillywhite, 1987; Stevenson et al., 1985), and striking (Greenwald, 1972). Physiological limitations thus profoundly constrain the foraging strategies of ectotherms (Lillywhite, 1987; Mushinsky, 1987; Pough, 1980; 1983a). Tradeoffs between burst speed and stamina, for example, are common in lizards (Huey and Bennett, 1986). Seasonal differences in foraging behaviors due to temperature have been found in a European semi-aquatic snake, *Natrix maura* (Hailey et al., 1982).

It seems clear that ectotherms are ecologically quite distinct from endotherms. Pough (1980, 1983a) suggests that reptiles and amphibians have ecological significance as energy producers in the form of biomass rather than as energy consumers like birds and mammals. The highly specialized morphology of snakes, the elongate shape and the highly kinetic skull in particular, may [as suggested already by Toft (1985) and Spellerberg (1976)] set snakes apart from other vertebrate terrestrial ectotherms .

Ecological differences within populations. As with any taxon of vertebrates, small or young snakes cannot eat the same food as adults. The solution to this problem within a taxon has profound evolutionary effects (Pond, 1977). Ontogenetic and sexual differences in diet have been found with some frequency in snakes. Ontogenetic changes can be so extreme that juveniles and adults of the same species are not members of the same feeding guild (Mushinsky et al., 1982).

Ontogenetic changes in diet may involve changes in prey taxa (Fitch, 1960; Godley, 1980; Henderson et al., 1988; Drummond and Macias Garcia, 1987; Macias Garcia and Drummond, 1988; Mushinsky et al., 1982; Raney and Roecker, 1947; Saint Giron, 1980; Mushinsky, 1987) or in prey size (Hess, 1966; Mushinsky and Hebrard, 1982; Mushinsky, 1987; Plummer and Goy, 1984; Voris and Moffett, 1981; Saint Giron, 1980). Given the size differences between adult and juvenile snakes and the consumption of intact prey, prey size differences are probably even more common than reported. Juvenile snakes do not have the metabolic scope of adults and tire faster (Pough, 1977, 1978), which certainly accounts for some of the dietary differences between adults and juveniles. Habitat differences would logically be

expected to be associated with dietary differences, also, although these have not really been explored.

In sexually dimorphic species where a positive correlation between snake size and prey size exists, sexual difference in prey size would seem to naturally result, although only recent workers have looked into this phenomenon (Mushinsky et al., 1982; Plummer and Goy, 1984; Shine, 1986b; White and Kolb, 1974). Shine (1986b) suggests that this phenomenon is probably widespread in snakes, and that sexual dimorphism is often of ecological significance in snakes.

Snakes and foraging theory. Because most foraging theories were developed to describe endotherms, these theories make assumptions which are not applicable to snakes (*e.g.*, that digestion can occur while foraging continues) (Schoener, 1971). Conversely, the physiological constraints of ectothermy are not included in the models (Huey and Bennett, 1986). Similarly, the physiological advantages of ectothermy, especially the ability to manipulate energy expenditure, are not included either.

General theories can be developed for a group, however, only when enough information has accumulated to foster generalizations. While energetics studies have provided a clear and consistent picture of the physiology of snakes, considerably more basic information about how snakes find, capture, and handle their prey must be available before theories of the sort which abound for endotherms can be applied to snakes and other less specialized ectotherms.

4. ADAPTATIONS FOR PISCIVORY IN SNAKES AND OTHER VERTEBRATES

Adaptations for Aquatic Habits

The benefits of being elongate and limbless. The shape and metabolic characteristics of snakes make them pre-adapted for aquatic habits (Seymour, 1982). For snakes, terrestrial serpentine locomotion becomes anguilliform locomotion in the water; no anatomical or behavioral changes are required (Bennett, 1982, Jayne, 1985; Seymour, 1982). Both forms of limbless locomotion are energetically cheaper than limbed locomotion, and aquatic locomotion is cheaper than terrestrial for snakes (Bennett, 1982; Gans, 1974).

Buoyancy and diving. Buoyancy comes naturally for snakes; staying under water, on the other hand, requires adaptation. The release of air from the lung and, perhaps, morphological changes such as decreased lung volume are required to achieve "negative buoyancy" (Drummond, 1980; Seymour, 1982; Zug, 1971). While decreasing lung volume would not seem to be desirable because it would necessarily shorten the time under water, snakes have such low oxygen needs, high anaerobic capacity, unusual tolerance of acid-base disturbance, and possession of the circulatory shunting known as the diving reflex (but see Baeyens et al., 1980), all of which allow them to stay under water for long periods of time (Seymour, 1982). Most of the hydrophiid sea snakes (but not *Pelamis platurus* (Kropach, 1975) utilize these tactics (Heatwole and Seymour, 1975; McCosker, 1975; Voris et al., 1978). Nevertheless, neither the fully aquatic marine snakes nor the semi-aquatic natricines exhibit

unusual long-term submergence capabilities (Baeyens, et al., 1980; Heatwole and Seymour, 1975).

Drummond (1979, 1980, 1983a) found that natricine neonates vary in negative buoyancy, and Fleharty (1967) found that *Thamnophis* adults of three species also vary in buoyancy. Both workers noted that the more highly aquatic species were less buoyant than the more generalized species. *Nerodia sipedon* (Drummond, 1980, 1983a) and *N. rhombifera* (pers. obs.) are also negatively buoyant from birth.

Other reptiles also use lung volume changes to control buoyancy. Buoyancy in turtles is also controlled by lung volume with aquatic species having less lung volume, and, consequently, a more flattened carapace, than terrestrial species. Bottom-walking turtles are somewhat less buoyant than swimming turtles (allowing bottom walkers to return to the surface easily); both are less buoyant than terrestrial turtles (Zug, 1971). Many turtles can remain submerged longer than can snakes, even the marine snakes (Heatwole and Seymour, 1982).

Skin and circulatory specializations. Aquatic and semi-aquatic snakes also have specializations of the skin to control osmotic balance (Seymour, 1982, 1987). Semi-aquatic and aquatic freshwater snakes have skins that are more permeable to water than terrestrial snakes, although the semi-aquatic *Agkistrodon piscivorus* has skin whose permeability is typical of terrestrial species (Dunson and Freda, 1985). The fully aquatic marine hydrophiine snakes possess specializations of the lung, heart, and skin not seen in terrestrial or semi-aquatic snakes. These specializations are required for deep (> 100 m) dives in sea water (Heatwole and Seymour, 1975;

Seymour, 1987), but are not necessary for the brief, shallow freshwater dives made by most aquatic and semi-aquatic snakes.

Adaptations Specifically for Feeding in Water

Dealing with friction and drag. Feeding in the water presents special problems. While movement through water is less energetically costly than terrestrial locomotion because of the lower friction, this reduced friction results in destabilization of the body when the animal strikes, as the body is pushed in the opposite direction of the strike (Seymour, 1982).

Water is a more viscous and denser medium than air, however, and the head moving through the water also results in more drag than moving it through the less viscous air. Drag can be reduced by reduction of head width and depth, especially depth (Seymour, 1982; Taylor, 1987). Movement of the open mouth through the water toward the prey should also accelerate the water, and prey, into the mouth so the water is pushed into a confined area (Vogel, 1981). Most piscivores have a long, narrow snout to minimize the cross-sectional area being pushed through the water (Taylor, 1987; Williston, 1914). The crocodilians exhibit this correlation of snout shape and piscivory especially nicely: the most piscivorous forms have the most slender snouts with the piscivorous *Gavialis gangeticus* at the slender end of snout width continuum, and the generalists, such as the Nile crocodile, *Crocodylus niloticus*, at the other end of the continuum (Taylor, 1987). The water snakes, sea snakes (Seymour, 1982; Taylor, 1987), the piscivorous turtles (Pritchard, 1984), and mammals such as the porpoises (Taylor, 1987) also exhibit this snout narrowing.

Teeth for piscivores. Many piscivores, but not all (see Taylor, 1987; Williston, 1914), tend to possess a large number of sharp, undifferentiated teeth. Piscivorous snakes fit this generalization, as they tend to have numerous, long, sharp teeth which, although highly curved or recurved, are also relatively undifferentiated (Savitzky, 1983). These teeth may assure retention of prey as discussed below.

Vision. The difference in refraction between air and water can be a problem for semi-aquatic species which need to focus in both air and water (Drummond, 1979, 1980, 1983, 1985; Hibbard, 1975; Schaeffel and de Queiroz, in press). The specialist garter snakes, *Thamnophis couchi* and *T. melanogaster* are able to accommodate well in both water and air (Schaeffel and de Queiroz, *op. cit.*) and are capable of relatively long (>5 cm) underwater strikes (Drummond, 1980, 1983, 1985). In general, these species utilize a forward, directed (spear fishing) attack more than lateral sweeping (trawling) attack.

The aquatic specialist, *Nerodia sipedon*, on the other hand, was found to be unable to focus underwater (Schaeffel and de Queiroz, *op. cit.*). Yet, vision is an important sensory modality for these natricines (Drummond, 1979, 1985; see also Burghardt, 1968; Czaplicki and Porter, 1974; Porter and Czaplicki, 1977). As Drummond (1980) noted, however, *precise* underwater vision may be of little use for snakes which forage at night in murky water.

Tactics for Capturing Prey

"Trawling". Attacking by means of a sideways thrust of the head been called "trawling" (or "netting") by Pritchard (1984) in regard to piscivorous turtles. Pritchard (*op. cit.*) notes that animals which attack in such a manner tend to have a flattened, relatively narrow skull. Snakes of the genus *Nerodia* are also renowned for this behavior, although Evans (1942) called it "fishing", a term which I will not use because of its lack of specificity. The sideways movement of the head is frequently continued so that the snake forms circles or figure-eights (Drummond, 1980; Evans, 1942; Kofron and Dixon, 1980; Hailey et al., 1982). Similar behavior has been reported for the homalopsine *Cerberus rhynchops* (Jayne et al., 1988), and for the natricines *Natrix maura* and *N. natrix* (Hailey et al., 1982; Hailey and Davies, 1986a,b,c), and the pelagic hydrophiid sea snake *Pelamis platurus* (Kropach, 1975). *Caiman crocodilus* also catches fish with a sideways snap of the jaws after herding fish against its body (Schaller and Cranshaw, 1982).

"Spear fishing". The head can also be thrust straight forward in the water. This has been called "spear fishing" by Pritchard (1984). Extreme neck elongation and flexibility, and reduction of the entire head or head width are associated with this technique (Pritchard, 1984; Taylor, 1987). Examples include the natricine specialist garter snakes studied by Drummond (1979, 1980), the natricine fish specialist *Thamnophis rufipunctatus* (Fleharty, 1967), the trionichid turtle *Chitra indica* (Pritchard, 1984), the chelid "snake-necked" turtles *Hydromedusa* and *Chelodina* (Pritchard, 1984), the extinct plesiosaurs (Boulenger, 1913 in Schmidt, 1950; Seymour, 1982; Williston, 1914), and possibly the hydrophiid genus, *Hydrophis* (Schmidt, 1950).

Spear fishing and trawling tactics both are associated with relatively long, narrow skulls and have been observed as alternative tactics in at least one species, *Natrix maura* (Patterson and Davies, 1982).

"Angling". Another method, usually from the bottom, but which conceivably could be used from crevices or vegetation, is "angling" (Pritchard, 1984; Taylor, 1987). This is a form of luring or aggressive mimicry, and, in tetrapods, is known only in the alligator snapping turtle (*Macroclemys temmincki*) (Pritchard, 1984). It is somewhat surprising that other piscivorous tetrapods, particularly snakes, have not converged upon this tactic as it seems to be ideal for underwater ambush foraging. One snake, the tentacled snake, *Erpeton tentaculatum*, an ambush forager, possesses tentacles on the head, but these are not used as lures (Cornelissen, 1970a,b; Winokur, 1977).

Porter and Czaplicki (1974) studying feeding by water snakes from bowls in the laboratory, noticed that the snakes often tongue flicked the surface of the water. This motion provoked approach by the prey fish, domestic strains of the goldfish, *Carassius auratus*. They considered this behavior to be a luring behavior, calling it "fly-casting". Drummond (1980) also saw tongue flicking of the surface in the laboratory, but not in the field. He did not report the approach of fish (he used *Pimephales promelas*) to the flicking tongue. No other workers have reported a possible luring function for tongue flicking in aquatically foraging snakes.

Development of a lure may not have been selected for because the underwater ambush tactics used by *Natrix* and *Nerodia* species as mentioned earlier, as well as those used by the homalopsine *E. tentaculatum* (Cornelissen, 1970a,b), work well enough. The motionless snake form appears not to stimulate vigilance in fish. It has

been my observation in the laboratory and the field that snakes stretched out or coiled in the water are readily approached by fish as long as they are immobile. This is true even immediately after the snake has lunged at fish. Some fish, particularly *Lepomis* species, even locate themselves near snakes when structures such as rocks or branches are not immediately available.

Foraging at the bottom and in crevices. Another solution to aquatic foraging is to forage at the bottom and in crevices (Seymour, 1982). Negative buoyancy is required for both tactics. Several species of sea snakes which forage in reefs use this tactic (McCosker, 1975; Voris and Glodek, 1980). Drummond (1979, 1980, 1983a) found that the negatively buoyant *N. sipedon* foraged in crevices extensively. Not all negatively buoyant snakes forage extensively in crevices.

Body shape and foraging tactics. Another trait correlated with pisviory is the concentration of the body mass in the rear portion of the body (Schmidt, 1950; Seymour, 1982; Taylor, 1987, Williston, 1914). This has been dubbed the "plesiosaur form" by Boulenger (Schmidt, 1950) as it is characteristic of the extinct plesiosaurs. A long neck and narrow head are part of the plesiosaur form. All spear fishers exhibit this characteristic to some degree, as lengthening of the neck and reduction of the head necessarily result in rearward concentration of the weight.

Shortening of the tail can facilitate weight concentration in limbed vertebrates forms (Williston, 1914). This distribution of weight stabilizes the body in water during striking. Turtles and crocodilians, piscivorous or not, exhibit this trait for aquatic feeding. Shortening of the tail is not characteristic of aquatic snakes.

Behavioral means are also used for stabilization of semi-aquatic snakes: species of the natricine *Nerodia* (Mushinsky and Hebrard, 1977a; B. Savitzky, pers. obs.), and *Natrix* (Hailey et al., 1982; Hailey and Davies, 1986a), frequently wrap their tails around vegetation to stabilize themselves while striking. Crocodilians ingest stones, a behavior which may be best explained as a means of stabilization underwater (Taylor, 1987).

Retention and control of prey. Retaining control of the prey is important for all predators, of course, but may be of special concern to aquatic predators as prey can disappear very quickly in water, especially murky water. Many aquatic predators prevent escape by tearing or shaking prey apart immediately (Taylor, 1987). Small prey can be ingested whole by suction processes in turtles or by inertial processes assisted by gravity in the crocodilians (Taylor, 1987). The tentacled snake attacks in a lateral but directed sweep toward an approaching fish so that it is partially engulfed at capture (Cornelissen, 1970a,b; pers. obs.). The henophidian *Acrochordus* species constrict fish. Their loose, rough skin assist in this process (Shine, 1986a).

Envenomating prey offers good control as long as the venom kills or cripples fast enough to prevent prey escape after envenomation. The hydrophiid snakes sometimes release their prey, particularly violently thrashing eels; their potent neurotoxin apparently makes subsequent escape difficult (Radcliffe and Chiszar, 1980; Klemmer, 1967). Some hydrophiid species habitually retain hold of prey anyway, however. These snakes apparently have difficulty locating dropped dead prey, which may account for the retention of prey (Radcliffe and Chiszar, 1980; Voris et al., 1978).

The hemotoxic venom of the only piscivorous crotaline, *Agkistrodon piscivorus*, does not quickly immobilize fish, (B. Savitzky, unpubl.), but this snake generally retains hold of its prey until dead (O'Connell et al., 1981). Even so, returning to shore with prey may improve success for this species (Bothner, 1974).

Prey control for nonvenomous snakes may be aided by an integumentary hinge above the mouth, dorsal to the supralabial scales. This hinge, described by Savitzky (1983), is characteristic of piscivorous natricine, xenodontine, and homalopsine snakes. It was originally hypothesized to serve as an oral valve, but in light of further behavioral and taxonomic evidence, it is now hypothesized to be associated with the wide lateral maxillary excursion which occurs when snakes "walk" their jaws down prey to the head prior to ingestion (Savitzky and Savitzky, unpubl.).

While most semi-aquatic and aquatic snakes can swallow prey under water, really large prey tend to be taken to land by semi-aquatic snakes (Bothner, 1974; Hailey et al., 1982; pers. obs.). Taking large prey to land may conveniently result in their death by suffocation before ingestion (Krevosky and Graham, unpubl.). Piscivores of various lineages tend to have longer quadrates, loose ligaments between the palatomaxillary arches and braincase, supratemporal elongation, and, as mentioned earlier, long, numerous, highly curved or recurved teeth, all of which facilitate ingestion (Savitzky, 1983).

Summarizing piscivory. Piscivory is associated with a variety of morphological and behavioral adaptations in snakes as well as other vertebrates. Both ecological and phylogenetic factors play a role in the presence of these traits in snakes. Piscivorous snakes can be placed on a generalist-specialist continuum fairly easily.

5. RESEARCH APPROACH OF THIS STUDY

Species, Research Goals, and Methods

Overview. In keeping with an ethological perspective, external validity was a concern. Therefore, a large, complex test enclosure was designed to simulate the structural features of the habitats where both species are known to feed. Because internal validity was also a concern, a standardized pool layout and testing protocol was used. I chose piscivory as a foraging strategy because it is relatively easy to observe in the field and laboratory. Consequently, a useful amount of literature is available. That piscivorous snakes feed relatively frequently also was expected to facilitate the collection of data. Finally, piscivory is also a strategy widely used by other taxa of snakes and by other vertebrates. Thus, generalizations across taxa can be readily made.

Species. The species chosen for this study were the natricine *Nerodia rhombifera* (Colubridae), the diamondback water snake, and the viperid, *Agkistrodon piscivorus* (Viperidae), the cottonmouth, are common, widespread members of Nearctic fresh water aquatic communities. The ecology of these animals is slowly being pieced together. The missing information is largely behavioral. These species utilize similar habitats (see Conant, 1975): they are sympatric or syntopic over much of their range (Conant, 1975). Their ecological similarities include high dietary overlap: both eat primarily fish and anurans. They have similar seasonal and diel activity patterns: during the active summer months they are primarily nocturnal.

They are of similar size and shape: adults are in the one meter snout-vent length (SVL) range and are heavy-bodied snakes (cf. stoutness scores of *N. sipedon*, which is more slender-bodied than *N. rhombifera*, to that of *A. piscivorus* in Pough and Groves, 1983).

In spite of being similar enough in appearance and habits (Conant, 1975) to be indistinguishable by many outdoorsmen (Burkett, 1966; Conant, 1975; pers. obs.), they are not closely related: *Nerodia rhombifera*, a natricine colubrid, is from a lineage generally regarded to be primitive to that of *Agkistrodon piscivorus*, a crotaline viperid (Brattstrom, 1964). Both are numerous where found, thus easing observations and avoiding problems of acquisition or population depletion. Finally, both species are plentiful at Reelfoot Lake, Obion and Lake Counties, Tennessee, which provided a source of subjects and a site for field observations. Reelfoot Lake is a hypereutrophic shallow lake in the coastal plains of western Tennessee, surrounded by cypress-hardwood forest and swamp habitat (Dennis, 1988; Denton, 1987; Hess, 1966; Petit, 1984 for description of the habitat and water conditions; Davis, 1937 for description of plant species; Baker, 1937; Denton, 1987 for description of fish species). It is a habitat typical of both species.

Research goals. The goal of this study, then, is to look at foraging behavior, specifically piscivory, in relation to habitat structure and to document ontogenetic changes. Habitat structure has been found to be critical for reptiles (Heatwole, 1966, 1977; Sexton, 1958). In fact, simple structural features alone can be used to differentiate the habitats of some lizards of the genus *Anolis* (Iguanidae) (Heatwole, 1977). Nevertheless, the role of habitat structure has not been given adequate

consideration in most studies of snake ecology (Mushinsky, 1987). Drummond (1980, 1983) found that structural details are important proximate determinants of foraging behavior in semi-aquatic snakes. Snakes use habitat structure in foraging in various ways (see Drummond, *op. cit.*; Patterson and Davies, 1982; Jayne et al., 1988; Reinert et al., 1984). For example, the rattlesnake, *Crotalus horridus* (Viperidae), has been found to lie in wait coiled with its head on the upper edge of a fallen tree trunk waiting for rodents which use such a log as a runway.

Methods. The methodology of this study is an elaboration of that of Drummond (1980, 1983a) as the basic goals, some of the taxa (natricines), and assumptions of that and this study are similar. His methodology is both straightforward and successful with semi-aquatic snakes: the snakes foraged in his naturalistic pool readily and in the same manner as in the wild. Using his methodology also facilitates the previously proposed comparisons between the generalist and specialist *Thamnophis* and *Nerodia sipedon* used in his study with the specialist *N. rhombifera* and the phylogenetically unrelated generalist *Agkistrodon piscivorus* used in my study.

In addition to laboratory studies, field observations of both species were made prior to testing to familiarize myself with the natural behavior of the species, and concomitantly with testing to verify laboratory findings. A field study based on techniques described in Kershaw and Looney, (1985), Riechert (1973), and Riechert et al. (1974) was also carried out for one summer for *Nerodia rhombifera*. A similar study was not possible for *Agkistrodon piscivorus* because of the effects of drought. Methods are detailed in Chapter II.

Discussion and Summary of the Goals of This Study

Other issues and assumptions. It should be noted that detailing habitat structure is tantamount to defining "microhabitat" for these snakes. "Microhabitat" has been cited as an ecological factor of particular importance to reptiles (Toft, 1985). By using a large naturalistic pool offering the species typical structural (microhabitat) features, to test both species, this study can readily document microhabitat differences, should they be present. Another question for this study then, is how do the snakes make use of habitat structure in general and during foraging in particular? Do differences in use of structure between the species lead to differential use of microhabitat and dietary differences?

This study also proceeded on the assumption that foraging behaviors are not necessarily phenotypic adaptations to the environment, but are to some degree phylogenetically conservative (Gould and Lewontin, 1979; Wanntorp, 1983). Comparisons with congeners of each species using literature data will be used to shed light on the aptational nature of the behaviors (Dobson, 1985; Gould and Vrba, 1982; Wanntorp, 1983; cf. to Greene, 1986a). *Nerodia rhombifera* and *N. sipedon* are both aquatic specialists which utilize fish heavily, although *N. sipedon* preys on frogs more than *N. rhombifera* (see Drummond, 1980, 1983a). Drummond (1980, 1983a) and Halloy and Burghardt (in press) found well defined differences between the generalist and specialist species of *Thamnophis* (Colubridae). One might expect such differences between *N. sipedon* and *N. rhombifera*, with the latter being the more specialized of the two. Both, however, are still basically aquatic specialists. Yet, Drummond (1980) found that *N. sipedon* was somewhat intermediate in foraging tactics between the generalist and specialist species of *Thamnophis*: while it engaged

in considerable underwater searching like the garter snake specialists, its attacks were short and not directed at particular prey, but were "blind" attacks into crowded prey. Published accounts of the foraging of *N. rhombifera* suggest similar tactics (Evans, 1942; Kofron and Dixon, 1980; Mushinsky and Hebrard, 1977a; Stoner, 1941; Trapido, 1943), although this species may spend less time on land or at the water margin than does *N. sipedon*.

Other work (Drummond, 1979, 1983; Schaeffel and de Queiroz, submitted) has documented the physiological basis of these differences: the specialist *Thamnophis* species can focus their eyes underwater whereas the other snakes, including *Nerodia sipedon*, cannot focus underwater. The specialists themselves, however, have different methods of underwater focusing, so that multiple modes of adaptation are present within the genus. It is not yet known whether or not *N. rhombifera* can focus underwater, but if its behavior really is similar to that of its congener, *N. sipedon*, it probably cannot. Thus, the ability to focus underwater may not necessarily be characteristic of piscivorous specialists. It would also appear that these two genera of natricines have evolved different solutions to the same foraging problem. Is there really a continuum from generalist to specialist piscivory or are there only different tactics for piscivory or are there both? This study will attempt to resolve this question.

As already noted, multiple modes of adaptation are present within the specialist *Thamnophis*. The problem becomes even more interesting or, perhaps, more confusing, in light of recent work which suggests that the genera *Thamnophis* and *Nerodia* should be combined into one genus (*Nerodia*) (Lawson, 1987). To add to the confusion, while *Nerodia* species are more closely related to other New World natricines (these genera have been recognized as forming a tribe, the Thamnophiini

[Rossman and Eberle, 1977]) than to Old World natricines such as *Natrix* (Dessauer et al., 1987; Rossman and Eberle, 1977), the foraging behavior of *Nerodia* appears to be more similar to that of *Natrix* than to that of *Thamnophis*.

In terms of looking at a continuum in piscivorous foraging, the generalist *Agkistrodon piscivorus* is a useful addition as it is from a different lineage (Brattstrom, 1964; Cadle, 1987). This snake is apparently the only piscivorous species in a lineage generally regarded as being highly evolved to prey upon endothermic terrestrial prey. Its closest relatives, New World congeners, are not even associated with water (Fitch, 1960; Burchfield, 1982; Conant, 1975). Comparing its foraging tactics to those of the generalist natricines should be interesting in light of generalizations that have been about prey generalists (Drummond, 1980; 1983; Drummond and Macias Garcia, 1988), and piscivory (Pritchard, 1984; Taylor, 1987; Williston, 1914). Just how does this species compare to the natricine generalists?

Again, of course, the foraging tactics *Agkistrodon piscivorus* may use for piscivory can be considered specifically as adaptations to piscivory only if not present in other members in its lineage (Greene, 1986a) and if not used in terrestrial predation. Enough information on crotaline foraging is available from the literature to allow reasonable inferences about the aptational (Gould and Vrba, 1982; Greene, 1986a) nature of the piscivorous behavior of *A. piscivorus*. Has this species developed unique behaviors which might be interpreted as adaptations for piscivory? Also, how does the cottonmouth use its well developed venom delivery apparatus in piscivory?

Summary. To sum up, this study is designed to provide important autecological information, specifically the relationship of foraging to habitat use, for

Nerodia rhombifera and *Agkistrodon piscivorus*. Included in this autecological information are sex and ontogenetic differences in foraging. Secondly, it compares the behavioral adaptations for piscivory in these phylogenetically unrelated but ecologically similar species. Thirdly, it looks at general tactics for piscivory in snakes and attempts to define a continuum by comparing the tactics used for piscivory within one lineage of piscivorous snakes, the tribe Thamnophiini (Rossman and Eberle, 1977), by comparing results from this study with data collected in a similar manner by another worker. Fourthly, the aquatic foraging tactics of *A. piscivorus* are compared to that of its terrestrial relatives using information from the literature to judge whether or not the species possesses behavioral differences which might be interpreted as adaptations for aquatic foraging.

6. BACKGROUND ON THE BIOLOGY, ECOLOGY, AND BEHAVIOR OF *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS*

Nerodia rhombifera.

Range, general habitat, and syntopy with other water snakes. The subspecies of the diamond back water snake *Nerodia rhombifera* studied herein, *N. r. rhombifera*, is found in a variety of aquatic habitats, usually lentic, throughout its range in the Mississippi drainage. As shown in Fig. I-1, its sister species, *N. taxispilota* is found in the Atlantic coastal plains (Mount and Schwaner, 19770) and is ecologically similar (see Camp et al., 1980). Swamp waterways and minnow ponds are commonly reported habitats for the diamond back water snake. (The other nominate subspecies have restricted ranges in Mexico, but are apparently found in similar habitats.) The

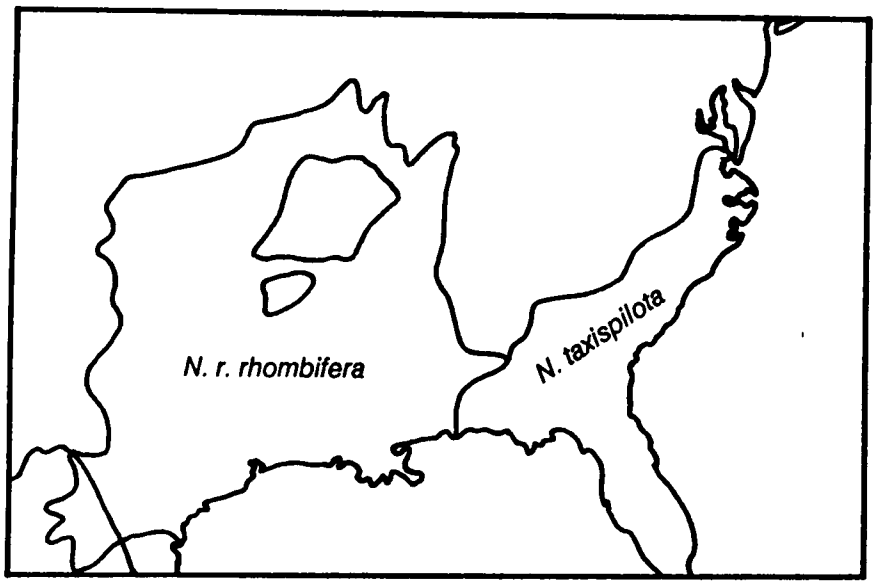


Figure I-1. The distribution of *Nerodia r. rhombifera* in the United States. The range of its ecologically similar sister species *N. taxispilota* is also shown. The other subspecies of *N. rhombifera* are found in Mexico. The map is based on Conant (1975).

diamond back water snake is usually quite numerous where found, often being the most common water snake (see Wright and Wright, 1957). While rarely found far from water, it is most accurately described as semi-aquatic due to its overall morphological similarity to terrestrial snakes and because it spends large portions of time out of water.

In swamp forest aquatic habitats, these water snakes are quite commonly part of a large assemblage of natricine snakes of the genera *Nerodia*, *Thamnophis*, and *Regina*. There is often considerable niche overlap among the *Nerodia* species; *Nerodia rhombifera* is generally one of the two largest and most piscivorous species of

the assemblage (Hebrard and Mushinsky, 1978; Mushinsky and Hebrard, 1977a; Mushinsky et al., 1980; Kofron, 1978). *Nerodia rhombifera* tends to take more of the larger sized fish than the other highly piscivorous similarly sized species, *N. cyclopion* (Mushinsky and Hebrard, 1977a).

Morphology. The dorsal coloring is fairly cryptic, being a drab olive-brown or buff. The ventral surface is brighter: yellow with black markings. Its dorsal pattern is more a chain-like series of rhombs than diamonds (see Conant, 1975; Wright and Wright, 1957). The species is sexually dimorphic, with the viviparous females being longer and stouter than males (see Blanchard, 1931; Fitch 1981) and possessing relatively larger heads (see Rossman,1980).

This species possesses the long quadrates, teeth, and supralabial groove associated with piscivory (see Savitzky, 1983), and a relatively long head that is large relative to its body length (Nakamura and Smith, 1960). It also readily achieves negative buoyancy from birth like its congener, *N. sipedon* (pers. obs.; see Drummond, 1979, 1980).

Yearly activity patterns. This species is reliably active from April through October at Reelfoot Lake. Winters are spent hibernating on land in crayfish burrows or hollow trees (Nelson, pers. comm.). Mating occurs in the spring and early summer. Females give birth from August to October.

These snakes are quite nocturnal during summer (Conant, 1975; Mushinsky and Hebrard, 1977b; Hess, 1966), but have often seen swimming parallel to and near shore during the day (Kofron, 1978). Basking on cypress limbs and snags near shore

in the open lake during the day is common (Cagle, 1937; Hebrard and Mushinsky, 1978).

Habitat use. These snakes appear to be associated with the peripheries of bodies of water and appear not to cross large open bodies of water regularly (Cagle, 1937; Hess, 1966; Nelson, 1983; pers. obs.), although Cagle (1937) found a shed skin on a cypress stump in an open area of Reelfoot Lake. Also, Kofron (1978) reported seeing diamondback water snakes among white-capped waves in an open brackish water bay. Nelson (1983), however, following snakes with implanted telemeters at Reelfoot Lake, never located snakes more than a few meters from shore. He declared their home ranges to be linear, i.e., along the lake margin. Kofron 1978) also found the snakes most frequently within 8 m of shore. Many were captured while crawling among rocks along the shore.

Hebrard and Mushinsky (1978) found that these water snakes preferred gently sloping shorelines that were basically devoid of vegetation. In contrast, however, Preston (1970 in Hebrard and Mushinsky, 1978) found these snakes along densely vegetated shorelines. The steepness of the banks were not specified, however. Porter and Czaplicki (1977), after studying prey capture in artificial bodies of water, speculated that the slope of the sides of a body of water may be an important factor in the ease of prey capture for this species.

Diet and foraging. The diet of this species has been rather widely studied using examination of gut contents. Data (summarized in Table I-1) indicate that,

TABLE I-1

DIET AND HABITAT OF SOME POPULATIONS OF *NERODIA RHOMBIFERA*

Locale	Habitat	Foods[a]	Source
Lonoke Co., AR (N=134[b])	fish hatchery ponds	fish; numerous frogs not eaten dietary shift in adults	Plummer & Goy, 1984
Reelfoot Lake, TN (N=20)	lake/hardwood forest, cypress swamp	catfish N=4, sunfish N=8 shad N=3, fish head N=2, frogs N>11, turtle N=1	Cagle, 1937
Reelfoot Lake, TN (N=64)	same as above	sunfishes and basses 45.6%, silversides 23.2%, white bass 12.5%, shad 11.8%, catfish 7.7%	Hess & Klimstra, 1975
Stillwater, OK (N=49)	lake	minnows 13.2%, catfish 29.1%, sunfishes and basses 19.2%, amphibians 7.7%, mammals 1.3%	Sisk & McCoy, 1964
Bowie & Red River Co., TX (N=60)	lake, fish hatchery ponds	catfish 40.6%, sunfishes 6%, amphibians 44.6%, unknown fish 3.8%	Bowers, 1966
Atchafalaya River basin, LA (N=126)	varied aquatic, including bay	catfish N=26, sunfishes and basses N=14, minnows N=53, poecilids N=66, other fish N=42, amphibians N=3, crayfish N=2	Kofron, 1978
Ascension Parish, LA (N=40)	swamp-bayous	sunfishes, basses, catfish, shad 81.7%, poecilids and minnows 13.5%,amphibians 4.7% dietary shift in adults	Mushinsky & Hebrard, 1977

[a]Foods = gut contents by volume (%) or by number (N=) obtained from all snakes.
[b]N = number of stomachs examined containing food.

while varying regionally in terms of prey species, is quite uniformly composed of around 95% fish. Catfish are a frequently reported prey class. The remainder of the diet is composed primarily of frogs, tadpoles, and crayfish. While most prey are presumed to be taken alive, scavenging on dead fish has been widely reported for this species (Cagle, 1937; Hess, 1966; Kofron, 1978). A gut content study of Reelfoot Lake snakes done earlier (Hess, 1966; Hess and Klimstra, 1975) found that the most important prey classes by volume were centrarchid fishes of the genera *Lepomis*, *Micropterus*, and *Pomoxis*, the small atherinid *Menidia audens*, the serranid *Morone chrysops*, and the clupeid *Dorosoma cepedianum*.

There is some discrepancy in the literature about the utilization of frogs by the species. While frogs comprise a small portion of the diets of most populations studied, they are usually not consumed in large quantities even when abundant (see Hess and Klimstra, 1975; Sisk and McCoy, 1964). Bowers (1966), however, found that frogs comprised 63% of the prey ingested by a population at a commercial minnow pond, whereas the more abundant minnows were not eaten. The species of minnow, *Notemigonous crysoleucas*, is readily eaten elsewhere in the wild (see Laughlin, 1959; Sisk and McCoy, 1964), and in the laboratory (pers. obs.). Bowers (1966) noted that the minnows stayed in deep water, but the frogs utilized the shallow water and the banks where the water snakes foraged. Thus, habitat utilization by both the predator and the prey was the proximate factor in diet here.

Hess (1966) found some dietary differences between males and females, but the differences were not clear cut. These differences were not mentioned in Hess and Klimstra (1975). The ontogenetic dietary shift mentioned above, however, resulted in dietary differentiation between the two sexes in a Louisiana population (Mushinsky et al., 1982). Ecological differentiation between the sexes resulting from sexual

dimorphism is widespread in reptiles; sexual selection rather than resource competition seems to be the selecting force (see Shine, 1986b; see also Reichenbach and Dalrymple, 1980).

As with many snakes, larger prey is taken by larger *Nerodia rhombifera*, although even large adults take small items also (Mushinsky et. al., 1982; Plummer and Goy, 1984). Mushinsky et. al. (op. cit.) suggest that these larger prey are found in deeper water and must be captured by different techniques than prey found in shallower water. Plummer and Goy (op. cit.) found a pronounced ontogenetic shift to larger prey at around 700 mm SVL in a population at a fish hatchery. Mushinsky et al. (1982) found a similar shift at about 800 mm SVL.

Nerodia rhombifera has been primarily classified as an active forager by those who have studied it in the field (see Mushinsky, 1987, p.308). This species, like other *Nerodia* species, is known for "trawling" foraging by swimming in circles or figure-eights while making sideways sweeps with the open mouth (Brown, 1958; Evans, 1942; Kofron and Dixon, 1980; Mushinsky and Hebrard, 1977a; Stoner, 1941; Trapido, 1943). Mushinsky and Hebrard (1977a) noted that the lower jaws of the snakes was sometimes used as a shovel which snapped shut upon any encountered prey. The attacks are undirected, that is, the attacks are made at groups of fish, but not at specific fish.

This behavior has almost always reported to occur in shallow water. Bowers (1966) believed that this technique would be most effective in shallow water where the fish could not escape below or above the snake. This behavior has been reported occur over bottoms covered with detritus. Here, the circling behavior was interpreted as a method of stirring up prey (Stoner, 1941).

Sit-and-wait foraging has also been reported in the species. Kofron (1978) reported an ambush or sit-and-wait foraging technique in which the snakes anchored their tails to branches or debris either above or in the water while keeping the rest of the body floating or submerged. Gillingham and Rush (1974) reported a similar technique in water snakes foraging at a drainage culvert. These snakes were waiting, bodies facing into the current, with the mouths open. Mushinsky and Hebrard (1977a) observed side to side open-mouthed sweeps of the water by "stationary" snakes. Open-mouthed attacks thus are not absolutely associated with active foraging, even in specialists. Similar behaviors have been reported in *Natrix maura* (Hailey et al., 1982; Hailey and Davies, 1986a,b).

Summary and Discussion of Water Snake Habitat Use and Foraging

Summary. The diamondback water snake appears to eat primarily live fish, but some populations also consume frogs. Opportunistic scavenging on dead fish has been reported by several authors. Local prey availability and details of the local topography seem to play a role in diet, however. Foraging is largely nocturnal. This snake is usually found in lentic bodies of water with gently sloping shorelines.

The snake is usually considered an active forager, utilizing a distinctive side-to-side sweep of the open mouth which has been seen in other congeneric species, but sit-and-wait foraging is also an option. Size and sex differences in diet have been found, although the differences involve only prey size, not type. Habitat and behavioral differences have been assumed to be associated with these differences but have not been documented.

Discussion. This species is a dietary specialist. The ontogenetic shift in prey size has been found to be rather abrupt, suggesting that there is a behavioral or habitat change with age. While this species has been classified as a habitat generalist, the fact that it generally utilizes only shallow, gently sloped lentic water suggests a kind of habitat specialization.

What could be expected from this species in the test pool? Given what is mentioned above and the fact that it is an aquatic specialist, the following predictions were made:

1. The snakes would actively forage below the surface in the open water. Use of cover was unpredictable since these snakes have been reported to use all of the types of cover areas present. Some foraging in crevices would also be probable.

2. These snakes would consume primarily live fish, but would also consume some dead fish.

3. Based on literature accounts for the species, foraging tactics would be mostly active open-mouth searching, but some sit-and-wait foraging, possibly while attached by the tail to vegetation and wood would also be probable. However, other specialist natricine piscivores have been found to make more directed, forward attacks underwater, especially while diving. *Nerodia sipedon*, a fairly close relative of *N. rhombifera*, however, although a specialist, was found to use primarily undirected, open-mouthed lateral sweeping attacks at fish underwater. Since *N. rhombifera*, is more of a fish specialist than *N. sipedon*, some more directed type of attack might also occur.

4. These snakes would be very adept at handling live fish, probably handling them readily in the water, including underwater. Handling times would be relatively brief.

5. Underwater ingestion would occur.

6. Large snakes (>700-800 mm SVL), who are usually females, would use the deeper water more than the males and juveniles. The largest females should also take larger fish than the males. Smaller snakes should use the deep open water less than the large females, and should take smaller fish. These predictions, however, are based on the assumption that large fish are in deeper water.

Agkistrodon piscivorus

Range, general habitat, and syntopy with water snakes. The cottonmouth also is found in a variety of aquatic habitats, generally lentic. Like the diamondback water snake, its range is throughout the Mississippi drainage (see Fig. I-2). While the cottonmouth is generally associated with water, it has been found to wander far from water. Its home range has not really been documented, but is almost certainly not linear.

Unlike *Nerodia rhombifera*, the cottonmouth is also found in the Atlantic coastal plains where *N. rhombifera* is replaced by *N. taxispilota* (Mount and Schwaner, 1970. There are three subspecies of the cottonmouth: *leucostoma* basically overlaps with *N. rhombifera*; *piscivorus* and *conanti* overlap with *N. taxispilota* (Conant, 1975).

This snake can be numerous in some locales, although usually less numerous than *Nerodia* species.

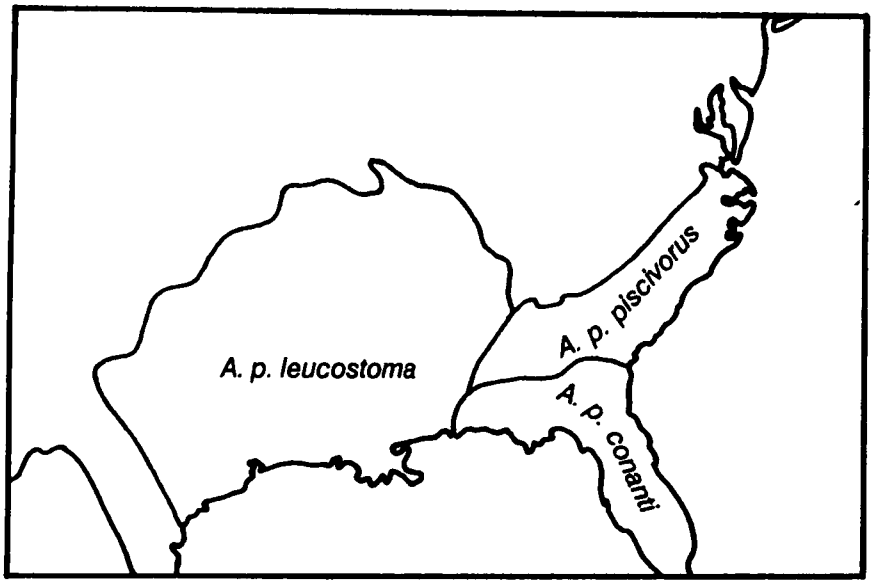


Figure I-2. The distribution of the three subspecies of *Agkistrodon piscivorus*, based on Conant (1975).

The cottonmouth is frequently syntopic with *Nerodia* species, including *rhombifera*. Competition may be reduced by cottonmouths preying on water snakes (Burkett, 1966).

Morphology. Like all crotalines, the cottonmouth is a heavy-bodied snake. Adults are in the one meter SVL range, and have wide, long heads relative to other species of *Agkistrodon* (Brattstrom, 1964). Adults are a dark brown or olive on the dorsum, and the wide crossband pattern is indistinct from the background. The head

is well marked in *A. piscivorus conanti* and in the young of all 3 subspecies, but in adult *A. piscivorus leucostoma*, only a broad dark band through the eye remains of head markings. See Gloyd and Conant (1943) for a more complete description of the American subspecies. Subspecific differences in habits were impossible to document from the literature (see Conant, 1975). The venter is yellowish with brown-black blotches (Conant, 1975; Wright and Wright, 1957). In the field, swimming cottonmouths are easily distinguished from water snakes by their buoyancy: they ride high in the water.

The species is sexually dimorphic, although slightly less so than *Nerodia rhombifera* (Fitch, 1981), and, unlike the water snakes, the male cottonmouths are larger than the females and engage in combat. Reproduction appears to be biennial (Burkett, 1966). Fewer, larger young are produced than in water snakes (Fitch, 1985; Wright and Wright, 1957).

Juveniles have a reddish-brown coloring with well demarcated crossbands resembling those of its congener, the copperhead, *Agkistrodon contortrix*. Juveniles also have a sulfur colored tail tip.

The cottonmouth possesses proteolytic venom and pit organs, considered to be specializations for predation on large, endothermic prey (Pough and Groves, 1983). The development of the retractable front fangs is associated with a reduction in tooth number, in part because the maxilla is reduced in size and the only teeth on it are the large fangs. It also has fewer and smaller palatine teeth. Its teeth thus are not the numerous, long, relatively undifferentiated teeth typical of piscivorous snakes (Savitzky, 1983). The placement of the pit organs in the skull results in reduction of skull mass, and the snout narrows in front of the pits in order not to block their infrared "vision" (Newman and Hartline, 1982). The cottonmouth possesses a

somewhat longer head relative to width and a longer quadrate than other members of its genus (Brattstrom, 1964), all of which are associated with ophidian piscivory (Savitzky, 1983). The size and shape of the fangs conform to those of other *Agkistrodon* species (Ernst, 1982).

Yearly activity patterns. Cottonmouths at Reelfoot Lake were reported to aggregate along Donaldson Ditch in the autumn, beginning in early September. Apparently they hibernated in the naturally formed hollows in the spoil bank of the ditch as well as in mammal burrows there. Autumn migrations and aggregations have been widely reported (e.g. Dundee and Burger, 1948; Martin and Wood, 1955; Werler and McCallion, 1951). Hibernation in limestone and sandstone outcroppings above a river was reported in Oklahoma (Dundee and Burger, 1948), in wooded hillsides (Barbour, 1956; Klimstra, 1959) and in pine stumps near water (Neill, 1947), and possibly in crayfish burrows along a river (Dundee and Burger, 1948). Like the water snakes, these snakes are viviparous, giving birth in autumn: young of the year were found in September and October at Reelfoot Lake.

The cottonmouth appears to have a long annual activity cycle. Neill (1947) noted that in Georgia the cottonmouth was the last species to hibernate. Tinkle (1959) noted that in a Louisiana population, the cottonmouth was the first active reptile of the year. Spring activity has been reported to begin in March in coastal southern Virginia (Martin and Wood, 1955), in April at Reelfoot Lake (Parker, 1948), and in early April in Oklahoma. Cook (1983) reported the Florida cottonmouths that he studied were active from mid-March until October. Annual activity periods are thus very similar throughout this species' range.

Nocturnal activity appears to be the rule in the warmer months throughout its range (Allen and Swindell, 1948; Wright and Wright, 1957, Burkett, 1966; Cook, 1983). The cottonmouths may go to some lengths to avoid hot, dry conditions. At Reelfoot Lake, State Wildlife Resources personnel reported that small aggregations of the snakes were often found in the moist root balls of fallen trees during such hot, dry periods. Wharton (1960) and Allen and Swindell (1948) reported that Florida cottonmouths often were found in dark, moist depressions at the base of palmettos during hot days.

Habitat use. At Reelfoot Lake, cottonmouths were known to frequent a dirt road leading into Donaldson Ditch as well as along the ditch itself on the northern side of the major open water area. The snake was reported to be rare along the southern shore of this area, but was known to occur along the western shore (Goodman, 1958). The cottonmouth was most reliably found along the ditches (which are manmade canals) on the muddy, unvegetated banks and among or on roots of trees along the banks. Cottonmouths were also reported to use flooded low areas of the forest at Reelfoot Lake also. Kofron (1978) found that a Louisiana population of cottonmouths used flooded forest also, remaining along drying pools after spring flood waters receded.

In Kentucky in a cypress forest along the drainage of a creek that feeds Reelfoot Lake, Barbour (1956) found that the the snake was "frequently found on the mud at the edge of a pool or slough, but more often in some pile of emergent trash or vegetation" (Barbour, 1956, p. 36).

Allen and Swindell (1948) reported a wide variety of habitat use in Florida cottonmouth. A photograph accompanying Allen and Swindell (1948) shows the snakes congregating on the flat, vegetation-free muddy banks of a drying slough in the Everglades. In Oklahoma, Trowbridge (1937) found the cottonmouths to congregate around small drying pools, but not along the larger streams. He believed that there was some migration from larger streams to the smaller drying streams during drought conditions. Hamilton and Pollack (1955) noted that a Georgia population of cottonmouths positioned themselves in water next to the bank, sometimes lying completely submerged at night.

Cook (1983), in an intensive study of a Florida population, found that the cottonmouths often were found coiled above the water on the bank during the day, but were at the edge or even in shallow water near the edge of a stream during the night. Tinkle (1959) found, in a Louisiana population, that whereas the cottonmouth was the only reptile found in a particular marsh, more cottonmouths were found on a narrow ridge surrounded by cypress swamp than in the marsh. In Kofron's Louisiana swamp and hardwood forest population, the cottonmouth seemed to be an inhabitant of the forest-water interface (see Kofron, 1978).

Kofron (*op. cit.*) considered the cottonmouth to be a habitat specialist. This generalization does not seem to hold true for the species as a whole (see Burkett, 1966). Wharton (1958), in an extensive study of populations of cottonmouths on Florida keys, found that these snakes were not at all associated with bodies of water as none were available on the keys. These snakes utilized moist areas under palmettos instead.

However, most habitat use seemed to consist of utilizing the bank area of a body of water, either a stream or a forest pool. Many authors specified that the pool

was a shrinking body of water containing presumably trapped prey. Thus, the species may be a habitat specialist, but one that is capable of colonizing unusual habitats to make use of unusual food resources. On the Florida keys where there were no bodies of water, the cottonmouths utilized dropped fish in a rookery of herons, egrets, and cormorants (Carr, 1936; Wharton, 1958). Burkett (1966) believes that whatever habitat use may be, moisture is a limiting resource for the cottonmouth.

Diet and foraging. These snakes are notably opportunistic foragers, eating almost anything that moves, and much that does not (Conant, 1929; 1934). Diet and habitat use are summarized in Table I-2. The ingestion of carrion and objects such as feathers, wood, egg shells have been widely reported (Burkett, 1966; Carr, 1936; Goodman, 1958; Laughlin, 1959). Toads, which are potentially toxic, have not been found in the guts of wild-caught snakes, but have been ingested without harm by captive specimens (Burkett, 1966). Cannibalism has been frequently reported (Allen and Swindell, 1948; Burkett, 1966; Klimstra, 1959; Penn, 1943). Cannibalism appears to be common in generalist species of reptiles and amphibians (Polis and Myers, 1985).

Few accounts of actual feeding in the field exist. Barbour did not report actual sightings of foraging, but "as evidenced by what they eat", he believed that they took food under the water, on the surface, on the land, and even in elevated vegetation (Barbour, 1956, p. 37).

Somewhat in contrast, Burkett (1966) suggested that cottonmouths do not often take live, healthy fish. One extensive account of foraging on live prey exists in the literature. Bothner (1974) described 3 cottonmouths capturing fish confined in

TABLE I-2

DIET AND HABITAT OF SOME POPULATIONS OF *AGKISTRODON PISCIVORUS*

Locale	Habitat	Foods[a]	Source
Pine Lakes IL area (N^b=84)	woodland swamp	fish 31.9%, amphibians 26.0% snakes, turtles, 18.2% mammals 17.9%	Klimstra, 1959
AR, LA, TX (N=46)	unknown: museum specimens	fish 18.4%, amphibians, 20.4% snakes, lizards, turtles, 29.9% birds 18.6%, mammals 12.7%	Burkett, 1966
Murphy's Pond, KY (N=42)	pond, bottomland forest	amphibians 69.1% fish, 12%, reptiles 4.8%	Barbour, 1956
Reelfoot Lake, TN (N=4)	sloughs	lizards, snakes, beetles, wood	Goodman, 1958
LeFlore & McCurtain Co., OK	forest streams, drying streams and pools	"great fish eaters" (sun perch,catfish), water snakes, frogs	Trowbridge, 1937
Ft. Benning, GA (N=9)	ponds	snakes, turtles 44.4% frogs 44.4%, rodents 11.1%	Hamilton & Pollack, 1955
"hill parishes", LA (N=100)	swamps, bayous, backwater pools running streams	frogs N=48, fish N=34, birds N=8, squirrels N=5 snakes N=4	Clark, 1949
Atchafalaya River basin, LA (N=25)	bottomland forest grasses, bayous	catfish N=16, other fish N=11, snakes=4, frogs=2, mammals=1	Kofron, 1978
Tall Timbers, FL (N^c=4	bottomland forest	frogs	Cook, 1983
Florida (large)	Everglades, various	"mostly fish and frogs",	Allen & Swindell, 1948
Sea Horse Key, FL (N=1122)	hammock	fish 46.7% (dropped by birds), mammals 28.2%, birds 8.7% reptiles 8.7%	Wharton, 1958

[a]Foods=gut contents by volume (%) or by number (N=) from all snakes examined.
[b]N=number of stomachs examined containing food.
[c]N=Number of observations of feeding.

a drying pool 15-20 cm deep in Georgia. Two snakes struck at fish from above or at the surface. The third moved about with its head underwater more of the time and was the most successful of the 3. Most fish were taken to shore for ingestion. Several prey were lost when ingestion was attempted in the water. Prey were held, but no mention of possible envenomation was made. It is not clear from the account whether the snakes swallowing in the water did so with the head above or below the surface.

Clark (1949) reported, without offering any details, that cottonmouths attack prey in the water and retain hold. Fish appear to be reliably retained in the jaws in laboratory studies (O'Connell et al., 1981). Cook (1983) saw only frogs consumed: 3 live, 1 dead while the snakes were positioned themselves on the stream bed during the night and early morning for feeding. No fish were eaten in his population.

Wharton's (1958) Florida keys snakes positioned themselves under heron nests and ate dropped dead fish as 47 % of their diet. The rest of their diet consisted of the wildlife and the digestible debris left on the island such as chicken bones . Most of the diet was some form of carrion, however. Kleptoparasitism occurred in the heron rookery. Bothner (1974), in contrast, noted that his foraging snakes were deferential of each other and avoided contact. Wharton's population, it should be noted, appeared to be slowly starving: only 10 % of the captured animals contained food, and the population lost weight over the years of his study. Cottonmouth populations on keys without rookeries were definitely not stable (Wharton, 1958). Thus, his animals may have been more willing to take risks for food than would well nourished cottonmouths.

Juveniles are apparently sit-and-wait foragers. They have been observed to caudal lure with and without motion of the sulfur-tipped tail in the field and

laboratory (Cook, 1983; Wharton, 1958, 1960). This behavior has been found to be very successful with frogs (Allen, 1949; Wharton, 1958, 1960).

The best information on feeding in the adults comes from laboratory studies. The cottonmouth has been a favored subject of Kardong (1975, 1977, 1982). He was able to define several phases in foraging: an approach phase, the glide phase during which the neck is positioned for striking, a rapid strike followed by bite, envenomation, and release of the prey (mouse), then a reapproach and ensuing ingestion. Phases were altered to fit circumstances. A common alteration was retention of prey after biting. From the above description it can be seen that the adult cottonmouths did not pursue a truly sit-and-wait strategy.

De Cock Buning et al. (1981) using a close relative of the cottonmouth, *Agkistrodon blomhoffi brevicaudus*, divided the process into more phases, adding, for example, a retraction phase between striking and re-approach. The descriptions of Kardong and de Cock Buning in no way conflict, however. The latter authors also performed a number of manipulations in order to determine the role of sensory information. It was found that heat, visual, or chemical information alone could alert the snake, but only chemical information alone would result in approach behavior. de Cock Buning et al. (1981) called *Agkistrodon* species "chemically oriented". All of these sensory modalities were important at some point in the foraging process, however, and lack of any sensory modality resulted in some disruption of the foraging process. For example, snakes with plugged pit organs ate mice before they were dead, sometimes with difficulty. Heat information apparently conveys information about when to begin ingestion.

De Cock Buning (1983) differentiated *Agkistrodon* species and some relatives from other crotalines such as *Crotalus* which he called "visually oriented". Other

workers have also noted that New World *Agkistrodon* species apparently rely more heavily upon chemosensory information, especially in the pre-strike phase of predation, than do *Crotalus* species (Chiszar et al., 1977, 1979, 1981, 1983, 1986; see also Graves and Duvall, 1983). De Cock Buning (1981, 1983) noted that "visually oriented species can compensate for the loss of heat information by vision..., whereas chemically oriented snakes cannot compensate for the loss of heat information" (de Cock Buning, 1983, p. 369).

Chiszar and colleagues found some evidence that mice and fish were handled so differently that different strategies, including central nervous system representations, might have evolved for terrestrial and aquatic prey (see O'Connell et al., 1981; Chiszar et. al., 1979, 1985). Other than the difference in post-strike retention of fish and mice, however, no major differences in the handling of the two prey types has emerged from their work. It is of interest, however, that caudal luring in the juveniles has only been observed in response to frogs (Cook, 1983; Wharton, 1960).

Summary and Discussion of Cottonmouth Habitat Use and Foraging

Summary. The common threads to the literature accounts appear to be (a) the consumption of a wide variety of prey, including fish, that are associated with aquatic habitats (b) using small confined pools in which fish and other aquatic prey may be trapped, (c) striking and holding fish after capture (d) using the edges, banks,

and areas near shore to prey upon whatever happens by, and (e) the frequent consumption of carrion.

Discussion. Looking at all of the accounts as a whole, the cottonmouth is a prey and habitat generalist. In Cook's population, however, it is a prey specialist; in Kofron's population, it is a habitat specialist; and, although considered to be a semi-aquatic snake, in Wharton's population, there are no bodies of water present, except the ocean, which it avoided. It also has been reported to consume more non-food items, carrion, and conspecifics than has been reported for other snakes.

This species clearly can adjust to a variety of ecological settings, and interpretations of its behavior must be made with this fact in mind. Only limited predictions about the behavior in the test pool could be made. Given what was mentioned above and the fact that it is an aquatic generalist, the following predictions were made:

1. This species would utilize the beach, edge and shallow water areas more than the deeper water. Since it was never reported to be associated with rocks, utilization of the wood and vegetation was expected to be higher than utilization of the crevices. While foraging in the cover areas was not expected to predominate, the variable habitat use and diet in this species made habitat use during foraging unpredictable.

2. The cottonmouth would forage aquatically for live fish, although it was also anticipated to utilize dead fish readily. As a generalist, the cottonmouth should require high prey concentrations (Drummond, 1980, 1983), and undirected attacks at

groups of prey would be the most likely tactic. Its head shape was not well suited for lateral sweeps through the water, however. Open-mouthed lateral attacks are certainly not typical of crotalines, either. Therefore, the details of the attack were not predictable.

3. Since it is so buoyant, it would not dive much, and so would strike from the surface, but would probably not strike successfully at live fish far below the surface.

4. Prey handling would take place above the surface of the water.

5. Envenomation of most live prey was expected. Because envenomation takes considerable time (generally, several minutes, B. Savitzky, pers. obs.), manipulation times would most likely be longer than for the water snake.

6. Ingestion times, however, for this snake should be shorter than for the water snake given the skull characteristics of the viperids. For this reason, it might also eat relatively larger prey.

7. The juveniles were expected to caudal lure. Ontogenetic changes in foraging are highly likely. The activity level of adults during foraging was not predictable, although it is expected to be higher than that of the juveniles.

Table I-3 summarizes and contrasts the biology of the two species of snakes used in this study.

TABLE I-3

SUMMARY OF COMPARISONS[a] OF *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS*

Trait	Description	
	N. r. rhombifera	*Agkistrodon piscivorus*
Phylogeny	semi-aquatic lineage	terrestrial lineage
Size	"stout-bodied"; = 1m SVL	"stout-bodied"; = 1m SVL
Sexual Dimorphism	females larger: FMR[b] = 111	males larger: FMR[b] = 96
Reproduction	annual; viviparous	biennial; viviparous
Litter Size	$\bar{x}$ = 27.1-37.1[c]	$\bar{x}$ = 5.6-7.7[c]
Head Shape	large, long, flattened rounded snout	large, long, triangular
Eyes	on top of head	on side of head
Teeth	long, recurved, numerous undifferentiated	proteroglyphic fangs; otherwise, reduced dentition
Specializations	supralabial groove	pit organs, venom
Buoyancy	negatively buoyant	positively buoyant
Habitat	aquatic: fresh lentic[d]	aquatic: fresh lentic[d]
Microhabitat	littoral zone	edge, banks, moist shore
Activity	summer: nocturnal	summer: nocturnal
Diet: Adults	mostly fish	frogs, fish, reptiles
Diet: Sexes	prey size differences	unknown
Diet: Ontogenetic Changes	prey size increases	juveniles lure, adult behavior uncertain
Aquatic Foraging	active: open-mouthed "trawling"	sit-and-wait or cruise
Ingestion	underwater capability	above water only

[a]These comparisons are based on information and references discussed earlier in Chapter I. The descriptions are broad generalizations only.
[b]Data are from Fitch (1981); FMR = female-to-male SVL ratio.
[c]Data are from Fitch (1985) and represent compilations of data from various sources.
[d]Both species are occasionally found in brackish water. *A. piscivorus* is known to cross salt water. Neither species, however, apparently exhibits adaptation to salt water.

CHAPTER II

METHODS

1. LABORATORY METHODS

Subjects

Maintenance. All of the *Nerodia rhombifera* and most of the *Agkistrodon piscivorus* were wild-caught by the author using Pilstrom tongs and a Furmont bag-stick at Reelfoot Lake. Neonate water snakes from 5 dams caught at Reelfoot Lake were tested also. Three cottonmouths were caught by me at a Federal Fish Hatchery in Perry County, Alabama. Three cottonmouths were caught by others in Mississippi, Florida, and Louisiana. The Louisiana snake was purchased originally from a dealer. Additionally, a litter of four neonate cottonmouths were obtained from Savannah River Ecology Lab. The cottonmouths consequently are not all of the same subspecies. Although it would have been ideal to have a more uniform sample, subspecific differences in ecology or behavior have not been reported. All snakes were in good health when captured and fed well in captivity. Weights and SVL measurements of the snakes at the beginning of the project are given in Appendix 1.

The snakes were maintained in ventilated plastic or glass containers, with fresh water available at all times. Although space limitations forced the group housing of some smaller snakes, care was taken to ensure that all snakes ate. Water snakes which were group housed at any time were permanently marked by scale clipping in a variation of the method recommended by Blanchard and Finster (1933). Most of the

snakes were maintained at 23-28° on a 12:12 light:dark cycle. The cottonmouth neonates and juveniles tested later in small square tanks were maintained at 28-30°. Wild-caught snakes were hibernated in glass aquaria in a delicatessen-type cooler in constant darkness at 10-15° from December to March in order to maintain natural activity patterns. The wild-caught snakes were tested only during the normal annual activity period, April through September. Neonates born in the laboratory and 2 juvenile cottonmouths were not hibernated and were tested in the winter months. These animals did not exhibit the diminution of activity frequently exhibited by wild-caught snakes during the winter months.

As the goal of this study was to record natural foraging behavior, the snakes had to be (1) acclimated to the environment, (2) motivated to feed, and (3) isolated from predator and social disruption. In order to ensure motivation to feed, the snakes were fed in their home cages on the same sizes and species of fish as were used for testing so that all snakes had had experience with all prey used during testing. Live fish were usually used for feeding, but all snakes were fed dead fish, small and large, at irregular intervals dependent upon availability. No pretesting deprivation was employed as many snakes, especially adults, seem to lose motivation to feed when not fed regularly. While the snakes were fed regularly, the time between feedings varied from 5-10 days so that the snakes did not become trained to feed only at rigidly specified intervals.

Pretesting habituation and handling. In order to acclimate the animals to the testing environments, all snakes were given 72 h or more continuous exposure to the testing environment with live fish before testing. Cottonmouths were marked on the

head and dorsum with Scotch Lite Reflective Liquid for individual identification and kept in the pool for at least one 5 d period before testing, as this species appears to require long habituation periods (Chiszar, pers. comm.) Snakes were observed continuously for at least 1 h upon introduction to the pool and were observed thereafter several times a day and in the evening shortly after dark. During these observational periods, I made no effort to avoid movement so that the snakes would habituate to my presence and activity.

In order to avoid social pressure, these observation periods were also used also to ensure that the animals were not fighting. Some cottonmouths were found to be incompatible with each other, chasing and displaying at each other (see Blem, 1987). Harassed animals were removed quickly with Pilstrom tongs. Trial groupings were made until several groups of compatible individuals were formed so that several snakes could be habituated in the pool at the same time and held together in a tank before and immediately after trials. Special care was taken with the sole neonate sized individual available in 1987 because cannibalism has been so frequently reported for this species (see Burkett, 1966). This individual was also the only cottonmouth small enough to be subject to predation by sunfish (*Lepomis* sp.), so that very large sunfish (>50 g) were not in the pool during this snake's tenure in the pool. The snakes were removed from the pool and housed singly or in groups in glass aquaria on the beach of the test pool for at least 24 h for the water snakes, and 72 h for the cottonmouths, in order to allow the guts to empty of any food that may have been eaten during the habituation period.

Test Enclosures

The need for more than one test enclosure. The main testing enclosure was a large naturalistic pool. While this pool was designed to prevent escapes, snakes are consummate escape artists; they also tend to secrete themselves in and under things and would be difficult to locate in the complex pool environment. Therefore, considerations of security and the need for ready retrieval of subjects made it necessary to use a second enclosure, smaller and more secure, for testing neonate and yearling snakes. The same test protocol was used for both testing environments.

Large test pool. The pool, (Fig. 1) was a plastic children's wading pool 1.83 m in diameter and .46 m high. It was surrounded in its entirety at the top by a plywood "beach" .3 m wide, painted matte gray in a scrubbable marine grade of paint. The beach was supported by struts of plywood and hardwood 2 x 4's so that it was sturdy enough to walk on. The junction of the beach and pool was secured with duct tape. The pool was enclosed in a 1.2 m high Lexan wall affixed with screws to the beach. An opening in the Lexan wall was made for entry and camera placement. This opening could be secured with a Lexan sheet that slipped into a groove formed from Lexan strips screwed into the Lexan wall. Three infrared and 1 Gro-Lite incandescent bulbs in metal reflectors were clamped onto the top of the wall and oriented to provide heat and illumination of the pool and plants. These lights were on automatic timers set on a 12:12 light:dark cycle. Snakes could raise their body temperatures higher than ambient by basking under the infrared lamps. Air

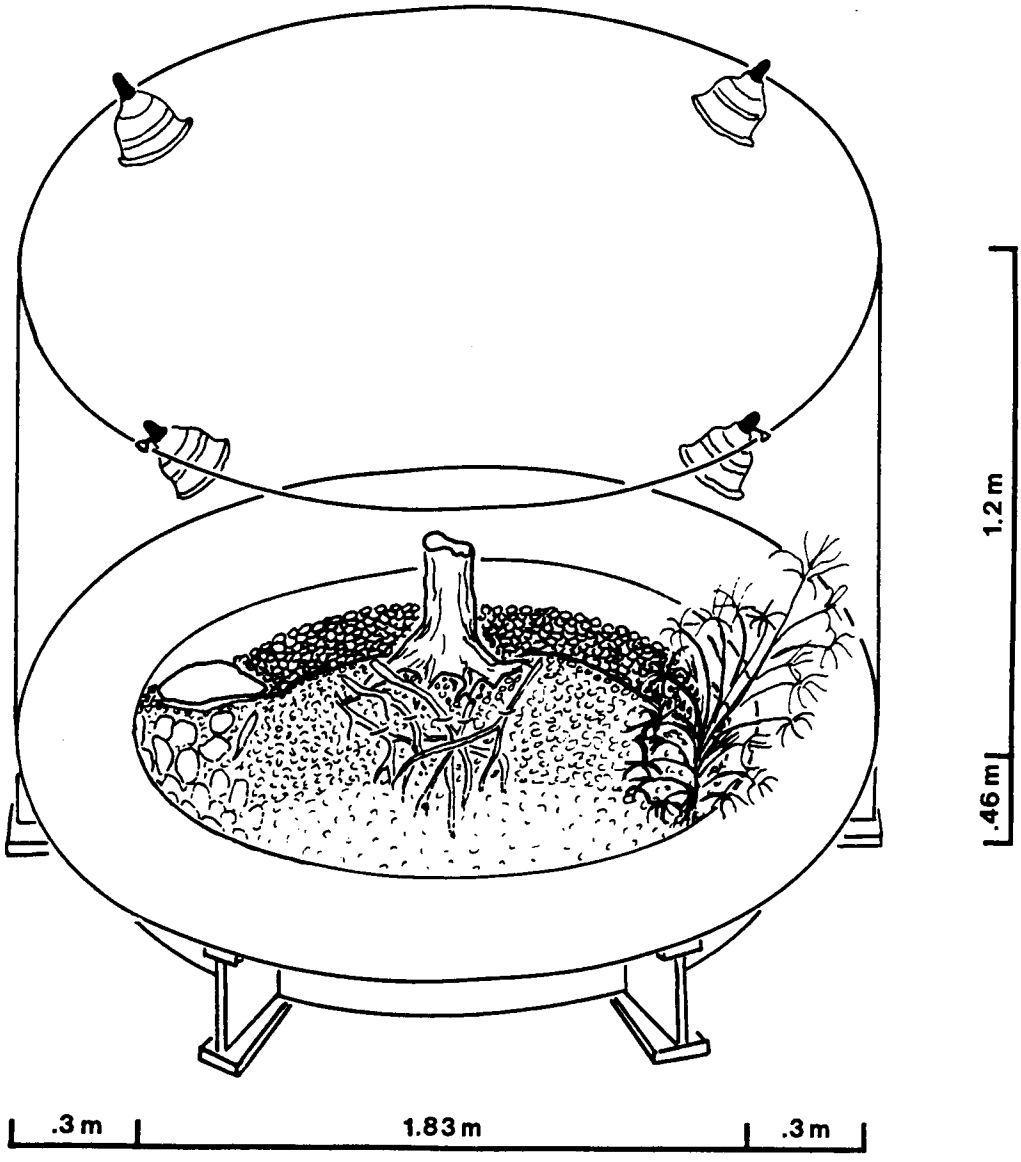


Figure II-1. The large test pool used for testing adult and sub-adult *Nerodia rhombifera* and *Agkistrodon piscivorus*.

temperatures in the enclosure were maintained at 24-28°, and water temperatures were maintained at 21-24°, which are within the activity range of both species used.

Based on Drummond (1980) and observations at Reelfoot Lake, a complex environment was created (see Fig. II-2) that formed a small covelet with a gently sloping-bottomed shallow area (< 15 cm deep), a flat-bottomed area 15-30 cm deep, and three cover areas of approximately the same size that extended from the edge to the deep areas and were each in part emergent and submergent. The substrate was washed "pea" gravel.

The pool was surrounded by a beach and a Lexan wall, neither of which are shown in Fig. II-2. The entire test habitat was divided into several habitat areas. The habitat areas and the proportion of the total habitat area pool that each comprised were as follows: Beach = 45%; Shore (S) = 13.5%; Edge (E) = 2%; Wood (W) = 6.5%; Vegetation (V) = 6.5%; Crevices (C) = 6.5%; open shallow water (OWS) = 10%; open deep water (OWD) = 10%. For predatory behaviors, cover areas were divided into edge and water covered areas as illustrated.

The cover areas were (1) rocks piled to form crevices, (2) wood stump and overlapping branches stripped of vegetation, and (3) grass-like clumps of *Cyperus* sp., a wild emergent aquatic which thrived under the Gro-Lites. As noted earlier, snakes at Reelfoot were seen to use similar cover types. While natural rock piles were not found at Reelfoot Lake, snakes showed a strong affinity for the manmade rock and concrete piles used as sea walls along the south shore of the lake. It was assumed that any preferences for particular plant species or rock types did not compromise the usefulness of this simulated natural habitat. Attempts were made to create areaslarge enough for any snake tested. With the possible exception of the rock crevices, the

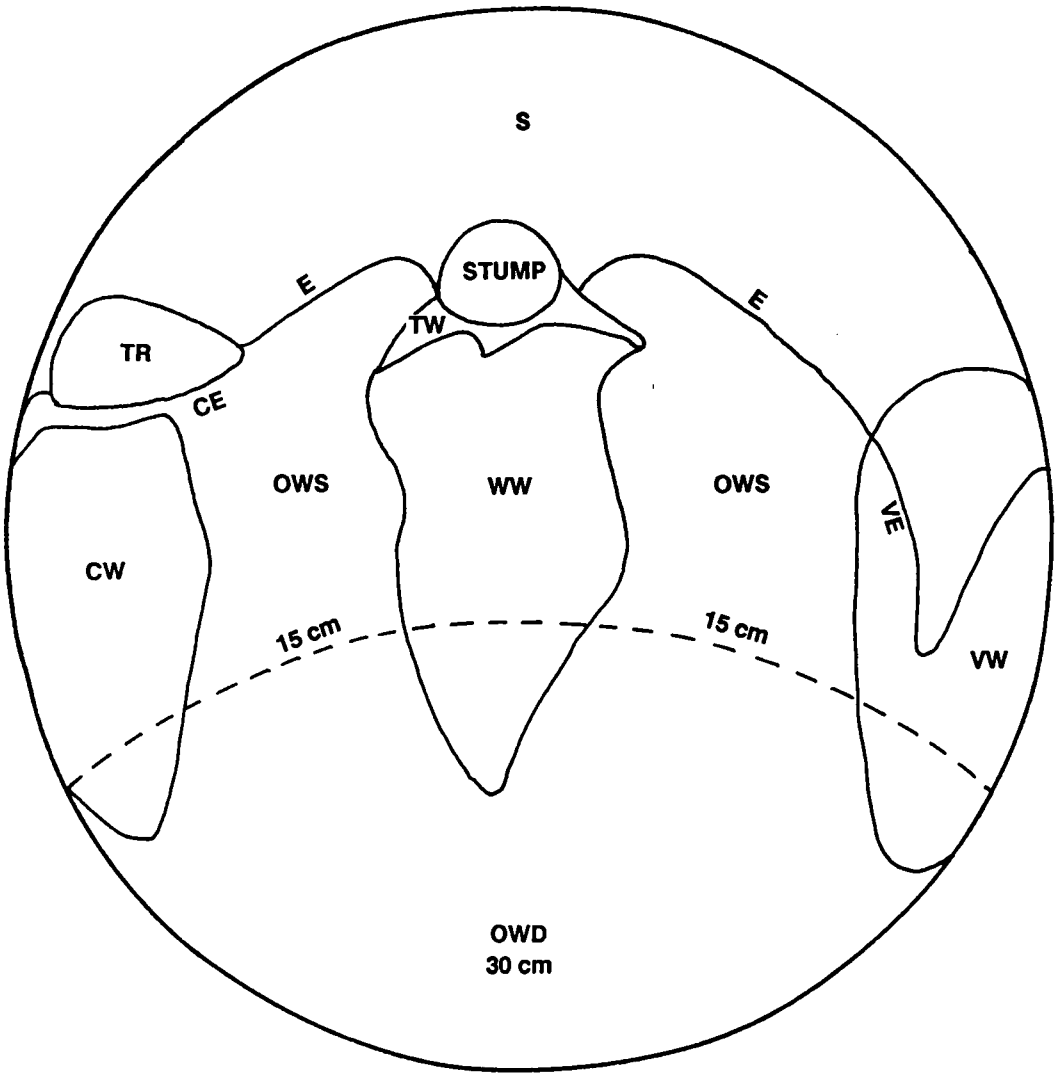


Figure II-2. Diagram of the large test pool as seen from overhead, showing the habitat areas. S=shore; E=Edge; WE=edge area of the wood; VE=edge area of the vegetation; CE=edge area of the rock crevices; WW=water covered area of the wood; VW=water covered area of the vegetation; CW=water covered areas of the rock crevices; OWS=open shallow water; OWD=open deep water.

cover areas all accommodated the largest snakes. The cover areas extended from the edge into deep water.

The regions between the cover areas in the test pool formed open water areas large enough to accommodate active foraging, even open-mouth circling, by at least moderate sized (600-700 mm SVL) snakes. The deep open water area was large enough to allow active foraging by even the largest snakes. A visible demarcation between shallow and deep water was made by creating a sharp drop-off in the gravel at the end of the shallow water area. The pool water was aerated to ensure adequate oxygen.

Small test tanks. These tanks (Fig. II-3), were 30 cm cubes of transparent plexiglas with locking screen lids described in Drummond (1979). Separate tanks were used for each species. In the basic foraging studies on both species, the tanks were outfitted with sloping "pea" gravel bottoms, and wood, rock, and vegetation cover areas similar to the large pool, but on a reduced scale. A narrow gravel edge was available. The *Cyperus* (a different species), was cut short in order to fit into the closed tank. The cover areas were arranged so that one side was in shallow water, and the other in deep water. Shallow water was 1-4 cm deep. The deep water area was only 7 cm deep at maximum. Again, the demarcation between shallow and deep water was made with sharply sloping gravel. The cover areas and deep open water areas were of such a size that neonate snakes could actively forage there. Open shallow water areas were too restricted in size to allow for open-mouth circling, however. Because of the size of the tank, no beach or shore was available. Structural categories were otherwise the same as for the large pool. These tanks were lighted

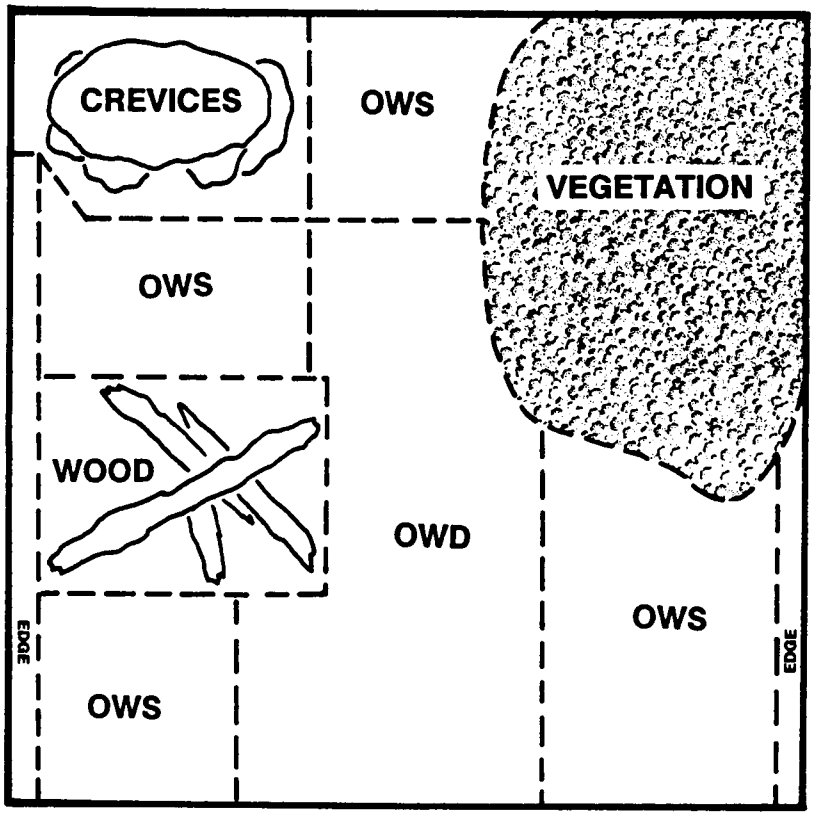


Figure II-3. Diagram of the habitat areas of the small test tank, as seen from above. Test tank was 30 cm square. Maximum water depth was 7 cm. The dashed lines represent the appoximate boundaries of the cover and open water areas.

during testing only by one red bulb on top of the tank and one incandescent about 45 cm away from the front of the tank. These lights provided fairly shadow-free light but little heat. The room where these tanks were placed was maintained at 24-28°.

Modified small test tanks. In follow-up tests for the cottonmouth juveniles, the small tanks were set up as illustrated in Fig. II-4 with a sloping gravel substrate of "pea" gravel with a flat "beach" area 7 cm across at the high end of the gravel at the back of the tank. The tank was supported on a styrofoam block under the tank at the back. Initially, a block of styrofoam 7 x 4 cm was placed on the right side of the beach in order to provide a dry resting area for the snakes. This was removed as some of the snakes shoved it into the water in order to rest on the gravel. A shallow pool outlined by slightly larger gravels was formed at one end of the beach . The tank was filled with water up to the edge of the beach, thus forming a body of water which increased in depth gradually to 7 cm deep at the front end of the cage. Tanks were maintained in a room at 28-30° with a 12:12 light:dark cycle. Different experimental protocols and a more limited range of behavioral and structural categories were used for these experiments and will be discussed in Chapter IV.

Prey

Live fish. Due to the large number of fish required and the large pool size, the fish had to be kept in the pool. Extra fish were housed in 30 or 75 gal aquaria in the same room. The numbers were kept as constant as possible; prey density was very

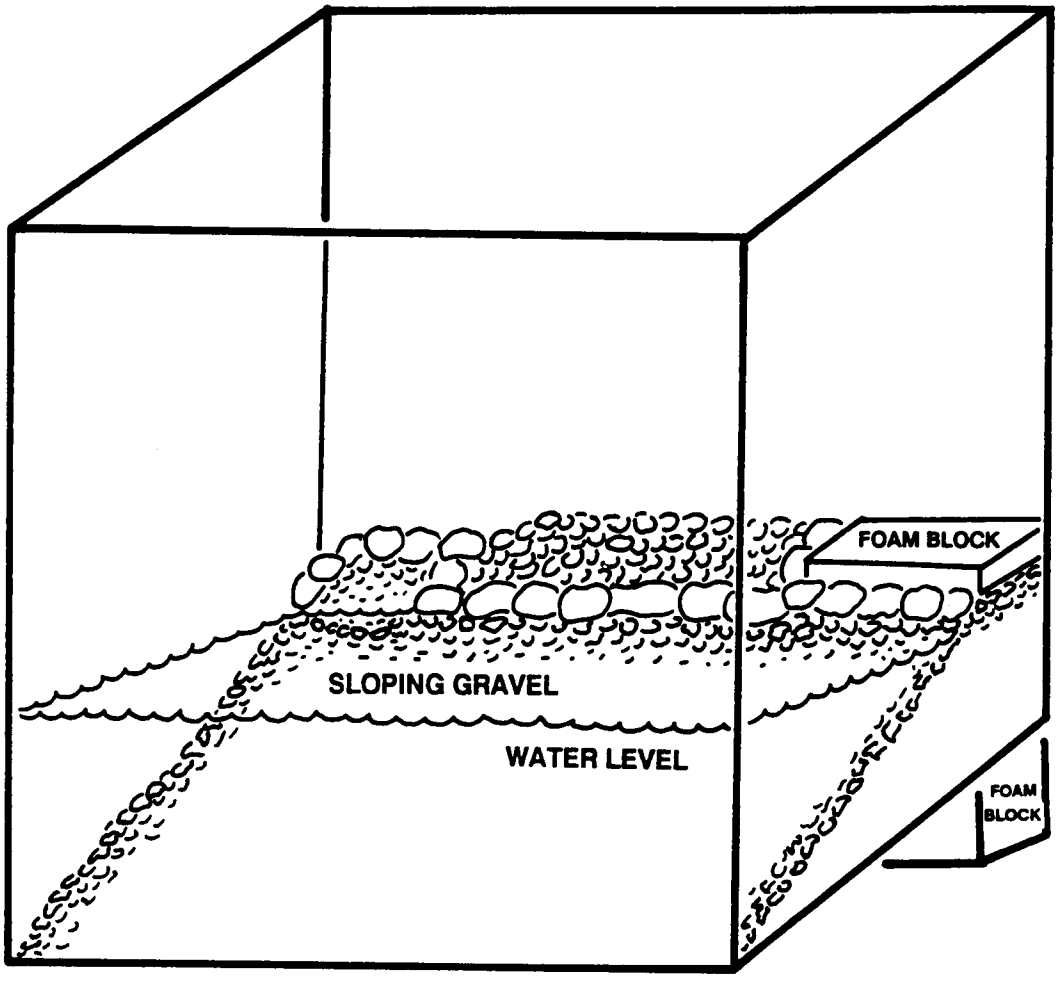


Figure II-4. Diagram of the modified small test tank used for testing young *Agkistrodon piscivorus*, showing habitat areas and water level. The small pea gravel substrate is surrounded by larger gravel along the water's edge and surrounding a small pool created by a depression in the gravel forming the shore.

high. About 2/3 of the 250-300 fish present during each trial were "medium" and "large" fathead minnows (*Pimephales promelas*) weighing approximately 1.5-2.5 g and 3.5-5.5 g respectively. The rest consisted mostly of golden shiners (*Notemigonus crysoleucas*), weighing 8-25 g, and "Baltimores" minnows (*Carassius auratus*), weighing 15-50 g. These were acquired from a local commercial source. A few (10-20) sunfish (*Lepomis* sp.), weighing 5-125 g, caught in local ponds, were also present. Only 2-3 fish over 50 g were present at one time. The fish formed loose aggregations of mixed sizes and species which used all parts of the pool.

Dead fish. Since pilot tests indicated that the cottonmouths reliably ate only dead fish, it was necessary to maintain a constant, large supply of dead fish, dispersed throughout the pool in such a way that habitat use was not biased by prey availability. Therefore, for each trial, dead fish of the above species, and large shad, *Dorosoma cepedianum* (25-125 g), all of which were frozen after dying of natural causes, were laid out at the beginning of each trial so that small (1.5-5.5) and large (>20 g) fish were placed in approximately the same quantities all over the pool, except deep within the vegetation. In order to conserve fish, uneaten dead fish were removed and re-frozen for later use at the end of each testing session.

Experimental Procedure

Pretesting pool preparation. Because the two species may react to the odor of the other, the pool was cleaned between tests of a given species. All traces of waste and shed skins were removed. The fish were removed and the pool was drained; then

the gravel was mixed and rinsed. The beach, walls, and rocks and wood were scrubbed with alcohol. The pool was not used for testing for 48 h after refilling so that the water could "age" for 24 h and return to temperature before adding fish; the fish then were given a 24 h habituation period.

Between within-species trials, only waste, shed skins, and excessive dead fish were removed. If needed, cover areas were rearranged to the prescribed configuration between trials. Additional cleansing of the water was done with a diatom filtration system as needed to maintain adequate clarity of the water in this eutrophic environment.

Lighting. Pilot studies indicated that the snakes foraged normally indoors in lighted rooms during daylight hours. Therefore, testing was done during the daylight hours. Although the snakes were tested with the four pool lights illuminated, room lights were turned off.

Minimizing observer disturbance. The lighted pool in an otherwise darkened room reduced my visibility to the snakes. This lighting was combined with black burlap drapes around the Lexan wall to hide my presence. It seemed to be sufficient as the snakes appeared not to be aware of me even when I moved. A video camera used for recording feeding was also shrouded by black burlap to make it less noticeable. While snakes occasionally reacted to movement of the camera by orienting toward it briefly, it did not appear to disrupt behavior. Nevertheless, camera movement was minimized by moving the camera only after the snake was clearly reacting to prey or was facing away from the camera.

Data Collection

Trials defined. Foraging was observed during trials. Snakes were tested singly or by twos. Data collection began after a 15 min habituation period, unless foraging began earlier. The occurrence of attacks, including tongue flicking dead prey, was the criterion for the onset of foraging. Trials lasted 45 min, divided into 30 s intervals. Virtually all snakes of both species had finished foraging by the end of the trial.

Beginning and ending trials. The snakes were released singly or by twos onto the beach. They were removed from an aquarium on the beach by hook or by allowing them to crawl out after partially lifting them with the hook. At the end of the trial the snakes were recaptured with tongs and returned to the aquarium unless they had secreted themselves somewhere out of the way. The snakes reliably stayed inactive long enough after ceasing activity so that testing the rest of a group could be completed without interference from previously tested snakes. No more than 5 snakes were in the pool at the same time during trials; no more than 3 were ever simultaneously active.

Sampling methods. Behavior and habitat use were recorded using instantaneous sampling, except that all attacks, which tended to be of very short duration (<5 s), were all-occurrence sampled. This combination of instantaneous sampling using short time intervals and all-occurrence sampling of very short duration behaviors should provide good estimates of behavioral frequencies (see Tyler, 1979).

Recording Data. A Casio brand repeating countdown timer gave an audible tone every 30 s to signal the beginning of each interval. At the sound of the tone the following information was noted: the location of the snake as determined by the location of its head, whether or not it was in motion, and its behavior. The information was then recorded by placing checks on a checksheet (see Appendix B) divided vertically into the habitat, movement, behavioral, and predatory categories, and horizontally into time intervals.

The predatory behaviors that were all-ocurrence sampled were checked off in the appropriate time intervals as they occurred. Some attacks were inferred when a snake's head was not visible but the snake was making jerky thrusting movements characteristic of attacks. Additional comments, including some aspects of prey handling, were handwritten as needed in a personal shorthand.

Videotaping. Every effort was made to videotape all foraging with the provisos discussed in the "minimizing observer disturbance" section above. While some foraging activity was consequently not filmed, all foraging episodes were recorded on the check sheet which was the primary tool for data collection. Samples of each snake's activity, both ordinary and extraordinary, were videotaped in order to have a permanent record of the behavior of the species. With the help of remote control, it was possible to operate the camera while recording data on the check sheet.

Habitat categories. The structural categories recorded consisted of the following:

1. **shore**- the area above water;
2. **edge**- the band, about 5 cm wide, where water meets shore;
3. **shallow**- water < 15 cm deep;
4. **deep**- water > 15 cm deep;
5. **substrate**- the bottom, underwater
6. **rock crevices**- rock crevices or on submergent rock;
7. **top of rock**- the top of emergent rock(s);
8. **wood**- the stump or branches;
9. **top of wood**- the top of emergent wood;
10. **vegetation**- the edge of vegetation;
11. **beach**- the beach.

These categories can be lumped for later data analysis. For example, Drummond's "overland" category can be generated by using all observations of behavior, with the exception of any food handling behavior, that occurs when the snake's head is over land substrate (see Drummond, 1980, p. 25) which would include my categories "shore", "edge", and "beach". Analogous lumping of structural categories can be used to generate Drummond's categories "over the water surface" and "underwater". These super categories proved useful in defining differences between aquatic specialists and generalists (Drummond, 1980, 1983).

Behavioral categories. Behavioral categories are the same as for Drummond except as noted. Additionally, Drummond (*op. cit.*) referred to any submersion of the

head as diving, which I did not. The differences were necessitated by the envenomation capabilities of the cottonmouth and the coincidental alterations of the skull as discussed in Chapter I. Prey handling was broken down into several categories, and some of this information was recorded by writing it in rather than by checkmarking as described.

The behavioral categories used are listed below; categories different from those of Drummond (1980) are marked with an asterisk (*):

1. **non-search**- is the time spent in the shelter on the beach or coiled up in cover areas;

2. **swimming**- is locomotion in water with the eyes above the surface;

3. **craning-cruising**- is a posture performed at the water's edge with the head over the surface without touching the surface (CCA)*, or while in the water with the eyes only above the surface (CCS)*; or with the head below the surface (CCD)*; the snake may be either still or moving;

4. **anterior dive**- is a dive in which the snake's head is below the water surface but some part of the body is on land or is supported by some other structure;

5. **mid-water dive**- is a dive in which the snake is moving through the water with no portion of his body supported by structure;

6. **crawl**- is locomotion on the underwater substrate;

7. **open-mouth searching** (OM)- is foraging in lateral sweeps through the water with the mouth open;

8. **orientation**- is a pointing of the head toward prey, usually after a definite projection;

9. **attack**- is a lunge at prey forward underwater and may take the form of an attack forward underwater, a **frontal attack**, sideways underwater, a **lateral attack**, or

from the air into the water, an **aerial attack**; the attack is **strike-hold*** in the cottonmouth when the prey is struck and held, and is **strike-release*** when the prey is struck and released, and **envenomation*** occurs when fangs are down and position of the prey in the snake's mouth indicates penetration by the fangs during strike-hold attacks, or the prey has obvious fang wounds upon release in strike-release attacks; and the attack is **live prey*** or **dead prey*** depending on whether the prey was alive or dead when attacked;

10. **capture**- is the retention of any prey item, alive or dead for more than 1 sec;

11. **prey handling**- is any manipulation of prey and is **on land*** whenever the snake's head is over dry substrate, is **in water*** whenever the snake's head is above or under water, is **underwater*** whenever the snake's head is under water 75 % or more of the time during prey handling; **prey size*** is the size of the prey relative to the predatory snake: *Size 1* fish have a maximum width less than 75% of the maximum width of the snake's head measured at the quadratomandibular joint, *Size 2* fish have a maximum width 75-125% of the maximum width of the width of the snake's head, and *Size 3* fish have a maximum width greater than 125% of the snake's head; **prey lost** occurs whenever prey is lost or dropped after capture;

12. **ingestion***- is the ingestion of any prey item and is **head first** when the prey is swallowed head first, is **folded*** when the prey is bent double and ingested from the middle, and is **tail first*** when the prey is ingested tail first.

13. **moving***- is the occurrence of body movement, either locomotion or postural realignment, but not just head movement.

Data Analysis

Data used for analysis. All snakes for whom data has been analyzed were tested at least twice. Trials for animals which were active lasted 45 min. Because of the number of animals required and the large number of trials which resulted in no foraging, trials were aborted after 15 min if the animals did nothing. Because virtually all snakes which foraged did so at or near the beginning of a trial and did not return to foraging, or any activity, after assuming a coiled or resting position, trials were stopped 15 min after the last foraging behavior. While this procedure produced trials of varying lengths, it resulted in the collection of the maximum amount of usable data. This data is equivalent to Drummond's "total search time" (see Drummond, 1980, p.30).

Some snakes never foraged or ate. Only data on snakes for whom I have at least 45 min of foraging, or total search time, are included for analysis. Some snakes foraged readily, and for them I have several hundred intervals of usable data. In order to use such data without throwing out information from animals for whom I have less data, all data are presented in terms of proportions of total trials.

Foraging v. non-foraging trials. Trials were divided into foraging and non-foraging trials. Foraging trials were those in which snakes showed "predatory interest" as evidenced by the occurrence of at least one attack or the tongue flicking of dead prey. This definition of predatory interest seems somewhat stricter than that used by Drummond (1980, p. 30) as he also considered the occurrence of any diving to indicate predatory interest, but I believe the definitions are really quite similar

since diving preceded many attacks for his specialist garter snakes. In this study, as in Drummond's, comparisons of searching behavior are limited to foraging trials. Within species comparisons of foraging and non-foraging trials will be discussed separately.

Interpreting prey handling times. Prey handling that occurred during an interval was recorded by placing a check in the square for that interval even if prey handling was not in progress at the beginning of the interval. Thus, prey handling times will be given in terms of time intervals required. Since intervals lasted 30 s, prey handling times can be converted to min by multiplying the number of intervals by .5. This will, of course, produce an overestimate of the actual time, so that the true time lies somewhere between the calculated time minus 1 min and the calculated time.

Determining pool area. A drawing of the pool was made, and the areas of the entire enclosure and its constituent habitats were calculated. The proportion of the entire enclosure occupied by each constituent area was then calculated. Most habitat areas were treated as rectangles; thus, areas and proportions are approximations. With minimal and systematic rounding, the proportions summed to 100%. The proportion of the total enclosure occupied by each habitat area are as follows:

1. beach- 45%;
2. shore- 13.5%;
3. edge- 2%;
4. cover areas (vegetation + wood + crevices)- 19.5%;

5. shallow open water- 10%;

6. deep open water- 10%.

Statistical methods. Some data were analyzed on a microcomputer using Statgraphics software supplied by the University of Tennessee. Tests used were the Wilcoxon one and two sample signed rank tests, and the Mann-Whitney signed rank test for independent samples. Some data were analyzed on a hand calculator using methods for analyzing proportional data described by Fleiss (1979) which provide a confidence interval for the difference between two proportions. If 0 falls within the calculated confidence interval, the proportions are considered to be statistically the same. Confidence intervals of 95%, 99%, and 99.5% were calculated. These tests were calculated in a very conservative manner more likely to produce Type II than Type I errors. Where possible, the G test described by Sokal and Rohlf (1981) was used. The results of the proportional data tests are presented with only the percentages and the significance level of the difference; G tests are presented with the value of the G statistic and its significance.

In accordance with Drummond (1980), most data analysis was by the nonparametric Kruskal-Wallis ANOVAs. These tests are rank order tests of the median that have been found to produce results very similar to parametric ANOVAs (Sokal and Rohlf, 1981). As described by Drummond (1980) and suggested by Gibbons (1976), these tests were performed at an overall significance level of .15-.25 for the test statistic (H), and the comparisons were then made at higher levels of significance. Since my analyses involved fewer comparisons than did Drummond's, higher overall significance levels were used (the maximum was $p < .11$ and most

overall p values were <.01). All comparisons were deemed significant only at $p<.05$. Results of these tests are presented in terms of the H statistic value, and the significance level of that value.

Parametric ANOVAs and ANCOVAs were performed in some cases, but only with transformed data: proportional data were arcsin transformed as described by Sokal and Rohlf (1981), and non-proportional data was log transformed in order to normalize it in accordance with the assumptions of parametric statistics. The confounding of many variables made the use of MANOVAs impossible, thus precluding the parametric analysis of interaction effects. Where used, ANOVA results are presented in terms of the F value and its significance.

There was pooling of some laboratory data, that is, subjects provided more than one observation to a data set, and sample size is then based on the number of observations rather than on the number of subjects, which can bias statistical results (see Machlis et al., 1985). To avoid such problems, Kruskal-Wallis ANOVAs were performed on each variable analyzed to check for individual differences. Whenever subjects produced a $p<.10$, subjects was considered significant, and analyses were performed on the medians from individuals to ensure that pooling did not bias the statistical results. The median was used because much of the data had a highly skewed distribution, and the median was a better measure of central value (Sokal and Rohlf, 1981).

For most analyses where individual differences were not significant ($p>.10$), tests were performed on pooled and unpooled data sets for comparison. Results were similar for most tests, although the significance of pooled data was sometimes higher than that of unpooled data. Lowered significance levels resulted in only 2 comparisons changing from significant to insignificant. The variance of pooled data

cannot be reliably calculated (Machlis et al., 1985), but that presents no problem for my analyses which largely rely on the value of the median. The type of data set and the number of subjects involved is given with the results of statistical tests. Since comparisons involve differing numbers of subjects in each group, the range of group sizes is given.

Another aspect of the habitat analysis requires explanation. Since the size of the various habitat areas relative to the total habitat area had been calculated, habitat use was analyzed by comparing the proportion of the total time spent in a habitat area to the proportion of the total habitat area accounted for by that area. If the proportion of time spent in an area was significantly less than the proportion of the total habitat area accounted for by that habitat area, than the snakes were considered to have been there "less than expected" and to be exhibiting "avoidance" of that area; conversely, if the proportion of time spent in an area was significantly greater than proportion of the total habitat area accounted for by that habitat area, then the snakes were considered to have spent more time there than "expected", and they were considered to be exhibiting some "preference" for that area. Two-tailed one or two sample Wilcoxon signed rank tests were used to determine the equality of proportions of unpooled data. When the direction of the difference is specified, one-tailed probabilities were calculated. Results of these tests will be given in terms of the test statistic "Z", the probability of the value being greater than that value of Z, and whether the test was one or two tailed. The Mann-Whitney tests were used for the comparisons between age groups and species. Results of these tests are also given in terms of the test statistic "Z".

2. FIELD METHODS

Preliminary Field Visits

Initial visits. Initial visits to Reelfoot Lake consisted of exploring the south shore by foot and by boat (kayack) in day and night looking for snakes. Several kilometers of continuous shoreline were walked during the day and then again at night. Even though visitors to the lake regularly killed snakes, the water snakes were found most consistently in the areas used by people. The nature of these areas was discussed in Chapter I. Most observations and collecting of the water snakes were made, therefore, near campgrounds and fishing camps. Cottonmouths were found by walking the dirt road to Donaldson Ditch and the ditch as described in Chapter I. Cottonmouths were found in sloughs in the National Wildlife Refuge in the northeastern part of the lake, but were too dispersed to study effectively.

Both species were found together in the above described sloughs and Donaldson Ditch. Most cottonmouths were collected in these areas. At the Perry County, Alabama site, cottonmouths were found primarily in a drainage stream at the edge of the forest. The water snakes, on the other hand, were found in the fish ponds rather than the stream, although one was was seen to cross a road heading toward the stream away from a pond. The cottonmouths, in contrast, were only occasionally found in the fish ponds although fish and frogs were very abundant there. These ponds offered little cover, however, being surrounded by dikes with grassy vegetation and no trees. At all sites, cottonmouths were either in forested areas or at the edge of forested areas.

Field Study

Overview of methods. In 1987, formal field study was undertaken using three study areas divided into grids of square quadrats as described in Riechert (1973,1974) and Kershaw (1985) in order to analyze the variables involved in habitat use. The variables considered were the amount, either sparse or thick, and the type of vegetation, either saw-grass or other (smartweed or lizard-tail), the amount (%) of wood, the amount (%) of open water, and water depth.

A site on the south shore in the Kiwanis Day Use Park was chosen for study of the water snakes because it contained several covelets known to be used by the snakes and several which were not used much by them. The area was monitored constantly during daylight by park personnel and locked at night; it therefore offered some security. It was also conveniently located next to the State Wildlife Resources headquarters where I stayed. The site was set up in June and monitored for a week at a time in June and in July-August, and briefly in October. Maps were made of the 2 most variable study areas showing all structures and water depths (see Appendix C). Each quadrat of all 3 study areas was numbered and described in terms of each variable listed above. The fairly distinct zonation of the littoral areas of the lake made the characterization of each block rather straightforward.

Cottonmouths could not be located in quantities sufficient for study in 1987 except in the heron rookery into which human entry was strictly limited for the protection of the birds. Therefore, no formal habitat study was undertaken.

Description of the study areas. After considering the size of the animals and the areas under study, a quadrat size of 2 x 2 m was selected. The quadrats were marked by stakes with red flagging. Stakes were left in place the entire summer with the exception of some stakes on land which were removed between visits for the safety of visitors. Park visitors vandalized the sites to some degree, but not irreparably. Maps for Study Grids I and II and a detailed description of Study Grid III can be found in Appendix C.

Study Grid I covered two covelets which had been found to be frequented by water snakes. This was considered fairly ideal habitat. It was 32 x 16 m which completely encompassed the coves and a small peninsular strip of land between the covelets. The water depth was largely less than 45 cm. The smaller west covelet had a shallow area with submergent vegetation and included a patch of smartweed so dense that the water was not visible. It was bordered on the west by dense smartweed. A few cypress trees, stumps, and one log were present in the water and on land areas. The larger east covelet had a very gradually sloping sandy bottom devoid of submergent vegetation. It was bordered by cypress trees, knees, and land on the south. The grid included a strip of grass-covered land 1 to 3 quadrats wide along the east covelet. This grid also included a large area of "sparse" smartweed. Sparse vegetation was defined as that in which the widest emergent parts of neighboring plants did not overlap. Large numbers of small fish and some larger fish were present in the shallowest areas night and day. Areas with submergent vegetation were at least as attractive to fish as areas devoid of submergent vegetation.

Study Grid II was only about 15 m east of Grid I, but was originally used significantly less by the snakses than was Grid I. This area was selected because of the amount of wood structures present both in very shallow and deeper water. It was

8 x 16 m extending from a largely vegetated shore with several large cypress trees and included a significant amount of water 45-60 cm deep. It consisted largely of cypress knees in open water, with some sparse smartweed in the shallow areas. It was bordered by saw-grass and dense smartweed on the east, and in the water in the north, large cypress trees. A very small amount of shoreline, but no dry land, was included along the south edge of the grid. Fewer fish were present here but, as everywhere in the lake, were sometimes quite abundant in the very shallowest areas.

Study Grid III was about 30 m east of Grid II and was originally found to be used by only a few water snakes. A cottonmouth had been found here the year before, however. This area was selected because of the heavy grass and shallow water areas with submergent vegetation. Grid III was 16 x 8 m and consisted of the west shore and a small water portion of a covelet somewhat wider but considerably longer than the east cove of Grid I. The shore and much of the water areas were thickly covered by saw-grass. Some land, mostly heavily vegetated, was included along the southeastern edge of the grid. The open water areas also had sparse saw-grass, and many areas had submergent vegetation. Although there were no trees or knees in the covelet, a patch of hardwood forest bordered the eastern side of the covelet. Fish were abundant primarily in the shallow areas with submergent vegetation.

Data collection. The study grids were examined in a systematic manner at hourly or bi-hourly intervals nightly. Additionally, the grids were visited in the daytime several times at each hour of the day on the hour except between 0300 and 0800, but not every day. At each check, the temperature of the air and water in both shallow and deep areas was recorded.

Each grid was scanned carefully first by headlamp, and areas of dense vegetation were then checked by gently parting vegetation, even in the saw-grass. The water snakes are calm enough at night that walking near does not cause them to flee. Snakes in the water will continue to forage or swim around as humans walk by. When snakes were found, the location was marked with flagging; it was written down in the field notes in terms of block number and as an "x" on a map of the grid. Behavior was noted using variables already described in the Laboratory Methods section. Snakes found foraging were observed until the foraging ceased. Few snakes from the grids were captured to avoid driving them away.

Captured snakes were placed in cloth bags until the grid check was completed. After the grid check, captured snakes were permanently marked by clipping subcaudal scutes (Blanchard and Finster, 1933) and were temporarily marked with Scotch Lite Reflective Liquid. They were measured, including head width and length, sexed, and palpated for food. They were then released where captured. Collected gut samples were placed in marked plastic bags and later were preserved in 10% formalin.

Between grid checks, the rest of the Kiwanis Park and nearby areas were examined by walking along the shore and/or in the shallow water along shore. Snakes found in these areas were captured when possible and examined as described above. The area in which they were found and their behavior when first seen were noted in terms of the behavioral and structural variables already mentioned. These snakes were also permanently marked. Some were held overnight; all were released the following day where captured.

Data analysis. The water dropped a little more than 15 cm between the June and July-August visits leaving large areas of the covelets dry. Therefore, the grids were significantly different on each visit and had to be analyzed separately.

Gut samples were examined to identify prey to the generic level. Prey size was determined by weighing to the nearest tenth of a gram on a top-loading electronic balance. The size of partially digested prey was estimated when possible by comparing the remaining portion with fish of the same genus captured alive by dip net and preserved in 10% formalin and then determining the size of the undigested fish. Since many partially digested prey were digested only at one end and not at the other, identifying these prey was relatively easy. Prey larger than the prey size 2 of the laboratory study were also measured for standard length (SL) and maximum body depth.

Data were analyzed by parametric ANOVAs, ANCOVAs, goodness-of-fit tests, and non-parametric ANOVAs using the Statgraphics statistical software. There was no pooling of data *sensu* Machlis et al. (1985). Presentation of data follows that of the laboratory data as discussed above.

CHAPTER III

FORAGING FOR FISH BY *NERODIA RHOMBIFERA* IN THE POOL

1. INTRODUCTION

The goals of the following analysis of water snake piscivory are to elucidate how *Nerodia rhombifera* attacks and captures fish, how it uses the habitat during the various phases of foraging, and how it manipulates and then ingests the prey. Size and sex differences in habitat use and predatory behaviors are also investigated. The analysis was guided by the premise that the water snakes are aquatic specialists from a lineage of aquatic specialists. In the interests of brevity, the generalized term "water snake" will be used to refer to *N. rhombifera* in this chapter.

2. SEARCHING FOR PREY

Qualitative Analysis.

Beginning the trial and locomotion. Foraging information was collected for 21 water snakes. The snakes often began foraging before the end of the prescribed habituation period, usually hurling themselves into the water upon release. Exploration of the pool thus tended to be confined to a rapid circuit of the deeper water areas, punctuated by cruise postures above and below the surface.

The snakes tongues flicked as they moved around whether above, below, or at the surface. The water snakes achieved negative buoyancy very easily, and were more

likely to move across the pool by locomoting across the underwater substrate than by swimming across the surface. They maintained enough positive buoyancy so that underwater locomotion, herein called substrate crawling, was somewhat of a combination of terrestrial lateral undulation and swimming. During substrate crawling, the snake proceeded by pushing against substrate pivot points (see Cundall, 1987) with enough force to propel itself forward through the water just above the substrate. This form of locomotion may by energetically cheaper than swimming because it allows the snake to generate more force by pushing against a solid object rather than against the water, but then minimizes frictional loss during the forward movement because the snake glides through the water rather than across the solid substrate. This method of locomotion would seem to make the best use of the frictional properties of the habitat.

The water snakes' movements gave the general impression of irregularity: they alternated periods of remaining still, either above or below the surface, with bursts of rapid movement, generally underwater. While the larger snakes tended to use more of the pool habitat than the smaller snakes, larger snakes still tended to stay in the deeper parts of the water covered areas. Extended periods were sometimes spent under water. Nevertheless, anterior and mid-water dives were remarkably brief and rare.

Orienting toward and attacking fish. Most underwater time was spent in a cruise posture. When their heads were above the water, they generally were motionless in a cruise posture, again with the head just at the surface or a few cm

above the surface. These apparent sentinel postures were not accompanied by much head movement.

When foraging in the more open areas, the snakes usually oriented toward fish underwater, often from a great distance (15-30 cm), then approached underwater slowly in a manner which could be called stalking, only to lie immobile on the underwater substrate until the fish swam near. While the snakes often tensed their necks before attacking, the necks were not formed into sinuous curves. Attacks often started out as single lateral or forward attacks, only to gain momentum and become open-mouth searching. Forward attacks resulted in propelling the snake forward a few centimeters.

Smaller snakes (<800 mm SVL) tended to settle into the crevices where they spent long periods of immobility in a cruise posture with the head just at, or slightly above, the surface, punctuated by periods moving around in the rock crevices, often being not visible for several intervals at a time. Sometimes it was difficult to determine whether these snakes were foraging or not: they often oriented toward fish but then did not react toward fish which swam by just below the surface. Many of these snakes, however, snapped at such fish, and were often successful in capturing fish which swam by. The water snakes, large and small, occasionally stalked prey underwater from the crevices, gradually moving the head toward fish. Often, however, the snakes simplay lay still with the head on top of a submerged rock and snapped at fish which came by.

Fish swimming above the snake were often attacked successfully by snakes lying on the substrate or in a low submergent cruise posture. These attacks occurred primarily in deeper water areas, primarily where the cover areas merged with the

open water. Such attacks involved in a lateral upward swing of the head and neck. Larger snakes (>800 mm SVL) made most of these attacks.

Quantitative Analysis

Habitat use during searching. Terminology and the methods used in the analysis of habitat use was described in Chapter II. Because a range of sizes (SVL) of both sexes was available, size and sex differences in habitat use were tested where warranted. Habitat use is summarized in Table III-1 and Fig. III-1 below.

The water snakes exhibited differential use of the habitat, based on the relative proportions of the total habitat comprised by each habitat area. The water snakes used the beach much less than expected ($M=0$, Wilcoxon signed rank test $Z=4.09$, $p<.0001$, one-tailed test); only 6 of 21 snakes used it at all during foraging trials. Two water snakes, the only gravid subjects, did spend a considerable amount of time there ($M=.57$ and $M=.13$). The other snakes who used the beach at all spent much less ($M=.0$-$.04$) time there. Although the gravid females did not really bask on the beach, the beach received direct infrared radiation from the heat lamps, and therefore, the gravid snakes may have utilized the beach more in order to attain a higher body temperature.

The water snakes also exhibited avoidance of the shore (Wilcoxon signed rank test $Z=3.94$, $p<.0002$, one-tailed test); only 4 snakes (all non-gravid) spent any time there, so that this species generally spent no time there ($M=0$). The water snakes as a group thus avoided the areas away from the water.

TABLE III-1

SUMMARY OF HABITAT USE BY FORAGING *NERODIA RHOMBIFERA* (N=21) IN THE LARGE TEST POOL

Habitat Area	Proportion of Observations[a]	Proportion of Pool Habitat	Difference
Beach	.00	.45	-.45**[c]
Shore	.00	.135	-.135**
Edge	.04	.02	+.02
Vegetation	.06	.065	-.05
Wood	.06	.065	-.05
Crevices	.23	.065	+.165**
OWS[b]	.03	.10	-.07**
OWD[b]	.13	.13	=.00

[a]The proportion of observations was the median value of the median values of the proportions for each subject (N=21) during foraging trials.

[b]OWS= open shallow water; OWD= open deep water.

[c]** $p < .01$, one-tailed probability of a significant difference, N=21, Wilcoxon one sample signed rank tests comparing the proportion of observations to the porportion of the pool habitat for each habitat area.

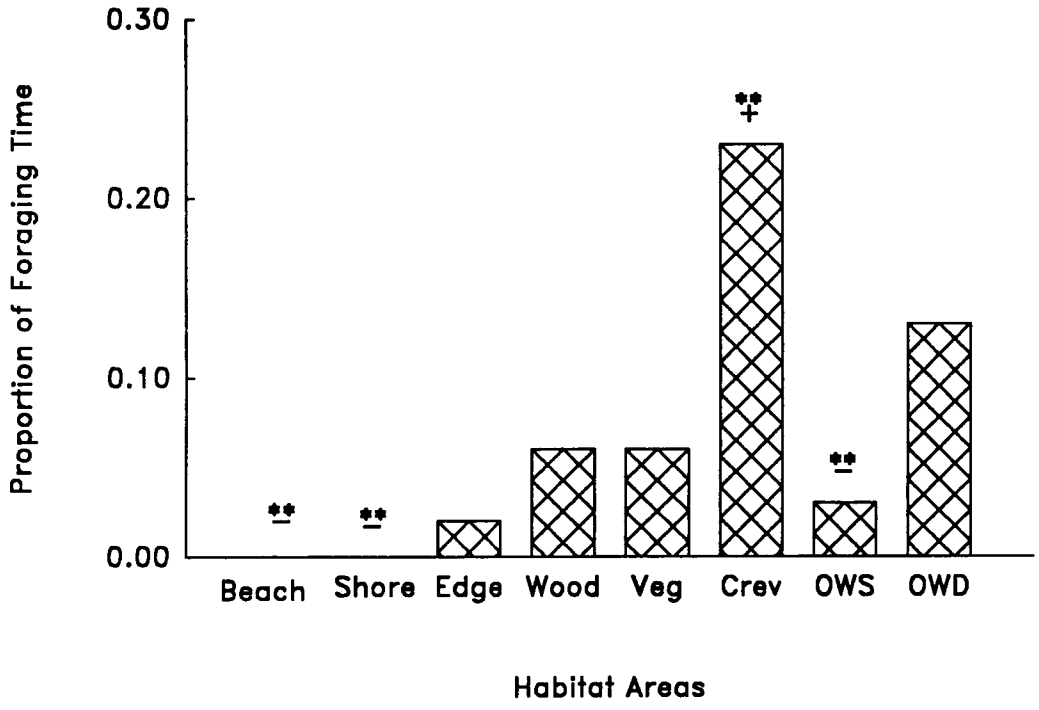


Figure III-1. The proportion of time that foraging *Nerodia rhombifera* spent in the various habitat areas. ** = significant difference ($p < .01$) between the amount of time spent in an area relative to the proportion of the total habitat area comprised by that habitat area; "+" denotes significantly more time spent in an area, "-" denotes significantly less time spent in an area. Veg=vegetation; Crev= rock crevices; OWS=open shallow water; OWD=open deep water. See Chapter II for details of the pool habitat.

The edge was used little, also (M=.04), but not significantly less than the expected (Wilcoxon signed rank test Z=1.96, p=.05, two-tailed test), however, so no avoidance was exhibited. It is of interest to note that 4 snakes (of both sexes in a large range of SVLs) spent no time there at all, however.

The snakes used the cover areas to varying degrees. The vegetation was utilized about as expected (M=.06), although 2 snakes never utilized it at all. The wood was utilized at the same rate (M=.06), although 4 snakes never utilized it at all. Only use of the crevices differed from the expected.

The crevices were used more than any other habitat area. This being so, the median value (M=.23), seems rather low, suggesting a lack of strong preference for this, or any, area in the pool. Use of this area was highly variable among individuals (s=.339), however, and the distribution deviated considerably from normal with the mean being considerably higher than the median ($\bar{x}$=.41). All individuals spent some time in the crevices, the only pool area for which this is true. Many, 10 of 21 subjects, spent the majority of their time (53-100%) there. Since I had noted that smaller animals tended to spend more time in the crevices, it seemed reasonable to test formally for a size (SVL) effect. Because of the sexual size dimorphism in this species, it seemed wise also to test for a sex effect. An ANCOVA was performed using SVL as the covariate and sex as the main factor. Both SVL and sex were relevant factors, although only the main factor was actually statistically significant (covariate SVL $F_{1,18}=3.92$, p=.06; main factor sex $F_{1,18}=9.26$, p<.01). The nearly significant value of the covariate SVL suggests that this factor might have been relevant in a different sample of snakes. It was the males, the smaller sex, that spent more search time in the crevices (male $\bar{x}$=.68, female $\bar{x}$=.24). A plot of time spent in the crevices v. SVL and sex is shown in Fig. III-2.

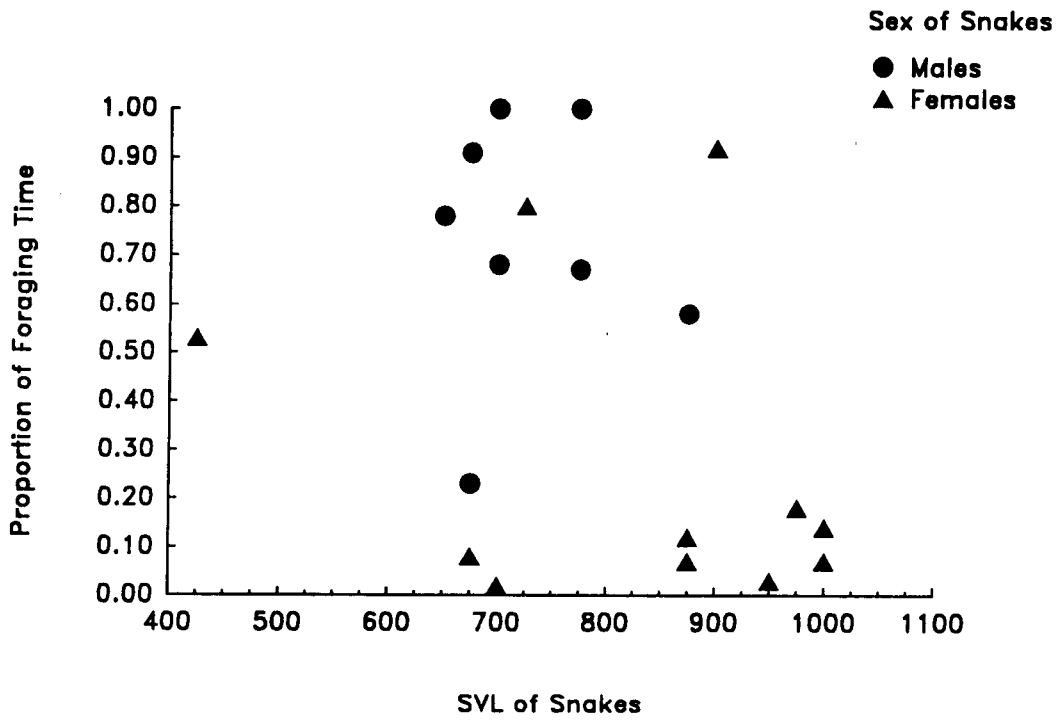


Figure III-2. Plot of utilization of the crevices by foraging male and female *Nerodia rhombifera* of various size classes in the large test pool. An ANCOVA showed that both SVL and sex were relevant factors, although only the main factor was actually statistically significant (covariate SVL $F_{1,18}=3.92$, $p=.06$; main factor sex $F_{1,18}=9.26$, $p<.01$).

Note that two distinct clusters appear in the plot: animals that spent less than 25% of the time in crevices, and animals that spent more than 50% of the time in crevices. As the plot illustrates, the sole individual under 500 mm SVL was a female who spent 53% of the time in the crevices. Only 2 females larger than 725 mm SVLspent more than 50% of the time in the crevices. The other 10 large females (including the gravid females) spent less than 20% of the time in the crevices. The scarcity of small snakes of either sex makes it difficult to know how much of a factor size really is.

The water snakes also spent a fair amount of time in the open water areas (M=.16). Most of this time (M=.13) was spent in the deep open water (OWD). Only time spent in the shallow water (M=.03) differed from the expected (M=.10): the open shallow water (OWS) was utilized less than expected (OWS Wilcoxon single sample signed rank test Z=3.72, p<.001, two-tailed; OWD Wilcoxon single sample signed rank test Z=.99, p=.32, two-tailed).

Sex, but not SVL, was a significant factor in utilization of the OWS (sex H=4.87, p=.03; SVL H=16.43, p=.13). That is, females (N=13, M=.07) searched in the shallow water areas more than did the males (N=8, M=0); 4 of the 8 males did not search there at all. These differences did not hold for the OWD, however (sex H=1.91, p=.17; SVL H=16.43, p=.14). Here, females and males searched at a statistically similar rate (M=.13), although the largest females (>900 mm SVL consistently utilized the deep water at a rate higher than the median (2418, 2420, 2421, 2422, 2444, 2447 M=.24), and 3 of the 8 males did not search there at all.

While searching in the deep open water, the snakes inevitably moved into deep water areas that were designated as cover areas. In fact, quite a bit of foraging occurred in these areas, especially in the crevices and the vegetation overhanging the

water, as the fish often remained in these areas even when the snakes were active there. Consequently, utilization of deep water was greater than indicated by the habitat analysis above.

Behavior during searching. Behavior during searching is summarized in Table III-2 below. The water snakes were in motion 34% of the time: they were moving significantly less than they were still (M=.7) (unpooled data, N=21, Wilcoxon two sample signed rank test Z=3.16, p<.02, one-tailed test).

While these snakes craned some, much of the time was spent in a cruise position, above or below the water. Placement of the eyes on top of the head allows this species to maintain a cruise posture in the water with the head just at the surface, and this was a very frequently seen posture. While the snakes tongue flicked constantly during movement, they did not follow chemical trails in an obvious manner. Many dead fish at the surface and along the edge and shore were never noticed. Dead fish in the water were not always recognized either. Actively foraging snakes sometimes even rested their heads on floating dead fish (DF) in deep water, without reacting to them. Nevertheless, it is quite possible, in fact, likely, that distant fish underwater were discovered chemically as well as visually.

Considering that these snakes are aquatic specialists, they did surprisingly little swimming, M=0, and the maximum value was only M=.04. Only 10 snakes were recorded swimming.

They also dived surprisingly little; in fact, only 11 individuals were recorded diving. The typical value for diving time was thus M=0, with the maximum value being M=.07, seen in a gravid female. Diving was of extremely short duration.

TABLE III-2

PROPORTION OF FORAGING TIME SPENT BY *NERODIA RHOMBIFERA* (N=21) IN SELECTED BEHAVIORS IN THE LARGE TEST POOL

Behavior	Proportion of Foraging Time[a]
Moving**[b]	.34
Swimming	.00
Diving	.00
Crawling[c]	.05
CCD[d]	.28
Attacking	.03
Above water[e]	.37
Below water[e]	.38

[a]Proportion of foraging time is the median of the median values for the proportion of foraging time for each subject (N=21).

[b]Proportion of foraging time spent moving. The time spent moving was significantly less than the time spent moving (Wilcoxon signed rank test, $Z=3.16$, $p<.02$, one-tailed probability).

[c]Crawling= crawling prone on the underwater substrate.

[d]CCD= underwater cruise posture: the body is on the underwater substrate with the head and neck are raised up, but the head is still underwater.

[e]Above water= the snake is in a water covered area with the head at or above the surface of the water; below the water= the snake is in a water covered area with the head below the surface of the water. The difference in the proportions for above and below the water was not significant (Wilcoxon signed rank test, $Z=.54$, $p=.59$, two-tailed probability).

While the instantaneous sampling techniques resulted in many dives not being recorded, which could result in underrepresentation of the true frequency of diving (see Tyler, 1979), the dives were so brief (<2 sec) that each one that was recorded resulted in such gross over-estimation of the actual time that it would have made up for approximately 14 unrecorded dives. Since the water snakes usually submerged from a cruise posture rather than diving while swimming, I doubt that mid-water diving was underrepresented. Anterior diving was rare also. These snakes simply went directly to the bottom when they submerged. Therefore, diving really was rare, and accounted for very little of the search time, however imprecisely the rate may have been estimated.

The water snakes displayed their aquatic specialization by the amount of time spent in the water in general and underwater in particular. These snakes were in water most (75%) of the time. They were submergent as much as emergent (M=.38 v. M=.37 total search time, respectively, Wilcoxon signed rank test, Z=.54, p=.59, two-tailed test).

Most of the submergent time was spent in an underwater cruise posture (CCD), moving or still (M=.28). The snakes substrate crawled some of the time (M=.05 of total search time). The remainder of the underwater time (approximately .06) was spent lying still resting or stalking on the substrate in open water and in cover areas. Attacks often occurred during this time as well.

As indicated by the habitat analysis, most of the searching time was spent in the crevices, deep open water (OWD), wood, vegetation, and shallow open water (OWS) in that order. Searching was often done by remaining still in an emergent immobile cruise (CCU) posture and lunging at fish which approached. Sometimes this ambush strategy involved wrapping part of the body in the wood or vegetation,

but this was not common. Lying stretched out on the substrate worked well, and was the more common position. (Snakes ambushing from the crevices were usually enveloped by the rocks, however.) Open mouth attacking accompanied by locomotion occurred mostly in the deep water where there was more room. Fish also fled to this area when the snakes became active, so prey density tended to be higher here.

3. ORIENTATION AND ATTACKS

Orientation

Relationship to the surface. Orientation The water snakes oriented to prey from above, below or at the surface. Orientation toward underwater prey 15-30 cm away was was noted. The snakes also sometimes stalked prey by moving slowly toward them, usually, but not necessarily, underwater. The snakes also often waited until the fish approached them. Orientation, then, was often obvious.

Problems in determining the occurrence of orientation. Nevertheless, because the snakes often maintained an immobile cruise posture below, at, or above the surface, and unreliably reacted to fish which swam by, it was not always clear whether this position at a given moment was a resting, foraging, or sentinel posture. Based on what followed this posture, it functioned as all of these. But determining the motivation of any given instance seems risky as several snakes spent all or most of the trial in such a posture in the crevices, disappearing briefly only to re-emerge from the

same or a different crevice, and never striking at passing fish while visible. When collected at the end of the trial, however, these snakes were found to have food in their guts. They thus had eaten while moving around out of sight in the crevices. Consequently, while I frequently was able to predict the onset of attacks, I often could not even accurately judge that an animal was motivated to feed. Therefore, no attempt was made to analyze orientation behavior statistically.

Attacks

Relationship to the surface and frequency. Attacks were categorized by whether they were made from out of the water on the edge or shore, from at or above water into the water, or from below water, and whether they were directed at dead or live fish. The posture from which they were made was taken into consideration also for the underwater attacks.

The water snakes attacked frequently, mostly underwater. In all, 370 attacks by 21 snakes were recorded. While the water snakes tended to attack frequently, non-capture attacks were recorded for only 14/21 snakes. Some unseen attacks in the crevices and vegetation almost certainly occurred. Of the 370 attacks, 311 (84%) were underwater attacks, 15 (4%) were attacks from or at the edge and shore, and the remainder (12%) were aerial attacks: 21 were made at the surface, and the remaining 23 were from above the surface. Most of the attacks (341/370) were at live fish. As noted previously, the water snakes ignored many of the dead fish encountered in the water and at the shore. Attacks were recorded in about 3% (based on individual medians) of the intervals.

Attack rates did not vary systematically by sex, SVL, or even by individual (pooled data 63 trials, Kruskal-Wallis ANOVAs all had $p > .05$). While some snakes utilized more attack types than did others, all snakes which captured more than 4 fish during the trials used AUW attacks to capture the majority of their prey. The attack types used by each snake are illustrated in Fig. III-3.

Attacks at dead fish. Twenty-nine dead fish were attacked: 10 at the edge, 2 on the shore, and the remainder in the water. Since only 15 attacks were made at the edge-shore area, 80% of the fish attacked in this area were dead. Relatively few dead sunken fish (DUW) were attacked; 8 were attacked from underwater, and only 1 was attacked from above the water. An additional 8 floating dead fish (DF) were attacked. DF attacks consisted of tongue flicking the fish at the surface, and so were part of the surface attacks. Most of the water snakes (80%) either attacked or captured at least one dead fish, and only one dead fish underwater (DUW) was not successfully captured after attacked. Nevertheless, the water snakes attacked far fewer dead fish than live fish, a significantly different rate of attack (.92 v. .08, $p < .001$). The water snakes, then, readily ate dead fish, but reacted more readily to live fish, not taking many of the dead fish encountered in the water.

Aerial attacks. The aerial attacks were made at fish very near the surface, usually from the emergent cruise posture (CCU). The water snakes did not sit at the edge or crane from the edge and attack fish: only about 4% of all attacks were at the edge. Instead, the snakes usually approached from the water or cover areas to discover fish at the edge. Live fish at the edge were hampered in their escape and were functionally trapped.

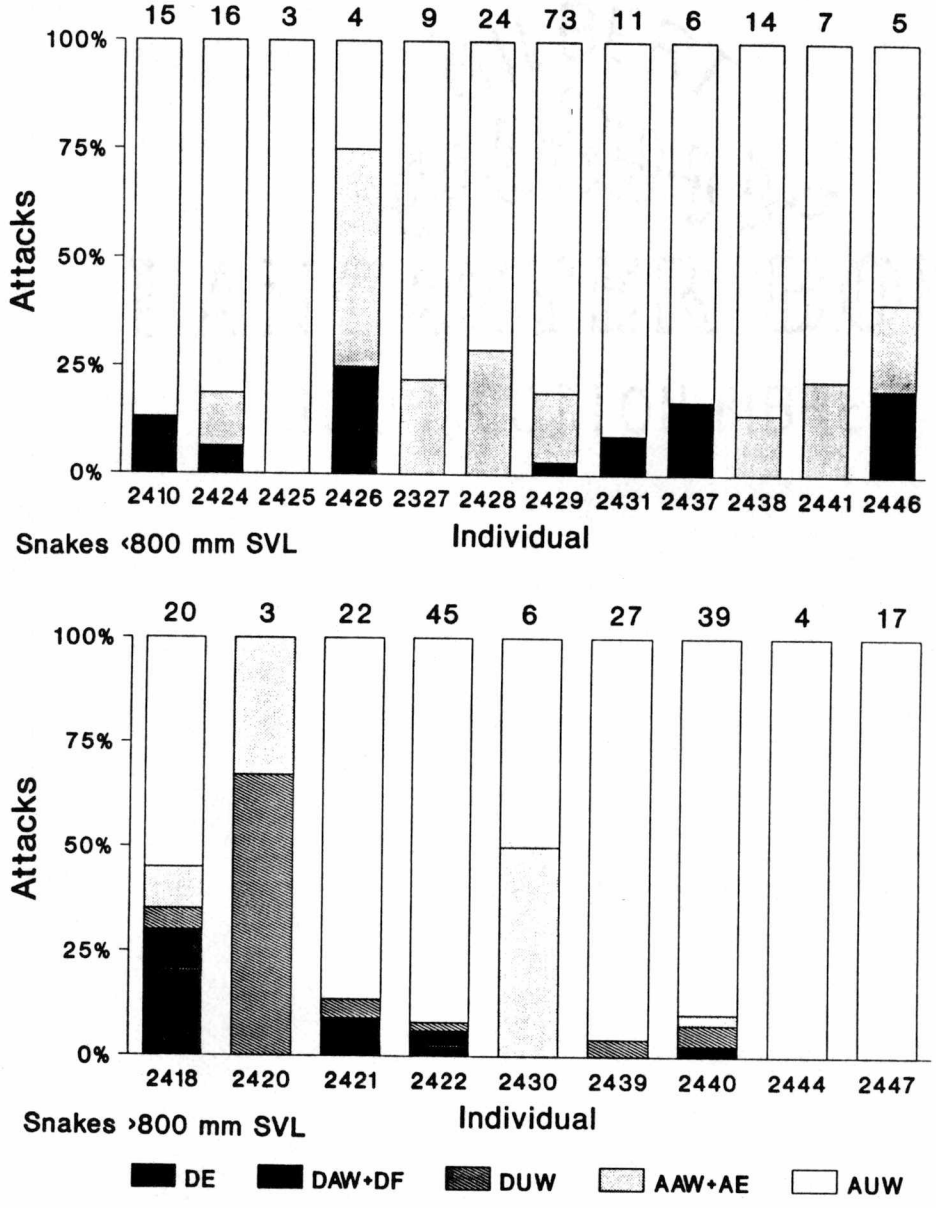


Figure III-3. The types of attacks made by individual *Nerodia rhombifera* in the large test pool. Open-mouthed (OM) attacks form a subset of the underwater attacks at live fish (AUW) attacks, and are not shown separately here. Other attack types are as follows: DE = dead fish at the edge; DAW = sunken dead fish attacked from above the surface; DF = dead fish floating on the surface; DUW = sunken dead fish attacked from below the surface; AAW = live fish attacked from above the surface; AE = live fish attacked at the edge; AUW = live fish attacked from underwater.

As mentioned above, the snake's head was often at the surface in such attacks (CCS), and the snake waited for the fish to come quite near before striking. The snake attacked laterally and forward at about similar rates. Most aerial attacks were ambush attacks, involving little expenditure of energy.

Underwater attacks. The underwater attacks were qualitatively as well as quantitively more important than the aerial attacks. While diving accounted for virtually none of the search time, 11% of the attacks occurred from dives, slightly more from mid-water dives than from anterior dives. As detailed earlier, underwater attacks often followed, or occurred during, movements that could be characterized as stalking. Some of these attacks are included in the the underwater attacks were made from a CCD posture, either moving or still, accounting for 41% of all attacks. Attacking while substrate crawling was also frequent, accounting for 25% of all attacks. Substrate crawling often appeared to be a stalking maneuver. About 12% of all attacks occurred while the snake was lying still on the bottom, or in an undetermined posture in a cover area. As with aerial attacks, underwater attacks were directed forward or laterally at similar rates. Forward and lateral attacks were in the 2-4 cm distance range. Some attacks were also directed overhead. These were made mostly by the larger snakes (>800 mm SVL) and were lateral upward sweeps of the head and neck. Some of these attacks took the observer by surprise as the snake did not appear to be attending to fish overhead. Many of the underwater attacks, then, were ambush attacks of slow "cruise" foraging, involving little energy expenditure. Attacks involving open-mouthed lateral sweeps would be characterized

as "trawling", while the closed mouthed forward thrusts would be characterized as "spear fishing".

Only a little over 1% of the attacks were categorized as pure open-mouthed OM) searching. These were really bouts of attacks delivered while moving in a manner that could not be categorized, but began from the CCD posture. Such attacks were quite intense, even frenzied. Many bouts of OM attacking also occurred during substrate crawling and diving. These bouts of open-mouthed attacking were intense also, although perhaps less frenzied in appearance than those categorized as pure open-mouthed searching because it was possible for the observer to categorize the mode of locomotion. In all, 49% of the attacks were categorized as open-mouthed because 1) the mouth was kept open, and 2) the head was swept around in an arc. Nevertheless, some of these attacks also dissolved into a frenzy so that there was a gradation from the OM attacks to the pure OM searching.

Open-mouthed searching did not seem to be a highly stereotyped behavior, but rather a frenetic bout of lateral attacking accompanied by circling behavior. While it sometimes started from a mid-water dive, it also started from substrate crawling, anterior diving, and the underwater cruise posture (CCD). In the pool it never did evolve into a pattern of regular movements which resembled the "figure-eight open-mouthed circling" reported in the literature (Kofron and Dixon, 1980; Mushinsky and Hebrard, 1977a; Stoner, 1941; Trapido, 1943). The behavior did not appear to entrap groups of prey or to or concentrate prey (Dixon and Kofron, 1980; Stoner, 1941; Trapido, 1943) although fish were often captured along the snake's body. The snake's mouth did not suggest a shovel (Mushinsky and Hebrard, 1977a), but, rather, an exquisitely sensitive trap.

Open-mouthed attacks always suggested a high level of motivation, even frustration (see Drummond, 1980). First of all, they were often of long duration. While these attacks did not last an entire interval uninterupted, the snakes attacked in such a manner for up to 6 consecutive intervals, stopping only long enough to close the mouth and change direction. Secondly, these attacks were not directed at particular fish but at groups of fish. Thirdly, OM attack rates were significantly and positively correlated with the rate of other attacks (Spearman $r=.474$, $p=.0002$). Finally, these predatory sweeps through the water sometimes occurred when no fish were even nearby, and were more frequent after a series of single attacks. These attacks often alternated with directed closed-mouth attacks, occasionally in a regular patterned manner. The OM attacks were sometimes, but not necessarily, often quite active, and probably energetically expensive. Overall, Om attacks were recorded in about 1% of the intervals (based on individual medians).

Unlike the rate of other attacks, the OM attack rate varied significantly by individual ($H=38.92$, $p<.02$). Interestingly, two of the individuals with very high OM attack rates were the gravid females. Among the other individuals with high scores were two of the males; the remaining three individuals with high scores were large females. Nevertheless, sex and SVL were not significant factors (sex $N=63$ trials, $H=1.03$, $p=.60$; SVL $N=63$ trials $H=17.85$, $p=.16$).

4. CAPTURING AND MANIPULATING FISH

Capturing Fish

Live v. dead fish. All of the water snakes who foraged captured fish. There were a total of 123 captures made by the 21 snakes. Most (82%) of the captured fish were alive. Since there were a total of 370 attacks, the success rate as measured by the the attack to capture ratio is only 33%. The more important thing to note here, however, is the strong tendency to capture live fish preferentially to dead fish. As noted above, the water snakes more readily attacked live fish. Most interestingly, live fish were lost at a lower rate than dead fish, as we shall see below.

Additionally, since most of the fish were alive, capture time was generally 0 intervals. That is, capture did not involve any pre-capture probing. Dead fish were also captured with little preliminary probing ($M=0$), even dead fish on the edge and shore were rarely tongue-flicked for an interval before being grasped. The water snakes seemed to recognize the dead fish as prey immediately or not at all. Almost all of the dead fish taken were Size 2 and 3 fish found on the shore, edge, and floating. Some of the dead fish taken underwater were captured during undirected Om attacks.

Unsuccessful ingestions. Live fish, of course, can escape, and some did, all but one within the first time interval after capture. Total prey loss was only 7.3%, 2 dead and 7 live. While more live than dead fish were lost, a greater proportion of the captured dead fish were lost ($G=8.02$, 1 d.f., $p<.005$, with Yates' correction). Thus,

the water snakes were significantly more likely to attack and capture live prey successfully than dead prey.

The primary cause of prey loss, then, would seem to be escape. Most prey, live or dead, were lost within 30 sec, so that not much time or energy was expended on lost prey. The water snakes generally attacked almost immediately after losing prey, and it was not uncommon to attack and/or capture more than one prey item in an interval. The prey loss rate would be much higher if prey lost after contact were included as many prey were often seen to pass through the jaws of the water snakes.

The water snakes lost two dead fish after capturing them in deep water. Apparently, even these aquatic specialists had problems with deep water captures: 25% of the dead fish captured underwater were lost, but none of the dead fish caught at the surface or above were lost, a difference that is significant (.25 v. .0, $p<.05$). As with the cottonmouths, the dead fish simply slipped out of the snake's mouth underwater. Live fish, however, were lost at about the same rate whether captured underwater or above or out of water (.063 v. .095, $p>.05$). Thus, while escape may have been the reason for the loss of live prey, the rate of prey loss was actually higher for dead than live prey, so that it would appear that inanimate (dead) prey was a more important reason for prey loss. The water snakes, then, again exhibited evidence of being adapted for the aquatic capture of live prey.

Prey escape was still important for the water snakes. Prey size and the direction grasped merit inspection as factors in prey loss. Relative prey size was important ($N=123$ captures, $H=6.7$, $p<.04$). No Size 1 prey were lost, and the differences in loss rate between Size 2, (5/49) and Size 3 (4/26) were not significant (Size 1 v. Size 2 and 3 $H=6.04$, $p=.01$; Size 2 v. Size 3 $H=.43$, $p>.05$). Thus, prey loss

was a problem with Size 2 and 3 fish only, but the rate of loss did not significantly increase from Size 2 to Size 3 prey.

The direction prey was grasped also was a significant factor ($N = 123$ captures $H = 11.53$, $p < .005$). Grabbing by the tail resulted in greater prey loss (4/16) than grabbing by the head (3/98) or mid-body (0/16), but grabbing by the mid-body did not result in greater prey loss than grabbing by the head (head v. mid-body $H = .56$, $p = .45$; head v. mid-body and tail $H = 11.2$, $p < .001$; mid-body v. tail $H = 4.17$, $p < .05$). When the fish were grabbed by the tail the fish would attempt to swim away, the action of the caudal fin caused its capter's head to be shaken rather violently. The snake either released the fish after the rough treatment, or the caudal fin may simply have ripped away from the snake's teeth. Either way, the fish escaped. Fish grabbed by the mid-body often thrashed enough to shake the snake about, but the shaking was less extreme than at the caudal end of the fish, so that the snake was more likely to retain hold of the fish.

Since the lost prey were held only 1 interval, prey would not seem to have been lost after unusually long manipulation times. The water snakes, however, had very short handling times, the longest, and an outlier at that, was 10 intervals; most handling times were 0-2 intervals. Handling times for lost prey were, in fact, longer (range = 1-2, $M = 1$) than for successfully ingested fish (range = 0-10, $M = 0$) (successful Size 2 and 3 ingestions $N = 66$ v. lost fish $N = 9$ manipulation times $H = 10.02$, $p < .002$). Since most of the lost prey escaped after vigorous resistance and were not simply dropped, it is difficult to interpret handling time as a cue for abandonment in the water snakes as in the cottonmouths. Nevertheless, the interpretation may still have some merit as it was unclear whether the fish were released or pulled free.

Where fish were captured. In line with their reputation as aquatic specialists, the water snakes captured most of their prey (88%) in water. The remainder were captured in the edge areas (10%) and on shore (2%). It was the dead fish that were captured on the edge and shore (12/22=54%) of the dead fish captured), while very few live fish were captured at the edge (3/123=2%) of the live fish), and none were captured on the shore. Just over half of the fish (52%) were captured in the open water areas, most (45.5% of the total captures) in the OWD. Significantly more fish were captured in the OWD than in any other area (.455 v. .244, $p<.01$). The next most important site for prey capture was in the crevices, where 24% of the fish were captured. Similar proportions of prey were caught in the water covered portions of the wood and vegetation.

Habitat use during capture naturally followed habitat use during attack in broad terms, but were attacks more successful in some habitats than in others? To answer this question, the proportion of non-capture attacks made in each habitat area was compared to the proportion of successful capture attacks using the methods of Fleiss (1979). Since I considered a successful attack to be one that resulted in ingestion after capture, the successful attacks here are those which resulted in ingestion. The comparisons indicated no statistically significant differences ($p>.05$) between the proportions. Thus, the water snakes were about equally successful in each habitat area, although they attacked at different rates in the various habitat areas.

The snakes did not attack from the various habitat areas in accordance with the success rate of the attacks in the habitat areas. If the snakes were foraging so that the attack to capture ratio would be as low as possible, then the proportion of fish captured in an area should be correlated with the success rate in that area. Thus,

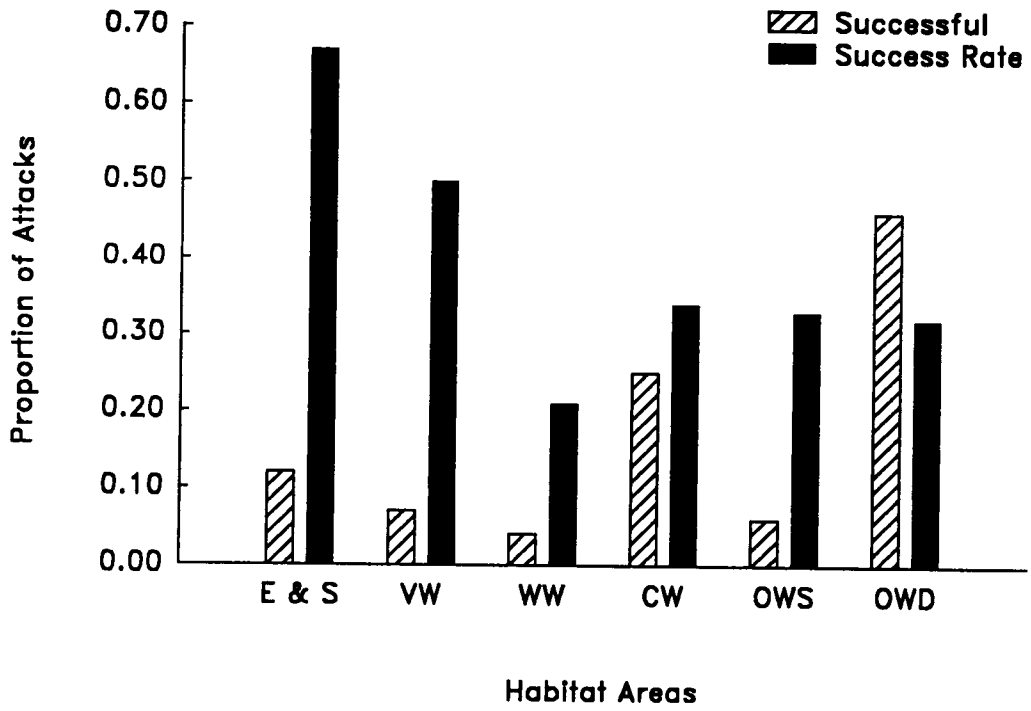


Figure III-4. The proportion of successful attacks (captures) and the success rate for attacks in each habitat area for *Nerodia rhombifera*. The success rate is the ratio of the successful attacks to the total number of attacks. See text above for definition of successful attacks. E & S = edge and shore combined; VW = water covered portion of the vegetation; WW = water covered portion of the wood; CW = water covered portion of the crevices; OWS = shallow open water; OWD = deep open water.

when the proportion of the fish captured in an area is similar to, or greater than, the success rate for attacks in that area, then too many attacks were made in that area, and when the proportion of fish captured in an area is very low in comparison to the success rate, then too few attacks were made in that area. As can be seen in Fig. III-4 below, the snakes under-utilized the edge and shore, and over-utilized the crevices and OWD.

How fish were captured. A similar type of analysis can be applied to foraging behaviors. Since open-mouthed attacks were made from a variety of postures, and because there was something of a gradation from a lateral attack to open-mouth attacking, I limited the analysis to attacks made from several postures without regard to the type of attack. I also limited my analysis to attacks made in the water as these are characteristic of this species. The "postures" were substrate crawling, diving, and cruise posture below, at, and above the surface. The proportions of the successful and unsuccessful captures for each attack posture were similar ($p > .05$) for most of the behaviors. However, the proportion of unsuccessful attacks from the CCD posture were significantly lower than the successful attacks, indicating that this attack, the most frequently used one, was relatively ineffective, at least in the pool. The proportion of successful CCS attacks is significantly higher than the unsuccessful attacks, indicating that this attack posture is relatively effective. Substrate crawling produced the highest proportion of successful attacks overall, although the proportion of successful attacks is not statistically different from the unsuccessful attacks. The difference, however, is in the correct direction and approaches significance ($p < .10$). This tactic, then, is relatively effective.

Fig. III-5 below illustrates the success rate and the proportion of all fish captured from that posture. As can be seen, the success of the postures was not correlated with their use. The two attack postures that keep the head at or above the surface, CCS and CCA, were the two most effective postures, but were two of the three least used behavior. CCD, which keeps the head below the surface, was over-utilized.

Thus, the postures and habitat use that result in the most exposure of the animal above the surface are the least used, even though they are the most effective, and the postures which keep the animal below the surface are over-utilized relative to their success rate. This suggests that these snakes may have avoided being above the surface. Even when below the surface, they are not using the more effective behavior, substrate crawling. The less effective CCD posture certainly allows the snake to scan for underwater predators as well as prey. Although this study cannot resolve the issue of predator avoidance since predators were not present during the study, it is noteworthy that the snakes' behavior in the absence of predators was more optimal for predator avoidance than for energy intake.

Factors affecting capture time. As mentioned earlier, capture time was very brief, so brief that none of the possible factors, i.e., subject, prey size, direction grasped, item, or even sex, were signifcant. Additionally, capture times were very similar for dead and live fish, $M=0$, with very few different values.

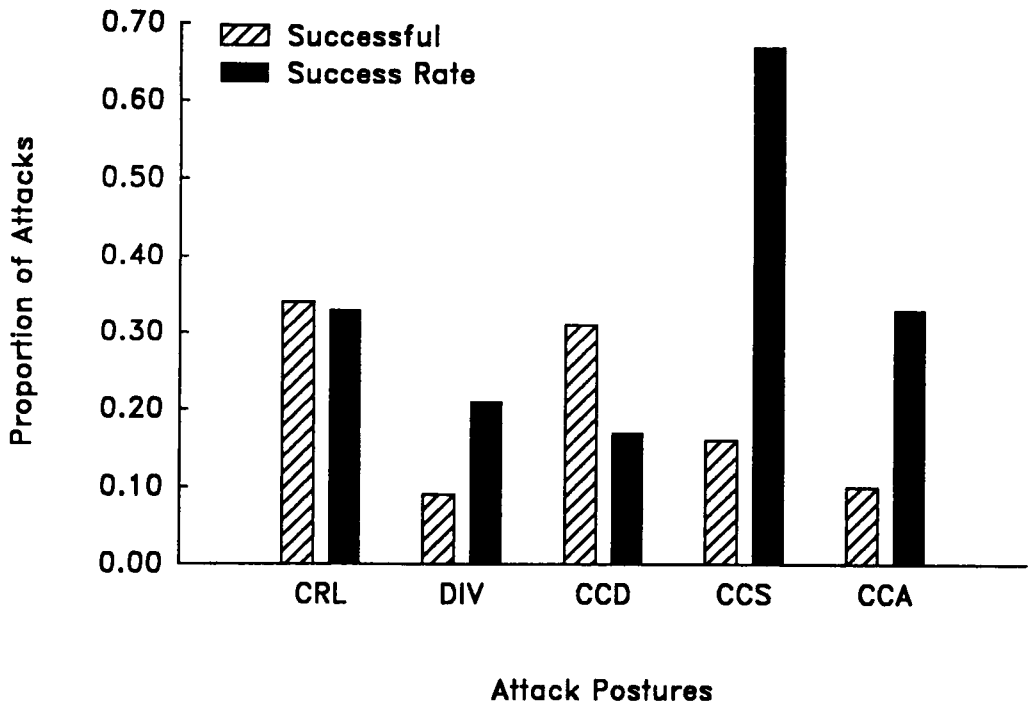


Figure III-5. The proportion of successful attacks (captures) and the success rate for attacks made from various attack postures by *Nerodia rhombifera*. The success rate is the ratio of the successful attacks to the total number of attacks. See text for the definition of successful attacks. CRL=substrate crawling; DIV=anterior or mid-water diving; CCD=submergent cruise posture; CCS=cruise posture with the head at the surface; CCA=cruise posture with the head elevated above the surface. Postures are described in detail in Chapter II.

Manipulating Fish

Manipulating live fish. Again, the factors affecting manipulation are most easily examined in terms of manipulation time. The analysis of prey handling will focus on the manipulation of live fish, since they were the typical prey type for this species. Overall, individual differences were not significant (123 captures, 20 subjects $H = 18.07$, $p = .58$); nevertheless, analysis will be based on individual medians.

Factors affecting manipulation time. The factors affecting manipulation are examined in terms of manipulation time. Although individual differences were not significant for the water snakes ($N = 15$ snakes, 114 ingestions, $H = 18.07$, $p = .58$), median values for each subject are used in all of the following analyses, unless otherwise stated. Prey manipulation was usually quick; in general, ingestion began immediately after capture (70% of the ingestions), so that no manipulation time was required ($M = 0$, $N = 123$ captures, pooled data), although one subject did spend 10 intervals manipulating a dead Size 3 fish. Since dead fish were lost at a higher rate than were live fish, the following analyses are done on live and dead fish separately.

As expected, the size of the prey did affect manipulation time: the large Size 3 live prey required more manipulation time than did the smaller Size 1 and 2 fish which were not significantly different ($N = 9$-16 snakes, overall $H = 6.43$, $p = .04$; Size 1 [$M = 0$, $\tilde{x} = .02$] and Size 2 [$M = 0$, $x = .5$] v. Size 3 [$M = 0$, $x = 2.7$ $H = 5.51$, $p < .02$; Size 1 v. 2 $H = 3.01$, $p = .0$). Dead prey required manipulation times that were very similar to those of live prey: Size 1 ($N = 1$) manipulation time $M = 0$, $\bar{x} = 0$; Size 2 ($N = 8$) $M = 0$, $\tilde{x} = 0$; Size 3 ($N = 8$) $M = 0$, $\tilde{x} = 2.0$).

As with the loss of prey, the direction in which prey were grasped also significantly affected manipulation time. Unlike the loss of prey, however, manipulation times were similar for fish grasped by the head (M=0) and mid-body (M=1), and were significantly shorter than manipulation times for fish grasped by the tail (M=2) (N=7-17, overall $H=9.71$, $p<.008$; head and mid-body v. tail grasp $H=9.55$, $p<.003$; head v. mid-body grasp $H<1.0$; $p>.05$). Thus, grasping a fish by the mid-body did not necessarily slow down the water snakes.

Males and females did not differ significantly in handling times as indicated by insignificant Spearman rank correlations between sex and handling time ($r=-.16$, $p=.12$), although the correlation suggests that females handled prey somewhat faster than did males.

Where fish were handled. The water snakes did not often appear to struggle with the prey, and pushing the prey against the body or the substrate was uncommom. Manipulation took place in and under water regularly. The ease of manipulation was evidenced in the low rate of location change during manipulation: most prey were manipulated where caught. About the same number of changes were to same depth water areas (5/13) as to shallower 3/13) or deeper (5/12). Some of the changes to same depth areas were into cover areas (4/13). Given the proximity of these areas to the open water areas where the fish were captured, it is difficult to ascribe much importance to this, however.

Methods for dealing with mis-grasped fish. Only one fish grasped by the tail, a live one at that, was dropped and re-grasped. That fish was taken to shore from

deep water first. Another fish, a dead one, was dropped and re-grasped, but was originally grasped by the head. Thus, dropping and re-grasping was not a standard tactic in prey manipulation for the water snakes, even with dead prey.

Fish grasped by the mid-body or tail were usually re-oriented by conversion (13/15 of prey re-orientations) by means of jaw manipulations. Mis-grasped Size 2 and 3 fish were far more likely to be converted before ingestion, than Size 1 fish, only 1 of which was converted, accounting for only 8% of the conversions. Interestingly, all mis-grasped fish were "correctly" converted to head first grasps. Conversion did require extra manipulation time: manipulation times were significantly higher for converted than unconverted Size 2 and 3 prey (pooled data $H=22.79$, $p<.0001$; conversion manipulation time, $N=15$, $M=3$, non-conversion manipulation time $N=40$, $M=0$).

Nevertheless, conversion was a relatively easy task for the water snakes as evidenced by the lack of struggle involved. As one evidence of the lack of struggle, conversions did not occur after a change of location, but were accomplished where the fish were captured in 82% of the instances. Change of location during conversion did not differ, then, from overall change of location (.18 v. .11, $p>05$). Additionally, conversion was also accomplished underwater quite readily as 73% of the conversions occurred underwater.

Item number and meal size. Meal size for the 21 water snakes which ingested prey was rather small, varying from 0-7 items, $M=2$. There was not a significant relationship between meal size and sex ($H=1.60$, $p=.21$), nor between item and SVL ($H=18.77$, $p<.07$). While snakes of different SVLs ate meals that almost differed

significantly in size, inspection of the ranks shows no pattern from smaller to larger snakes, suggesting that individual differences had more to do with meal size than did SVL.

Item number might be expected to be correlated with some of the same factors as it was for the cottonmouths. Prey size, direction in which grasped, and capture time were not significantly correlated with item number in the water snakes, however, although they exhibited a weak tendency to to take larger fish earlier in a meal (pooled data, N=48 meals, Spearman rank correlation r=-.09, p=.30).

Manipulation time was significantly correlated with item number. That is, prey taken earlier in a meal required more manipulation time than prey taken later (pooled data, N=48 meals, Spearman rank correlation r=-.2327, p=.01), suggesting a practice effect.

5. INGESTION OF FISH

Where and How Fish Were Ingested

Description of ingestion. The swallowing of live and dead prey will be analyzed together as they were qualitatively and quantitatively similar. The water snakes did not obviously struggle with their prey during ingestion. No prey were lost once ingestion had begun. The head was usually kept low, parallel to the substrate throughout the entire process. A few very large prey items were pushed against objects during ingestion, however. The water snakes did not exhibit exaggerated sinuous movements of the neck although neck movements were important in

swallowing prey. Such movements appeared to begin late in the ingestion process after most of the prey item had entered the gullet.

Where fish were ingested. Since little relocation occurred during prey handling, most prey (89.5%) were ingested in the area where captured. Habitat use was consequently statistically the same for prey ingestion as for prey capture; landward areas were used infrequently and had to be combined for statistical analysis in order to avoid small cell values (N = 123 captures and N = 114 ingestions, habitat areas: Shore + Land + Edge, Cover Edge [VE + WE + CE], Cover Water [VW + WW + CW], OWS, OWD $G = .46$, $df = 4$, $p > .9$). Almost 87% of the fish were ingested in the water covered areas, with 48% ingested in the open water areas, mostly in the deep open water (42%). No fish were taken to the beach for ingestion, and only about 3% were ingested on the shore.

Not only did the water snakes preferentially ingest in the water, they preferentially ingested under the water. The location of the snake's head in relation to the surface of the water, either above or below, was noted for 104 of the 114 successful ingesions. Of these ingestions, 74%, took place under water. Since many of the ingestions for which there is missing information took place in water covered areas, the rate of underwater ingestions is at least as high for those ingestions also.

There was a negative correlation (albeit of borderline significance) between ingesting underwater and prey size, which means (because of the way data were coded) that large prey were more likely to be ingested above the water (Spearman $r = -.1887$, $p = .057$). The direction of ingestion was not significantly correlated with the location of the ingestion relative to the surface (Spearman $r = -.0926$, $p = .35$), and neither was the sex of the snake (Spearman $r = .0652$, $p = .51$).

Factors Affecting Ingestion Time.

Individual differences and relative prey size. Individual differences were not a significant factor in ingestion time (N= 21 snakes H=25.31, p=.19). Nevertheless, individual medians will be used in most of the following analysis.

The relative size of the prey was an important factor in ingestion time (N=12-17 snakes overall H=6.10, p<.05). Ingestion times were significantly longer for Size 2 than Size 1 prey (H=4.50, p<.04) but Size 2 and 3 did not require significantly different ingestion times (H=.78, p=.38). Size 2 (M=1.5) and 3 (M=2) prey, then, formed a homogeneous group that was significantly different from Size 1 (M=1)(H=5.9, p<.02). This contrasts with manipulation time where Size 1 and 2 prey formed a homogeneous group that differed from Size 3 prey.

The orientation of fish. The direction prey were ingested was not a significant factor in ingestion times (N=3-21 snakes H=.14, p=.93). Somewhat surprisingly, head first ingestions had a higher rank score than did mid-body ingestions; tail first ingestions had the highest rank score. This, however, may be because all Size 3 and 37/40 Size 2 fish were ingested head first, whereas Size 1 fish were also ingested mid-body and tail first. Therefore, 55/89 (62%) of the documented head first ingestions were of the larger Size 2 and 3 fish which require longer ingestion times; size effects are thus confounded with the direction of ingestion. Nevertheless, median ingestion times for all groups were similar: M=1.5 for head and mid-body first ingestions, and M=2 for tail first ingestions. The most extreme ingestion times were

one instance each of 16, 6, 5, and 4 intervals for Size 3 fish, and 7 intervals for a Size 2 fish. All other documented ingestion times (N=94) were 3 intervals or less. Figure III-6 graphically summarizes the direction of ingestion in relation to prey size.

The most interesting fact about the direction of ingestion was the low number of non-head first ingestions. All snakes ingested some prey head first, and 89/99 of documented ingestion were head first. Only 4 snakes ingested a total of 7 fish mid-body first; and only 3 snakes ingested a total of 3 fish tail first. As noted earlier, all of the conversions resulted in head first ingestions. The water snakes were quite efficient at attaining head first ingestions.

Sex and item number. Sex and prey item number were consistently found not to be significantly related to any aspect of ingestion, including time, direction of ingestion, and relation to the surface during ingestion.

Total handling time. Since most studies of prey handling look at total handling time rather than breaking prey handling down into three parts as was done here, it would be well to so analyze total prey handling time here in order to make comparisons later. Since a fair amount of discussion of these factors has already been undertaken and the results are predictable, the results for total handling time are presented in tabular form in Table III-3 below.

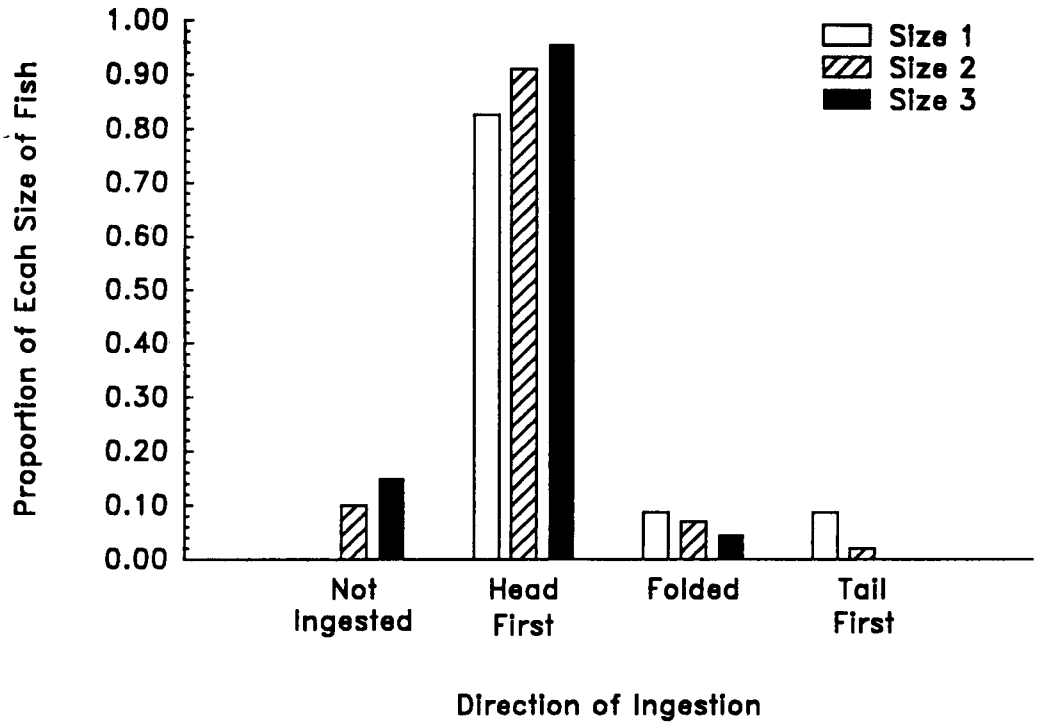


Figure III-6. Prey loss and the direction of ingestion for each prey size in *Nerodia rhombifera*. Prey size was relative to the head size of the snake which captured or ingested it. See Chapter II for details on the determination of prey size.

TABLE III-3

ANALYSIS OF TOTAL HANDLING TIME[a] FOR *NERODIA R. RHOMBIFERA* (N=21) IN THE LARGE TEST POOL

Factor	No. of Ingestions (No. of Snakes)	Median	Significant Comparisons[b]
Prey Size[c***d]			
1	41(12)	1	1 < 2*
2	40(17)	2	2 < 3***
3	13(18)	5	
Direction of Ingestion[e]			
H	89(21)	2	
M	7(4)	1.5	
T	3(3)	1.5	
Item*	1-7/trial(21)	2	r=-.20, p=.04*[f]

[a]Handling time is in terms of 30 sec intervals. Because behaviors were instaneously sampled at the beginning of an interval, handling time intervals represent times between interval/2 - .5 min, and interval/2 min.

[b]Kruskal-Wallis non-parametric ANOVAs were computed. If the overall significance level was less than .15, it was considered significant, and comparisons between the levels were then made. All comparisons were considered significant at $p<.05$.

[c]Prey size is relative to snake size. Size 1 are the smallest fish, and Size 3 are the largest fish. See Chapter II for details.

[d]*** = $p<001$; * = $p<01$; * = $p<.05$.

[e]H = head first; M = mid-body first or folded; T = tail first.

[f]Spearman rank correlation was computed.

6. SUMMARY OF AQUATIC PREDATION IN THE DIAMOND BACK WATER SNAKE

The water snakes in the large, naturalistic test pool preyed mostly, and most successfully, on live fish. Of 123 captures made by 21 individuals, 82% were of live fish. The water snakes attacked frequently; the ratio of successful to total attacks was about .335 (based on individual medians). There were no sex or size differences in capture success and prey size captured.

The water snakes achieved negative buoyancy very readily. Possibly as a consequence, they swam and dived very little, generally locomoting across the pool underwater by substrate crawling. The water snakes spent most of the time in water covered areas, spending similar amounts of time above and below the surface.

The crevices were used significantly more than any other habitat area, but the preference was not really pronounced. The beach and shore were avoided, the OWS area was used significantly less than expected, and the other habitat areas were used about as expected. The water snakes thus used the water covered areas of the pool rather uniformly. The males used the crevices significantly more than did the females, and the females used the OWS more than did the males. Both sexes utilized the OWD at statistically similar rates.

The majority of fish were captured in water covered areas, especially the OWD. The water snakes were very adept at attacking, capturing, handling, and ingesting live prey in water, and underwater, even in deep water. Some dead fish were lost or unsuccessfully captured in deep water, however.

Overall, the snakes were stationary significantly more than they were in motion. Fish were attacked by both mobile and motionless snakes. Some stalking of

prey was seen. The OM searching ("trawling") for which the genus is most noted was not a ritualized behavior, and did not necessarily involve strenuous activity. Some underwater forward attacks ("spear fishing") were made, but individual fish were not pursued through the water.

The water snakes were about equally successful capturing fish in all habitat areas, but not from all postures. Given the success rates in the various environments and from the different postures, the water snakes could have improved their foraging success by foraging more from the the edge-shore area and the vegetation. They also should have attacked more from the CCS and CCA postures, and attacked less from the CCD posture.

Relative prey size significantly affected prey loss, manipulation and ingestion times, and the direction prey were ingested. The direction prey were grasped significantly affected prey loss, manipulation times, and prey loss. There was an interaction between prey size and direction of ingestion.

All of the Size 3 fish, most of the Size 2 fish, but only one Size 1 fish, were ingested head first, often after converting prey to a head first position. No attempted conversions resulted in mid-body or tail first ingestions.

Manipulation time was significantly correlated with item number, although item was not correlated with any other aspect of foraging studied. No sex differences in predatory behavior other than the use of crevices and OWS were found.

Prey were manipulated and ingested where they were caught, so that habitat use for capture and ingestion was the same. Underwater ingestion was significantly more common than above water; large prey were less likely to be ingested below water than were smaller prey, however.

CHAPTER IV

FORAGING FOR FISH BY *AGKISTRODON PISCIVORUS* IN THE POOL

1. INTRODUCTION

The goals of the following analysis of cottonmouth piscivory foraging are the same as for that of *Nerodia rhombifera*. However, the analysis was guided by the premise that the cottonmouth, the only member of the crotalines to forage on fish, is a generalist predator that also forages terrestrially. Consequently, while this analysis basically parallels that done for *N. rhombifera*, the differences in foraging between the two species led to focusing on different aspects of the foraging process in *A. piscivorus*. In the interests of brevity, the common name "cottonmouth" will be used to refer to *A. piscivorus* in this chapter.

2. SEARCHING FOR PREY

Qualitative Analysis.

Beginning the trial and locomotion. The 15 cottonmouths tended to explore the entire pool area before capturing prey. While the animals freely swam across the deep water from the vegetation to the rocks and vice versa, and occasionally "cruised" in the deeper water, most of the time was spent "margin-wandering" along the edge and in the very shallow water or the shore near the edge. Little diving, or any

submersion of the head, was seen. The vegetation and wood areas, especially along the edge and in the very shallow parts were utilized extensively also.

Locomotion was accompanied by almost constant tongue flicking and side-to-side head movements. While in the water, the snakes frequently held their heads high in an exaggerated cruise posture to scan the surface of the water and the beach. The cottonmouths were so buoyant that they could raise the entire head-neck region of the body above the surface while the rest of the body was entirely supported by water, thus cruising while floating. They were also able to cruise from the substrate, however. Submersion was accompanied by the release of large masses of bubbles.

Orienting toward and attacking fish. Cottonmouths are generally regarded as bold because they tend not to flee when approached by man. However, the snakes seemed very wary in the test pool, whipping their head around and holding it high when any significant vibration or motion occurred. This constant vigilance made it impossible to determine whether orientation toward fish involved predatory interest or not. The snakes were also very observant of the activities of any conspecifics in the pool. Feeding conspecifics were never approached closely, however, and no kleptoparasitism occurred. While the cottonmouths often oriented toward fish some distance away from above the surface and even moved towards groups of fish breaking the surface, very few attacks were delivered at such fish. Dead fish were also sighted from across the pool and were subsequently captured, however.

Quantitative Analysis

Habitat use during searching. The methods and terminology used for habitat analysis were explained in Chapter II and are similar to those used in Chapter III. Because the sample of snakes was biased in terms of sex and size, these factors were not statistically analyzed. Habitat utilization is summarized in Table IV-1 and graphically in Fig. IV-1 below.

Most notably, the cottonmouths exhibited a strong preference for the edge area: foraging snakes were at the edge, including the edge of the large rock, in 51% of the observations, significantly more than expected ($M=.51$, $Z=3.44$, $p<.0001$, one-tailed test). The juvenile spent all of its time at the edge, especially favoring the large rock.

The snakes were also on the shore bordering the edge in 8% of the observations, which is not significantly different from the expected ($M=.08$, $Z=1.59$, $p=.11$, two-tailed test). The snakes then, spent most of the time in the edge and shore areas combined, being there in about 60% of the observations. The cottonmouths actually used the water's edge even more than already determined because, for example, a cottonmouth at the edge of the wood would have been scored as being in the wood, not at the edge.

The cottonmouths were not simply avoiding water, however, as use of the beach accounted for almost none of the search time ($M=0$). Five of the 15 snakes included in this analysis spent no time at all on the beach. No snake spent more than 8% of its search time on the beach. Since the beach comprises about 45% of the total habitat area, the cottonmouths used the beach significantly less ($M=.0$, $Z=3.44$,

TABLE IV-1

SUMMARY OF HABITAT USE BY FORAGING *AGKISTRODON PISCIVORUS* (N=15) IN THE LARGE TEST POOL

Habitat Area	Proportion of Observations[a]	Proportion of Pool Habitat	Difference
Beach	.00	.45	-.45**
Shore	.08	.135	-.055
Edge	.51	.02	+.49**
Vegetation	.33	.065	+.265**
Wood	.08	.065	+.015
Crevices	.04	.065	-.015
OWS[b]	.02	.10	-.08**
OWD[b]	.00	.10	-.10**

[a]The proportion of observations is the median value of the median values of the proportions for each subject (N=15) during foraging trials.

[b]OWS= open shallow water; OWD= open deep water.

** $p < .01$, one-tailed probability of the Wilcoxon one sample signed rank tests comparing the proportion of observations to the proportion of the pool habitat for each habitat area.

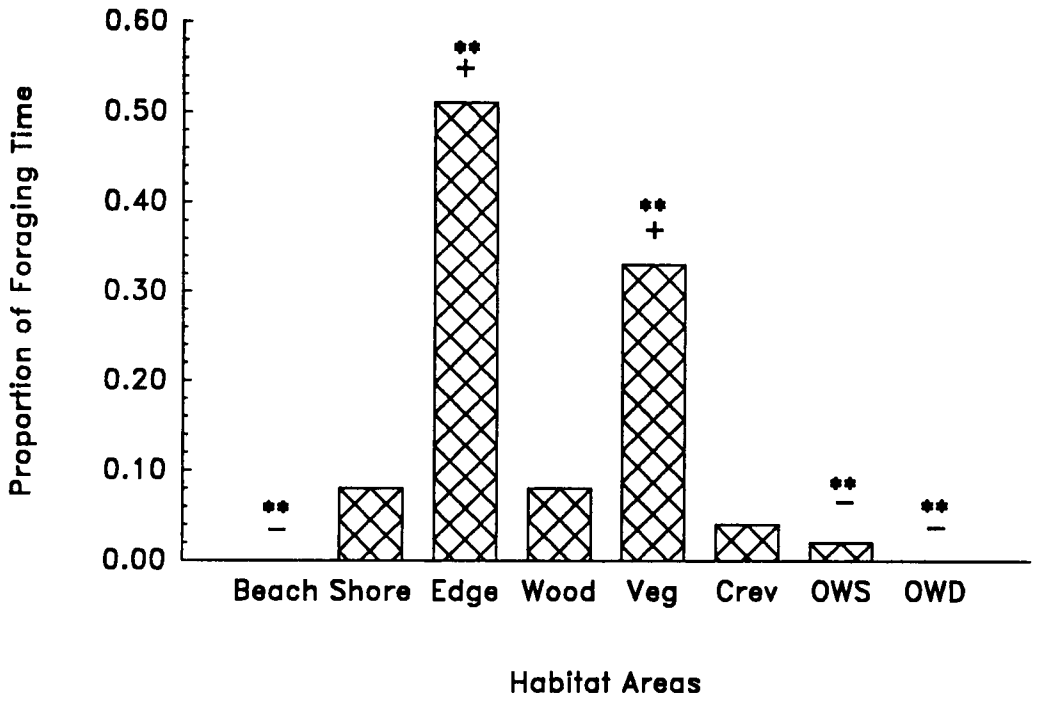


Figure IV-1. The proportion of time that foraging *Agkistrodon piscivorus* spent in the various habitat areas of the large test pool. ** = significant difference ($p < .01$) between the amount of time spent in an area relative to the proportion of the total habitat area comprised by that habitat area; "+" denotes significantly more time spent in an area, and "-" denotes significantly less time spent in an area. Veg = vegetation; Crev = rock crevices; OWS = open shallow water; OWD = open deep water. See Chapter II for details of the pool habitat.

$p < .0001$, one-tailed test) than would be expected. The beach was used extensively for basking and resting by inactive cottonmouths, however.

Open water was also used little, accounting for only about $M = .02$ of the observations. Use of the open water areas was less than expected (Wilcoxon signed rank two sample test: shallow water $M = .02$, $Z = 3.21$, $p < .003$, one-tailed test; deep water $M = 0$, $Z = 3.44$, $p < .0001$, one-tailed test). Most of the cottonmouths, 12 of 15, spent some time in the shallow water, however. One subject (2502) even spent $M = .17$ of the observations there. Only 8 of 15 snakes spent any time in the deep water, and the most time spent there was $M = .07$, observed in 2502 again. Consequently, the cottonmouths spent significantly less time in the deep water than in the shallow, even though the median values for both were low (.0 v.02, $Z = 2.86$. $p < .01$, one-tailed test.

There was differential usage of some of the cover areas (wood, vegetation, and crevices). The vegetation was used the most ($M = .33$). Use of the wood was much lowere ($M = .08$). Use of the crevices was also low ($M = .04$). Since each of these cover areas accounts for about 6.5% of the total habitat area, only use of the vegetation differed from the expected, being used more than expected (vegetation $M = .33$, $Z = 3.15$, $p < .005$, one-tailed test; wood $M = .08$, $Z = 1.25$, $p = .21$, two-tailed test; crevices $M = .04$, $Z = 1.7$, $p = .09$, two-tailed test). Wood and crevices were utilized at similar rates ($M = .04$ v. $M = .02$, $Z = 1.60$, $p = .10$, two-tailed test). The vegetation area was the location where snakes were most likely to end a trial (21 of 54 trials), which probably accounts for the apparent preference exhibited for this area as the snakes moved around in the area before ceasing activity there. There is, unfortunately, no way to distinguish this activity from predatory searching.

Behavior during searching. The cottonmouths were in motion much of the time (M=.58); motion was slow and even. The snakes did not coil or bask during pauses. Locomotion along the edge and in shallow water was primarily by lateral undulation, while locomotion along the shore and on the beach was primarily by rectilinear locomotion. The craning-cruising posture was assumed during most locomotion and pauses. Eye and pit organ placement on the head seem to force the cottonmouth to locomote with the head in a cruise posture. Locomotion proceeds with the head low and parallel to the surface only when the cottonmouth is following a chemical trail, which was seen mostly in the vicinity of a dead fish. Although craning and cruising postures were not differentially analyzed (Drummond [1980] had had difficulty distinguishing between them in his species), true craning over the water was extremely rare in the cottonmouths. Thus, margin-wandering cottonmouths kept most of their body, not just the head, along or near the edge, and were thus in a "cruise" posture when it was inclined over the water or in a "peering" posture when the body was not. Behaviors during searching are summarized below in Table IV-2.

Swimming, which includes floating, accounts for a surprising amount (M=.11) of the search time. This rather high value says more about the cottonmouth's buoyancy than its aquatic abilities. Given that these snakes spent only about 2% of their time in open water areas, it is clear that much of the "swimming" occurred in the water covered areas. Basically, these animals were so buoyant that they did not venture into the water, they ventured onto it.

Not unexpectedly, then, these snakes rarely dived, and only the slow serpentine diving, similar to that of the generalist natricines, was observed. These snakes, in fact, spent little time under water, and often only the head was submerged. Cottonmouth heads were under water in less than 2% of the observations, including

TABLE IV-2

PROPORTION OF FORAGING TIME SPENT BY *AGKISTRODON PISCIVORUS* (N = 15) IN SELECTED BEHAVIORS IN THE LARGE TEST POOL

Behavior	Proportion of Foraging Time[a]
Moving[b]	.58
Swimming	.11
Diving	.02
Crawling[c]	.00
CCD[d]	.01
Attacking	.02
Above water[e]	.35
Below water[e]	.02

[a]Proportion of foraging time is the median of the median values for the proportion of foraging time for each subject (N = 15).

[b]Proportion of foraging time spent moving. The time spent moving was not significantly different from the time spent not moving (Wilcoxon signed rank test, Z = 1.76, p = .08 one-tailed probability, N = 15).

[c]Crawling = crawling prone on the underwater substrate.

[d]CCD = underwater cruise posture: the body is on the underwater substrate with the head and neck are raised up, but the head in still underwater.

[e]Above water = the snake is in a water covered area with the head at or above the surface of the water; below the water = the snake is in a water covered area with the head below the surface of the water. The difference in the proportions for above and below the water was significant (Wilcoxon signed rank test, Z = 3.38, p < .001, two-tailed test).

the time spent attempting to pick up dead fish from under water. In contrast, the cottonmouths spent significantly more time (35%, $Z=3.38$, $p<.002$, one-tailed test) in the water covered areas with their head out of the water. When it did occur, submergence was accomplished in a slow, deliberate manner so that the tip of the snout went under first. The angle formed by the head and the surface of the water was usually close to 90°, often resulting in extreme arching of the neck.

Given the low values for utilization of the open water, it almost goes without saying that searching underwater rarely occurred there, especially in the deep water. Substrate crawling was extremely rare ($M=.003$). The maximum observation time spent substrate crawling by any individual was only 2 intervals in a trial, and only 4 of 15 snakes substrate crawled at all. The extreme buoyancy of the snakes certainly accounts in part for the small amount of time spent underwater, particularly substrate crawling, just as it also accounts for the fairly large amount of time spent swimming. Adult cottonmouths do have the capability of achieving negative buoyancy, however, since the snakes did some substrate crawling and routinely rested motionless in a coil on the bottom underwater.

The use of the habitat by foraging cottonmouths can by summed up simply: these snakes spent most of their time cruising slowly along the edge of the water, avoiding the beach and the open water areas, but not the water covered areas. The cottonmouths spent little time underwater anywhere. Active cottonmouths exhibited a preference for the vegetation over any other cover area, but the significance of this is open to question.

3. ORIENTATION AND ATTACKS

Orientation

Reaction to fish. As noted, cottonmouths oriented toward any disturbance. The snake often approached the source of the disturbance after at least briefly observing it from a distance, motionless. If the disturbance was a fish, the snake might or might not strike at it. Strikes were also sometimes made at inappropriate objects, including themselves. Some strikes seemed to be redirected behavior: one ingestion of a previously ignored dead minnow at the edge occurred seconds after a large sunfish briefly flopped out of the water nearby. Pieces of wood were occasionally bitten and held, but never more than one interval. Interestingly, all of these misdirected strikes were made in the months of April and May.

Problems in determining the occurrence of orientation. The cottonmouths tended to move slowly whether motivated to feed or not; rapid head movements and erratic striking were the only visible signs of excitement during searching. It was often quite difficult to predict whether the snake would strike or not. While the cottonmouths generally oriented toward trapped fish flopping around near by, many such hapless prey were not pursued. It was also difficult to predict whether or not a cottonmouth would attempt to pick up a dead fish, unless another had been recently ingested. The snakes often tongue flicked an area around or on a dead fish, only to pass over or near the fish without apparent recognition or interest even though other dead fish were eaten during the trial.

Attacks

Underwater attacks. Attacks and their outcomes are summarized in Table IV-3 and attack types for each snake are shown in Fig. IV-2. Only 3 bouts of underwater attacks were made at live fish (AUW): 2 involved mid-water (serpentine) diving, one of which resulted in the incidental capture of a dead fish, and the other lasted 2 intervals but did not result in a capture; the third bout, also unsuccessful, involved 2 intervals of anterior diving from the wood in shallow water.

Underwater attacks at dead fish (DUW) simply involved submerging the head from a cruising posture (CCD) and attempting to grasp submerged fish. While the snake might locomote with its head underwater in the process, it was not counted as substrate crawling. The cottonmouths reacted to relatively few of the available submerged fish (N = 19 attacks), and were remarkably unsuccessful in grasping the submerged fish (see below).

Aerial attacks. The remaining 80% of the attacks at live fish, including the successful attacks, were aerial attacks made from above the surface. Virtually all of the attacks were made from the edge or shore, none were made in deep water (> 15 cm). No attempts were made to attack fish well below the surface, although given the numbers of fish in the pool, undirected attacks into the aggregations of fish would probably have been reasonably successful.

TABLE IV-3

SUMMARY OF ATTACKS MADE BY *AGKISTRODON PISCIVORUS* IN THE LARGE TEST POOL

Types of Attack	Number of Fish Captured	Number of Unsuccessful Attacks	Number of Fish Lost	Calculated Success Rate[b]
From underwater				
AUW[a]-Dives	0	3	0	
DUW[a]-CCD[a]	17	2	5	.75
DUW or AUW-Crawl[a]	0	0	0	
From above water				
DAW[a]	21	0	2	.91
DF[a]	18[c]	10	1	.62
AAW[a]	2	2	0	.50
Out of water				
DS[a]	2	0	1	.67
DE[a]	88	8	6[d]	.86
AS[a]	1	0	0	1.00
AE[a]	5	1	0	.83

[a]CCD = striking from an underwater cruise posture; Crawl = striking while crawling on the underwater substrate; DAW = striking at dead fish from a cruise posture with the head above the surface; DF = striking at floating dead fish; AAW = striking at live fish from a cruise posture with the head above the surface; DS = striking at dead fish on the shore; DE = striking at dead fish at the edge; AS = striking at live fish on the shore; AE = striking at live fish on the edge.

[b]Success rate = captures/captures + no capture + lost.

[c]One of these fish was captured only after being pushed to shore.

[d]One of these fish was lost after it was dropped into the water and the snake was unable to re-grasp it underwater.

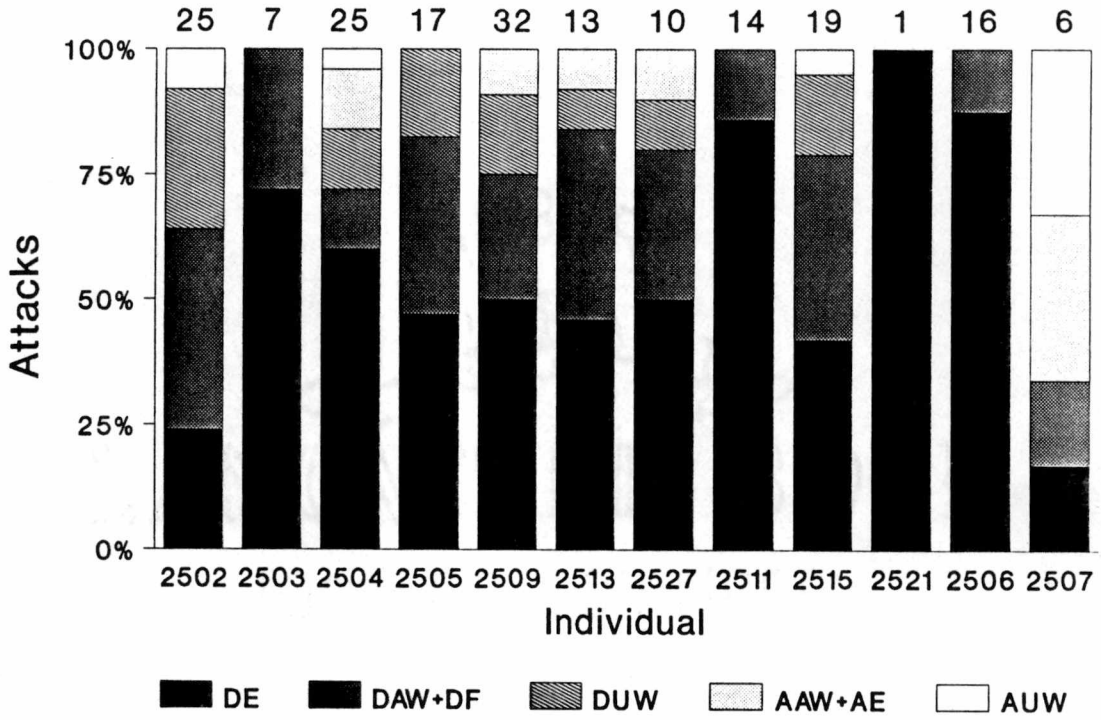


Figure IV-2. The types of attacks made by individual *Agkistrodon piscivorus* in the large test pool. Attack types are as follows: DE = dead fish at the edge; DAW = sunken dead fish attacked from above the surface; DF = dead fish floating on the surface; DUW = sunken dead fish attacked from below the surface; AAW = live fish attacked from above the surface; AE = live fish attacked at the edge; AUW = live fish attacked from underwater.

Out of water attacks. A number of fish at the edge and shore were tongue-flicked, and grasping was attempted but subsequently aborted (N = 16). Some of these were very small minnows. These were unsuccessfully attacked because the cottonmouth could not get the fish into its mouth. In part, the problem was that the fish often dried and stuck to the substrate. In part, however, the cottonmouths simply could not maneuver the fish into the jaws. Some large fish were apparently too large, and were simply tongue-flicked briefly and then ignored.

Comments on attacks at live fish. A surprisingly low number of attacks (N = 14) were made at live fish. It is surprising because there were so many live fish (250-300) in the pool, and many became trapped at the edge in shallow water or writhed at the edge while dying. The most surprising aspect of the live attacks, however, was their strong seasonality: 11 of the 14 attacks at live fish occurred during April and May, and all of the successful attacks at live fish occurred during this time period. A seasonal bias in testing does not account for the seasonal bias in attacks at live fish. Although the cottonmouths made few attacks at live fish, most of the aerial attacks (AAW, AS, and AE) were successful. As discussed above, the AUW attacks were all unsuccessful. The AUW attacks were made in the summer and were desultory in manner, although the snakes had clearly oriented toward the fish before attacking.

Not counted in the above tally of live attacks but might be construed as an attack, was a strange behavior seen in late September in 2 cottonmouths (2526 and 2530). One of these snakes (2530) was captured at Reelfoot Lake only 2 weeks previously. While at or near the edge in a cruise posture, these snakes oriented

toward fish at the surface across the pool and then slowly approached with their mouths open in a wide gape. As the water became deeper, both snakes swam with stiff necks, gradually lowering their heads while maintaining the gape and stiff neck. One snake did submerge his head below the surface slightly. As the snakes neared the fish, the fish, of course, dispersed. As the fish dispersed, the snake gradually closed its mouth. The snake returned to shore. Snake 2530 exhibited this behavior for 5-6 intervals in 2 trials and also made one other live attack; 2526 exhibited this behavior for 2 intervals during one trial and made no other attacks.

4. CAPTURING AND MANIPULATING FISH

Live v. dead fish. The capture of live and dead prey are quite different problems and will be discussed separately. As described in Chapter II, both live and dead fish were available in all parts of the pool, except the beach, in large numbers. Prey captures are summarized above in Table III-3.

Capturing dead fish. Of the 154 captures made by 12 snakes, 146 were of dead prey. All 12 of the cottonmouths which fed during trials ate some dead prey. Individual differences in the time required to grasp prey were not significant ($H=8.44$, $p=.67$). Therefore, pooled data were used for this analysis. Capture of dead prey was, of course, basically the grasping of dead fish. This behavior resembled the reapproach to a previously envenomated prey item (de Cock Buning, et al., 1981; Kardong, 1975). The snake approached the dead prey cautiously with the head low, tongue flicking the area near the prey. Dead fish at the edge and on the shore were

often apparently recognized from some distance visually, as several snakes were seen to orient toward dead fish on the edge or shore and then locomote across the pool toward them. Given the number of dead and live fish in the pool, it is unlikely that a single dead fish could be located chemically from across the pool.

After approaching the fish, the snake tongue flicked the prey all over, or, minimally, in the eye to snout region of the head, and usually poked or even pushed the fish with its snout before attempting to pick the fish up. Size was a significant factor in the time required to grasp the fish. Size 3 fish were probed from 1-6 intervals ($M=0$, $\bar{x}=1.08$, s.e.$=.33$), significantly longer than were Size 1 or 2 fish (Size 1 $M=0$, $\bar{x}=.23$, s.e.$=.06$; Size 2 $M=0$, $\bar{x}=.23$, s.e.$=.11$) (pooled data $N=146$ captures, overall $H=11.35$, $p<.01$; Size 3 v. Size 2 or Size 1 $H>8.40$, $p<.01$; Size 1 v. Size 2 $H=.13$, $p>.05$). This probing is also seen after envenomating a live prey item, fish or rodent, and probably serves to assure the snake that the prey item is dead.

The tongue flicking and probing continued until the fish was grasped, usually by the head. However, the time spent picking up the prey was not statistically related to the direction in which the fish was eventually picked up (pooled data $N=146$ captures, $H=1.22$, $p>.54$) or ingested ($H=1.37$, $p>.15$). Although the differences were not statistically significant because of the large variance, it is interesting that the fish picked up by the tail had received less probing ($\bar{x}=.14$, s.e.$=.075$) than did the fish picked up by the head ($\bar{x}=.43$, s.e.$=.116$) or by the mid-body ($\bar{x}=.60$, s.e.$=.31$).

The time spent probing was not significantly related to how many items were eaten before or after this item (Spearman $r=-.097$, $p>.05$).

Unsuccessful ingestions. Not surprisingly, the success rate of such captures was high: over 85% (N=131) of the 146 captures led to ingestion. There were 15 losses of dead fish after capture. Prey loss occurred when the snake dropped the fish and abandoned it. Occasionally, the snake tongue flicked or even probed the fish gently with its snout for one or more intervals before abandoning it. Size was a major factor in the abandonment of fish: the larger Size 3 fish were lost at a higher rate (7/28=.25) than the smaller Size 1 (3/62=.05) and Size 2 (5/51=.10) fish (pooled data N=146 captures, overall H=5.97, p =.05; Size 1 and 2 v. Size 3 H=5.64, p<.02).

Some of the abandoned Size 3 prey (3/15) were very large, possibly too large for the snake to swallow; these prey items were held from 1-6 intervals before being released. One very large prey item that was dropped after 4 intervals was later picked up again and successfully ingested, however, suggesting that motivation can be a factor in the ingestion of difficult prey.

Since snakes ordinarily ingest prey head first, it might be expected that prey grasped by the mid-body or tail might be lost more frequently than prey "properly" grasped by the head. While fish dropped after being grasped by the tail or mid-body accounted for 27% of the prey lost, the direction in which the fish were initially grasped was not a significant factor in the loss of fish (pooled data N=146, H=2.70, p>.25).

The cottonmouths had quite a bit of trouble dealing with the fish in the water, whether floating or sunken. First, they had problems even grasping fish in water. Even though fish were not captured while diving, but from a cruise position, the snakes often could not grasp either floating fish (DF) or fish on the bottom (DUW) in water more than a few cm deep, accounting for 33% of the losses and 55% of the unsuccessful attacks. In such a case, the snake could be seen to bite repeatedly at the

fish, usually making contact, but not successfully clamping the jaws around the fish. One snake only managed to grasp a large DF shad after pushing it to shore, all the while biting at it. Second, even when fish were successfully grasped underwater, the cottonmouths had trouble maintaining the grasp and often dropped the fish before getting to the surface. Two individuals spent 4 intervals attempting to bring up prey from under water. While the success rates for DF and DUW fish were still relatively high, in the 70% range as shown in Table IV-3, the success rates for DF and DUW captures were lower than success rates for fish captured from above water.

The loss of some of the remainder of the abandoned fish (4/15) cannot be explained by any of the mentioned factors. These fish were held from 1-4 intervals ($M=3$) which is significantly longer than the median handling time for fish that were ingested ($M=1$) (pooled data $N=146$, $H=13.68$, $p<.001$). Based on the significance levels of the size and manipulation time, manipulation time appears to be a more significant factor than size in the abandonment of prey, here. A possible interpretation of this result is that time spent on handling provides the cue for abandonment of prey. Given the time spent on unsuccessful attempts, and the occurrence of such losses before and between successful ingestions, but never as the last prey item, lack of motivation *per se* does not seem to be a sufficient explanation for the problem.

Where fish were captured. Ultimately, over 60% of the dead fish were captured out of water, most in an edge area. The habitat was divided into more categories for habitat analysis for prey capture than for general habitat use as the cover areas being divided into edge and water-covered areas. This analysis clearly

shows the importance of the water's edge for the cottonmouth Since the prey captures are effectively pooled data, overall habitat use in the table is the median of pooled habitat use. Fish were captured in the various habitat areas in proportions that approximate the overall habitat use. Nevertheless, the proportions of habitat use and prey capture for the edge and wood areas differ significantly. Fewer prey were captured on the edge and more were captured in the wood than would be "expected" based on the snakes' use of that area. Thus, the cottonmouths did not adjust habitat use to prey capture success. Habitat use during prey capture is summarized in Table IV-4 below.

Since dead fish had been carefully placed around the pool, the total number available over all trials in each area was known. The proportion available that was successfully captured was thus easily calculated and can be used as a measure of success. As can be seen in Table IV-5, the cottonmouths were quite successful at capturing dead fish out of water, capturing over 50% of the available prey in the shore and various edge areas, but they captured fewer of the the dead fish available in the water covered areas, except for the water covered area of the wood, where they enjoyed reasonable success. The wood area as a whole was utilized heavily for prey capture. The capture of live fish was not included in this table because so few live fish were captured, and all of these captures were made in water less than 3 cm deep. The cottonmouths clearly are not very adept at aquatic foraging for any kind of prey, even dead prey.

TABLE IV-4

HABITAT USE FOR PREY CAPTURE BY *AGKISTRODON PISCIVORUS* (N = 12) IN THE LARGE TEST POOL

Habitat Area[a]	No. of Captured Fish (Dead\Live)	% Total Captured	Habitat Use[b]
Shore	1\1	1.4	4.0
Edge	40\3	30.9	53.0**
[Out of Water Total]	**[41\4]**	**[32.3]**	**57.0**
VE	14\0	10.1	
VW	14\0	10.1	
[Vegetation Total]	**[28\0]**	**[21.4]**	**27.0**
WE	20\1	15.0	
WW	16\1	12.2	
[Wood Total]	**[36\2]**	**[29.0]**	**8.9****
CE	4\1	3.6	
CW	8\0	5.8	
[Crevices Total]	**[12\1]**	**[9.9]**	**1.7**
OWS	7\1	5.8	2.2
OWD	7\0	5.0	1.2
[Open Water Total]	**14\1**	**10.8**	**3.4**
Total	131\8	99.9%	

[a]VE = edge area of vegetation; VW = water covered area of vegetation; WE = edge area of wood; WW = water covered area of wood; CE = edge area of crevices; CW = water covered area of crevices; OWS = open shallow water; OWD = open deep water.

[b]The values given fabitat use are pooled medians.

**The percentage of prey captured in these areas differed significantly from the percentage of time spent in the area, $p < .01$, using the method of Fleiss (1979).

TABLE IV-5

AVAILABLE DEAD FISH CAPTURED IN THE LARGE TEST POOL BY *AGKISTRODON PISCIVORUS* (N = 12)

Habitat Area	Available[a]	% Captured
S	64	4.7
E	128	33.6
VE	96	17.7
WE	96	21.9
CE	96	6.3
VW	160	8.8
WW	128	12.5
CW	128	6.2
OWS	160	5.6
OWD	160	6.9

[a]Available = total fish available in each habitat area over all trials in which prey were consumed, N = 32 trials and 12 snakes. Fish were placed in the environment in a prescribed manner at the beginning of each trial. Due to the death of some fish, numbers are not exact, although excess dead fish were removed between trials.

S = shore; E = edge; VE = edge of vegetation; WE = edge of wood; CE = edge of crevices; VW = water covered portion of vegetation; WW = water covered portion of wood; CW = water covered portion of crevices; OWS = open shallow water; OWD = open deep water.

Manipulating Fish

Manipulating dead fish. The factors affecting manipulation are most easily examined in terms of manipulation time. Individual differences were important factors in manipulation time ($N = 146$, $H = 19.22$, $p < .06$). Therefore, data were analyzed using the median values for each individual. Prey manipulation often required a considerable amount of time, up to 9 intervals, and less than 1 in only 12% of the successful captures. The size of the prey would also be expected to affect manipulation time, and it did: manipulation times increased with prey size, although the differences in the manipulation times for Size 1 ($M = 1$, $\bar{x} = .94$, s.e. $= .19$) and 2 ($M = 1$, $\bar{x} = 1.26, .12$) fish were not significantly different (unpooled data $N = 9$-11 snakes, overall $H = 19.44$, $p < .0001$; Size 1 v. Size 2 $H = .45$, $p = .50$; Size 1 and 2 v. Size 3 $H = 14.96$, $p < .001$; Size 3 $M = 3$, $\bar{x} = 3.01$, s.e. $= .35$).

As with the loss of prey, the direction in which prey were grasped did not significantly affect the manipulation time (unpooled data $N = 7$-12 snakes, overall $H = 1.46$, $p = .48$). Nevertheless, initially grasping the fish by the mid-body did lead to more extreme manipulation times ($M = 1$, $\bar{x} = 1.56$, s.e. $= .38$) than did grasping by the head ($M = 1$, $\bar{x} = 1.42$, s.e. $= .22$) or tail ($M = 1$, $\bar{x} = 1.29$, s.e. $= .19$). This makes sense because fish grasped by the mid-body are almost impossible to swallow unless they are small enough to swallow folded. It is possible to swallow dead fish tail first, however; the sole difficulty in tail-first ingestions of at least dead fish appears to be getting the caudal fins into the mouth (pers. obs.).

Where fish were handled. In general, the cottonmouths often appeared to be struggling with the prey during manipulation as evidenced by their almost constant, sometimes agitated, movement during prey manipulation. This movement led to changes of location in 23-100% of the ingestions (unpooled data, N = 139 ingestions by 12 snakes, M = .33). More of the changes were to shallower rather than to deeper or similar depth water areas (M = .83 and M = .00 and M = .00 respectively, $p < .01$).

During manipulation, prey were often pushed against objects to assist the work of the jaws in alignment of the prey for swallowing. Virtually all of the manipulation process took place above water: the prey were sometimes held at the surface of the water, but never below during handling.

Methods for dealing with misgrasped fish. Fish grasped by the mid-body or tail were often re-oriented by means of jaw manipulations. While the prey were usually converted to a head first grasp (N = 9), some of the conversions were from mid-body to tail first grasps (N = 6), and one to a mid-body grasp. Since fish grabbed by the mid-body had to be folded for swallowing, it is somewhat surprising that one fish, a Size 2 fish at that, was converted from a tail to a folded position in only 1 interval. This snake (2509) in the end was responsible for 4/5 of the mid-body first ingestions.

One observed solution to the manipulation problem was to start over; that is, drop the fish and pick it up again. As mentioned, dropping often signaled abandonment of the prey, but dropped prey were about as likely to be picked up again (N = 17) as abandoned (N = 15). Prey were dropped and regrasped up to 3 times during prey manipulation in 12% of the successful ingestions of dead fish. About

40% (N=7) of all dropped fish had been initially grasped up by the head, suggesting that dropping was a solution to difficult ingestions in general. In fact, dropping (and re-grasping) occurred significantly more when handling times were longer (pooled data N=131 successful captures, H=34.54, p<.0001).

As with fish dropped and abandoned, prey size was a significant factor when fish were dropped and re-grasped (pooled data N=131 successful captures, H=29.85, p<.0001); and dropping occurred significantly more frequently with the large Size 3 prey (Size 1 [1/58] and Size 2 [2/46] v. Size 3 [8/27] H=12.87, p<.0001).

Unlike fish dropped and abandoned or overall handling time, fish grasped by the mid-body were dropped during manipulation (usually to be re-grasped by the head) significantly more often than fish grasped by the tail or head (pooled data N=131 successful captures, overall H=4.7, p<.10; head [9/91] and tail [2/20] v. mid-body [6/20] grasp H=4.59, p<.03).

Item number. Meal size varied from 1-20 items, M=4. Item number, that is, whether the prey item was the first, second, and so on, might be expected to be correlated with some of the above mentioned factors. Prey size which has heretofore consistently proved to be important was not, however, significantly correlated with item number, although the snakes exhibited a weak tendency (pooled data, N=146 captures, r=-.09, p>.27) to take larger fish earlier in a meal. Looking at strictly individual differences, first prey items in an individual's meal were not significantly different in size from that individual's median prey size (N=12 individuals, paired sample signs test z=.67, two-tailed p=.50).

Another interesting correlation was that between item number and direction the prey was initially grasped: prey captured earlier in the meal were more likely to be grasped by the head than those captured later (pooled data, $r = -.1812$, $p = .02$, $N = 131$ captures), thus the cottonmouths exhibited some evidence of taking more care with earlier prey items.

The time taken to probe and to manipulate were weakly and negatively correlated with item number, so that the snake spent less, but not significantly less, time in these activities for prey eaten later in a meal (pooled data, $r = -.10$, $p > .26$ and $r = -.07$, $p = .39$, $N = 131$ captures).

Capturing and Manipulating Live Fish

Capturing live fish. Given the few attacks on live fish, the success rate for the capture of attacked live prey was remarkably high. Eight live fish were captured by 4 individuals, which, at worst, makes the success rate 40% (8/20), counting all attacks. All attacks would be classified as "spear fishing" attacks delivered to fish at or just below the surface in very shallow water. No live fish were lost after capture. Many of the unsuccessful attacks were very abbreviated attacks, however. These involved snaps and very short lunges in the direction of active fish at the surface. Two of the snaps were at very large fish which splashed quite a bit of water about, and these snaps may have been defensive rather than predatory. Therefore, the success rate for true predatory attacks may have been higher, but discrimination of the 2 types of attacks is not possible in this situation. Nevertheless, it should noted that 2 of the 8 live captures occurred when the fish flopped out onto the shore or edge near the

snake. Only 2 snakes caught more than 1 live fish. One of these snakes, a large adult (2504), made all of the captures on the same day as part of a meal of 12 fish.

A small juvenile, still young enough to have a sulfur-tipped tail, captured 3 of the live fish. Seventy-five percent of the fish captured by this juvenile were alive; it also attacked one live fish (and 0 dead fish) unsuccessfully. This juvenile was the only snake which immediately moved to the edge when placed in the pool and stayed there for some time, relatively immobile; it also craned over the water for minutes at a time. As mentioned earlier, this craning was not typical for cottonmouths.

Given the seasonality seen in the attacks on and capture of live fish, motivation appears to play a role in the capture of live fish. Motivation might also be expected to affect the order in which live fish were taken during a meal. While the live fish were not the last items in a meal, they were not the initial items, either. Thus, the item number offers little information about the role of motivation in the capture of live prey.

Where live fish were captured. All live prey were captured by aerial attacks from a cruise posture in water 0-3 cm deep, and mostly (75%) from the edge; all captured prey were successfully ingested. One live fish, a very large (> 100 g) *Lepomis*, was caught on shore after it became trapped in rock crevices and flopped out of the water in its attempt to escape. Three of the live fish captured were captured in the wood.

Envenomation of fish. The above mentioned large *Lepomis*, captured serendipitously by a large adult (2513), was the only fish envenomated during the large pool trials. The snake struck and envenomated the fish on the dorsum just posterior to the head and anterior to the dorsal fin. The strike seemed deliberately placed, as the snake was poised within striking range of the flopping fish several seconds before striking. Almost all fish envenomated by cottonmouths are so envenomated (B. Savitzky, unpubl.) The stiff dorsal fins of fish such as the *Lepomis*, the only potential cause of injury to the snake presented by the fish, were avoided by this placement of the strike. The fish was held in the mouth for 12 intervals before being released and was motionless when released. Fang marks were quite obvious. The remainder of the prey handling process was exceptionally long as detailed below.

Strikes are generally delivered to the neck-shoulder region of rodents, so that fish and rodents appear to be handled similarly with regard to strike placement. This placement of the strike in rodents resulted in massive hemorrhages in the pleural and abdominal cavities as revealed by post-envenomation autopsies (B. Savitzky, unpubl.). While the full extent of internal hemorrhage in fish was not verified, internal and external evidence of internal hemorrhage was found in all fish with puncture wounds.

Manipulating live fish. Prey manipulation of the still living, small (Size 1 and 2) fish captured by the adults was brief: M = 1 interval. However, manipulation required 3-8 intervals (M = 5 intervals) for the Size 2 fish consumed by the juvenile, possibly in part because this snake moved from the edge to the beach during this

time. In contrast, the Size 2 dead fish eaten by the juvenile required only 1 interval for manipulation.

Snake 2513 also spent an inordinate amount of time handling his live-captured fish after envenomation: 5 intervals were spent tongue flicking and poking at the fish after it was released, although it was quite dead. Another 7 intervals were spent trying to grasp it satisfactorily, and then another 29 intervals were required to manipulate it before swallowing. While this fish was quite large, similarly large dead fish were ingested by other large or larger cottonmouths. No other prey item needed close to the 41 intervals required here for pre-ingestion handling: the next largest amount of time required was only 9 intervals (by another snake). The handling times for successfully ingested dead Size 3 fish successfully ingested by this snake was only 2 intervals, and the median handling time for dead Size 3 fish for other snakes was similar (M=1-7 intervals, group M=2.5). Prey captured alive thus may be given extra pre-ingestion handling time, although sample sizes are too small to establish this for certain. While it would make sense for the snake to spend extra time examining the fish after envenomation to assure its inanimation, the reason for prolonged alignment times is unclear.

Where live fish were manipulated. Although the live fish were captured at or near the edge, the cottonmouths moved to higher ground in 50% of the live fish captures. Additionally, one snake moved from the crevice edge to a strip of smooth edge. The cottonmouths exhibited a strong tendency to handle live fish out of water altogether as 50% of the manipulations were on the shore or land. The juvenile even dragged two of its live prey up to the beach. Only one fish, a Size 1 ingested by a

large adult (2504), was manipulated in the water, but this was very shallow (less than 3 cm).

5. INGESTION OF FISH

Where and How Fish Were Ingested

Description of ingestion. The swallowing of live and dead prey will be analyzed together as they were qualitatively and quantitatively similar. While snakes are adapted for swallowing relatively large, whole prey, viperids like the cottonmouth are regarded as adapted for swallowing especially large prey (see Pough and Groves, 1983). Less struggling was seen during swallowing than during manipulation, but the snakes still moved around quite a bit during swallowing. No prey were lost once swallowing had begun. During the last part of ingestion, the head was invariably raised high with the snout pointing almost straight upward, and large amplitude sinuous movements of the neck assisted in the movement of the prey down the gullet.

Where fish were ingested. The relocation that occurred during prey handling resulted in the cottonmouths ingesting prey landward of the site of capture. Fish were ingested where manipulation ended, and over 70% of the ingestions occurred out of water altogether. Habitat use for prey capture and ingestion are illustrated in Fig. IV-3. The edge, including the edge in the wood and vegetation, was the site of over 56% of the ingestions. This landward shift was most pronounced in the juvenile, who, as mentioned earlier, retreated to the beach with 2 of his live prey. This was the

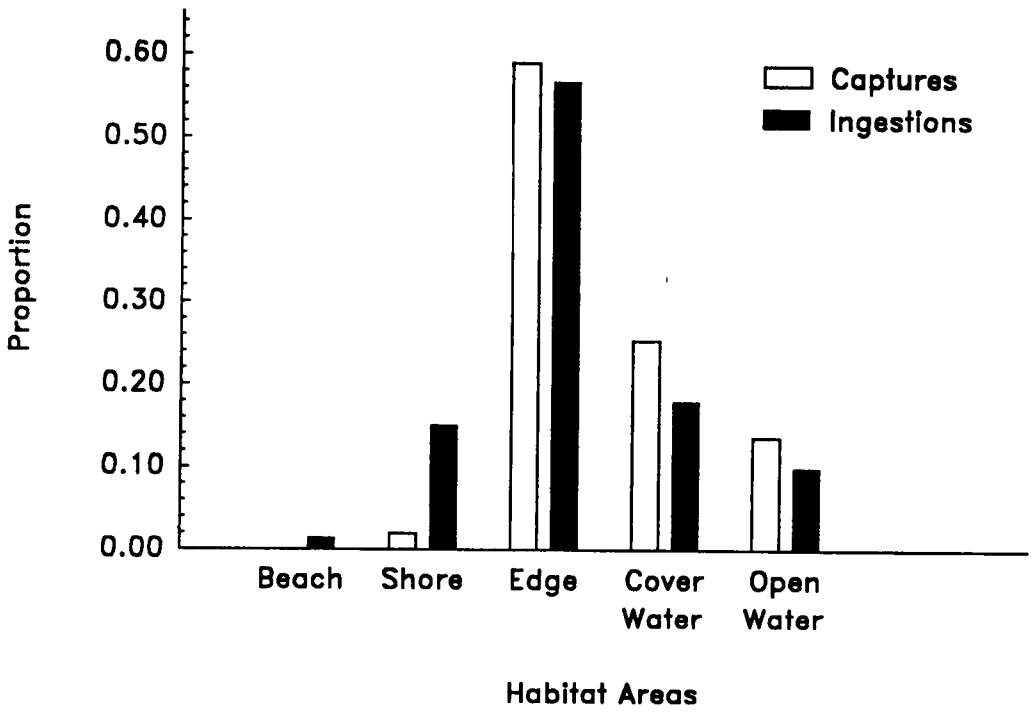


Figure IV-3. Habitat use during prey capture and ingestion for *Agkistrodon piscivorus* in the large test pool.

only cottonmouth to retreat to the beach. Adults shifted to shore frequently, however, so that the rate of ingestions on shore was significantly higher than the rate of captures (.14 v. .02, $p<.01$). Wherever ingestion took place, the cottonmouths always ingested with their heads out of water.

The landward shift was extreme enough that the difference between habitat use for prey capture and ingestion was statistically significant (habitat areas were combined to avoid low cell values: Shore + Land, Edge, Cover Edge [VE + WE + CE], Cover Water [VW + WW + CW], OWS, OWD $G=20.78$, $df=5$, $p<.005$). Fig. III-3 illustrates the the landward shift for prey ingestion.

Factors Affecting Ingestion Time

Individual differences and relative prey size. There were significant individual differences in ingestion times ($N=139$ ingestions by 12 snakes, $H=24.01$, $p=.01$); thus data analyses were based on the medians for each individual.

As expected, prey size was the most important factor in the time required for ingestion, with ingestion increasing with prey size. Size 3 fish required significantly more time than the smaller size fish (Size 1 $M=1$, Size 2 $M=1.5$, and Size 3 $M=5.5$) for which ingestion times were statistically the same (unpooled data, $N=9$-11 snakes, overall $H=15.42$, $p<.001$; Size 1 v Size 2 $H=1.92$, $p>.16$; Size 2 v. Size 3 $H=10.14$, $p<.01$, Size 1 v. Size 3 $H>.15$, $p<.001$; Size 1 and 2 v. Size 3 $H=14.52$, $p<.001$). The large size 3 fish envenomated by 2513 required 18 intervals to ingest, but this was not the longest ingestion time, and the fish was one of the largest ingested during this

study. It does not appear that post-envenomation ingestion time was unusually long as was the manipulation time.

The orientation of fish. Since snakes generally ingest prey head first, it was not surprising that direction of ingestion also was a factor in ingestion time. But before saying more, it should be noted that all snakes ingested at least some of their fish head first, and 9 (75%) ingested some tail first, but only 2 (17%) ingested any mid-body first. Clearly, ingesting head or tail first was much more common than ingesting mid-body first and suggests that cottonmouths avoided ingesting mid-body first. The fact that 1) most initial mid-body grasps (70%) were changed to head or tail first ingestions and 2) 67% of the snakes initially grasped at least one fish by the mid-body further supports the idea that mid-body ingestions were actively avoided.

Not surprisingly then, fish ingested mid-body first required more time to ingest than fish ingested head or tail first (head range = 1-2; M = 1, mid-body range = 2-4, M = 3, and tail range = 1-5.5, M = 3) which required statistically the same amount of time (unpooled data N = 2-12 snakes, overall $H = 4.21$, $p = .12$; mid-body v. tail $H = 4.21$, $p > .12$; mid-body and tail first v. head first $H = 4.09$, $p = .04$). However, no Size 3 fish were ingested mid-body first. Size 1 and 2 fish, on the other hand, were ingested mid-body first at a statistically similar low rate (4.8% v. 2.0%, $p > .05$). Thus, there would appear to be an interaction between size and direction of ingestion for Size 3 fish but not for Size 1 and 2 fish. Confounding of variables prevents the parametric analysis of this effect by MANOVA.

While it at first was somewhat surprising to find that tail first ingestions statistically required no more time than did head first ingestions, inspection of the data showed that no Size 3 fish were ingested tail first. Statistically similar

percentages of Size 1 and 2 fish were ingested tail first, however (23.5% and 19.4% respectively, $p > .05$). Thus, there again appears to be an interaction between size and direction of ingestion for Size 3 fish but not for Size 1 and 2 fish. Fig. IV-4 graphically summarizes the direction of ingestion and prey size.

Item number. The last factor in ingestion time to be analyzed is item number. As with the time spent probing a fish and then manipulating it, a negative correlation was found between item number and ingestion time. But while the previously analyzed portions of total handling time were each found to be insignificantly correlated with item number, the correlation between ingestion time and item number was significant (pooled data, $N = 141$ ingestions, $r = -.17$, $p < .05$). These negative correlations run counter to an explanation in terms of motivation.

Total handling time. As in Chapter III, the analysis of total handling time will be presented in tabular form below in Table IV-6. Only those ingestions for which complete information was available are included in the analysis.

6. SUMMARY OF AQUATIC PREDATION IN THE COTTONMOUTH

Cottonmouths in the large, naturalistic test pool preyed mostly on dead fish. Of 154 captures by 12 individuals, 95% of the captures were of dead fish. The grasping of dead prey qualitatively resembled that of envenomated live prey. As with envenomated prey, prey were investigated carefully by tongue flicking and poking

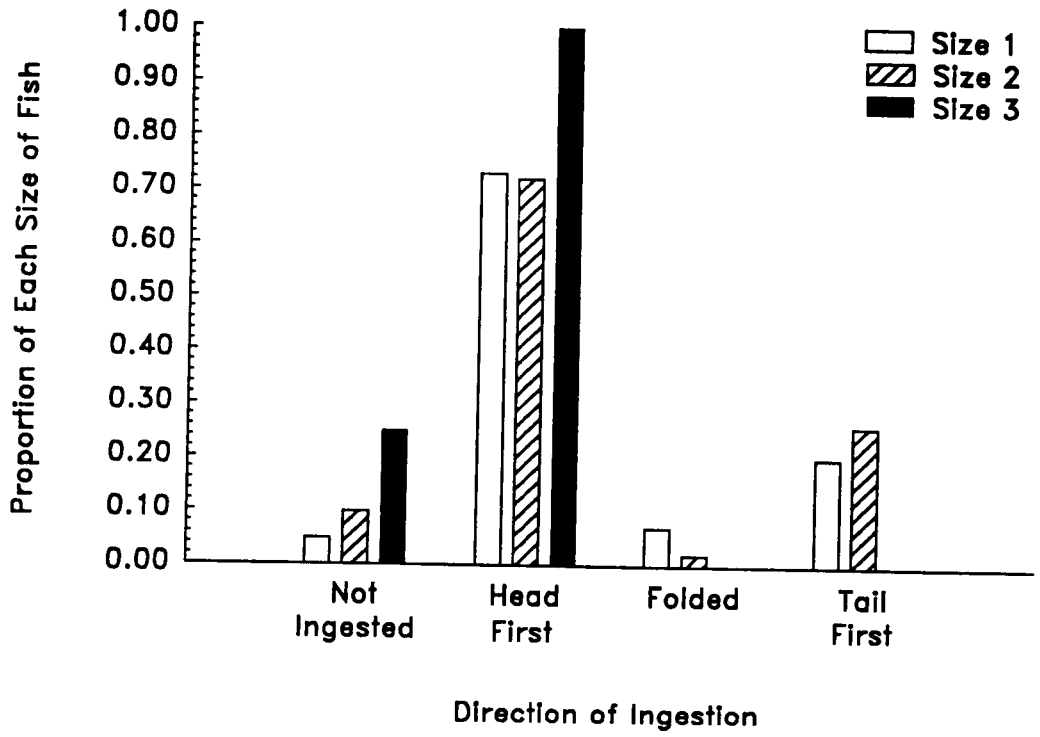


Figure IV-4. Prey loss and the direction of ingestion for each prey size in *Agkistrodon piscivorus*.

TABLE IV-6

ANALYSIS OF TOTAL HANDLING TIME[a] FOR *AGKISTRODON PISCIVORUS* (N=12)

Factor	No. of Ingestions (No. of Snakes)	Median[a]	Significant Comparisons[b]
Prey Size[c]*[d]			
S	58(9)	2	Size 1 < Size 3***
M	51(11)	2	Size 1 and 2 < Size 3***
L	30(10)	11.75	Size 2 < Size 3***
Direction of Ingestion[c]			
H	110(12)	3.5	
M	5(2)	5	
T	24(9)	4	
Item*	1-20/trial(12)	4	r=-.18, p=.04*[f]

[a]Handling time is in terms of 30 sec intervals. Because behaviors were instaneously sampled at the beginning of an interval, handling time intervals represent times between interval/2 - .5 min, and interval/2 min.

[b]Kruskal-Wallis non-parametric ANOVAs were computed. If the overall significance level was less than .15, it was considered significant, and comparisons between the levels were then made. All comparisons were considered significant at $p<.05$.

[c]Prey size is relative to snake size. See Chapter II for details.

[d]*** = $p<.001$; ** = $p<.01$; * = $p<.05$.

[e]H = head first; M = mid-body first or folded; T = tail first.

[f]Spearman rank correlation was computed.

with the snout before grasping. All live fish were captured by aerial attacks at fish in water no more than 3 cm deep. The sole juvenile snake was responsible for 37.5% of all live captures. All captures of live fish, and 85% of the attacks at live fish were made in the spring.

The very buoyant cottonmouths spent significantly more time in the edge areas than anywhere else, and rarely dived or crawled on the underwater substrate. The vegetation was preferentially used, and the other cover areas were used about as expected. Cover areas were used about equally. Open water, shallow and deep, were used very little.

The majority of fish, live and dead, were captured in very shallow water or out of water altogether. The snakes captured more of the available fish on the edge than anywhere else. The snakes had difficulty grasping or maintaining hold of fish under water, and they tended to lose prey in the water. Manipulation and ingestion of prey was entirely above water, and largely out of water altogether. Ingestion generally took place landward of capture so that habitat use for ingestion was significantly different from habitat use for capture.

As is typical of snakes, most prey were grasped head first. While some misgrasped prey were dropped and abandoned, some were dropped and re-grasped. Manipulation, with or without conversion, was often difficult and time consuming. Prey size significantly affected manipulation and ingestion times, prey loss, and dropping during manipulation with the large Size 3 fish being different from the smaller Size 1 and 2 fish. The direction in which prey were grasped significantly affected dropping during manipulation and ingestion time, with fish grasped by the mid-body being dropped more, and requiring more time to ingest, than fish grasped by the tail or head. There was an interaction between prey size and direction

ingested, with Size 1 and 2 fish again forming a homogeneous group which differed from Size 3. Fish eaten earlier in a meal were significantly more likely to be grasped head first but required significantly more time to ingest than fish eaten later in a meal.

7. A BRIEF SUMMARY COMPARISON OF *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS*.

The two species approached the problem of piscivory in very different manners. The approaches first of all involved quite different habitat utilization. The water snake, *Nerodia rhombifera*, foraged primarily on live fish in the water, above and below the surface. The cottonmouth, *Agkistrodon piscivorus*, on the other hand, foraged from the edge and very shallow water areas, primarily on dead fish. The two species also utilized different attack strategies. The water snake tended to use lateral strikes ("trawling") or rather short forward underwater attacks. The cottonmouth, in contrast, utilized forward ("spear fishing") attacks, but only to fish at or just below the surface. Neither species pursued individual fish through the water. The water snake, however, did make some directed forward underwater attacks at individual fish a few centimeters away, and frequently oriented underwater toward fish 15-30 cm away. The two species handled prey quite differently also. The water snake handled and ingested prey readily underwater, whereas the cottonmouth handled and ingested prey only above the surface, and generally out of water altogether. Both species behaved about as predicted in Chapter I, except that the cottonmouth relied on dead fish much more than expected.

CHAPTER V

ONTOGENETIC CHANGES IN FORAGING IN *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS*

1. ONTOGENETIC CHANGES IN THE FORAGING OF SNAKES

Introduction

Goals of this chapter. This chapter will address ontogenetic changes in foraging in *Nerodia rhombifera* and *Agkistrodon piscivorus*. Ontogenetic changes in the water snake were examined by means of both field and laboratory studies. Ontogenetic changes in the cottonmouth were examined in two laboratory studies. After a brief general discussion of ontogenetic changes, the two species will be discussed separately.

Documented ontogenetic changes. As discussed in Chapter I, ontogenetic changes have been found in snake feeding that involve either changes in prey size or prey type. Another possibility, one which has heretofore not been explored, is ontogenetic changes in foraging behavior. Whereas changes in behavior would be expected to accompany changes in prey type, such changes have only occasionally been explored (Franz, 1977).

In the large test pool in this study, the sole juvenile cottonmouth behaved differently from the adults in several ways: 1) it spent most of its exploratory time on the edge, particularly favoring the large flat rock; 2) it exhibited the lowest rate of

aquatic behaviors and was never observed swimming; 3) it attacked live prey preferentially to the numerous dead prey of suitable size nearby.

Less clear-cut results were found for the water snakes in the large test pool. Due to the pronounced sexual dimorphism in this species, size and sex covary. Differential utilization of the rock crevices and open water areas was associated with these factors. No sex or size effects were found in predatory behaviors (attack types), however. Nevertheless, because of the differences in habitat use, males captured more of their prey in the crevices, whereas females captured more of their prey in the open water.

As discussed in Chapter I, ontogenetic changes involving prey size have been found in field studies of this species (Mushinsky et al., 1982; Plummer and Goy, 1984). These changes have sometimes been found to result in dietary differences between the sexes (Mushinsky et al., op. cit.), but sometimes not (Hess, 1966; Plummer and Goy, 1984). Ontogenetic changes thus are expected. The results of Mushinsky et al. (1982) and Plummer and Goy (1984) suggest that these differences should result in sexual differences at SVLs over 700 mm.

Behavioral Ontogenetic Changes: What Might be Expected?

Changes due to increased metabolic scope. As discussed in Chapter I, ontogenetic changes can be expected because, first of all, young snakes do not have the metabolic scope of adult snakes (Pough, 1977; 1978). Therefore, neonates should use less active foraging tactics than older snakes. In the water snakes, this would be foraging in a cruise posture in shallow water with the head at the surface. This

foraging tactic was also the most successful foraging tactic used by the water snakes in the test pool in terms of the capture to attack ratio. In the cottonmouth, the less active tactic would be a crane or cruise posture from the edge over the water, or, possibly, lying coiled in the water at the edge. The juvenile cottonmouth in the test pool only utilized a craning tactic from the edge, and was quite successful (90% successful captures).

Changes due to decreased predation risk. Predation avoidance is a second important foraging consideration. Juvenile snakes undoubtedly are preyed upon heavily. Neonate snakes are only occasionally found in the field even in years when reproduction is known to have occurred, suggesting high rates of predation shortly after birth (Brown and Parker, 1982; Mushinsky and Miller, unpubl. ms.; Parker and Plummer, 1987; pers. obs.). Unfortunately, there is not much documentation of predation on snakes of any size (but see Godley, 1982). However, fish, birds, and small mammals are all known to prey upon snakes (Fitch, 1960, Godley, 1982; McGrew, 1963). Neonate snakes might, therefore, forage from cover in very shallow water in order to limit exposure to predatory fish. Foraging at night should limit exposure to herons and egrets which are diurnal predators in these areas. Staying in the water near refuges would minimize exposure to predatory mammals, most of which are nocturnal (raccoons, opossums, mink, etc.). Small minnows, poecilids, and anurans would be available as prey here. Neonates of cannibalistic species may avoid larger conspecifics, and therefore might utilize different habitat areas than do adults. Based on the test pool results, the water snakes might use the rock crevices extensively, although the snakes enjoyed the highest success rate in the vegetation.

Contrary to these predictions, the juvenile cottonmouth in the test pool foraged in the open along the edge, the area also used by the adults, and did not use cover at all. Perhaps this venomous snake is relatively immune to predation by any but conspecifics, to which the juvenile was not exposed in the test pool.

Changes due to decreased need for food. Thirdly, as discussed in Chapter I, the growth rate of juveniles can vary with food intake. Increased size would reduce their vulnerability to predation, and would improve survival during hibernation (see discussion in Parker and Plummer, 1987). Yet, neonate snakes may have higher food requirements per gram of body mass than adults (see Mushinsky, 1987). Neonate snakes, then, should, all things being equal, forage in the manner which results in the highest food intake.

Changes due to decreased risk of cannibalism. Finally, some species of snakes, such as the cottonmouth, are quite cannibalistic (Allen and Swindell, 1948; Penn, 1943; Klimstra, 1959; see also Burkett, 1966). While cannibalism has not been observed in *Nerodia rhombifera*, it has been seen in group housed *N. sipedon* when normal prey were present (Brown, 1958; pers. obs.) and in other natricines (Schwartz, 1985) when normal prey were not present. Neonate snakes should behave in such a way to minimize this risk. As with other forms of predation, the risk is probably greater for smaller than for larger snakes.

2. LABORATORY STUDIES ON ONTOGENETIC CHANGES IN *NERODIA RHOMBIFERA*

Experiment 1.

Introduction. The goal of this first study was to establish the habitat use and foraging repertoire of neonate water snakes that were both prey and habitat naive, to document any differences between neonates and adults, and to test the predictions developed above.

Subjects. Two to three week old water snakes born in the laboratory from dams 2443, 2444, and 2447 caught at Reelfoot Lake, TN were tested. These snakes were removed from the dam's cage within 24 h of birth and housed separately in clear plastic boxes 18.5 x 13.5 x 5 cm with a cardboard substrate, cardboard shelter, and a small water bowl. Snakes were weighed and measured within 3 d of birth. Some individuals did not forage and were dropped from the study; information was obtained from 6 neonates from dams 2443 and 2447, and 8 from dam 2444. Weight and length information is in Appendix A.

Methods. Due to the small size of the neonate water snakes, studies of their foraging were done in the small tanks described in Chapter II. This tank offered the same habitat areas as the large pool, except that there was no shore or beach. These areas were not used much by the adult water snakes, and the neonates were assumed not to use these much either. An exposed rock did offer a dry area for the snakes.

The behaviors and habitats were recorded in the same manner as in the test pool study (see Chapter II for details). Since the goal was to test naive snakes, all snakes were tested only once. Only one snake was tested at a time. A shorter 5 min habituation period was used as neonates were previously found to become active almost immediately. The neonates also were active for such short periods that the maximum trial length was reduced to 45 intervals (24.5 min) and many trials were stopped earlier so that only exploratory foraging information would be collected.

Due to the incandescent lights (see Chapter II for details about lighting during testing), air and water temperatures were 28-30° during the trials. These lights were turned off between trials and water in the tanks was replaced with cooler water as needed so that water temperatures stayed within the stated range.

Prey densities were high. The prey were 30 non-gravid mosquito fish *Gambusia affinis*, collected in a local pond, and 30 "small" minnows *Pimephales promelas*. Both species of fish were known to be readily accepted by neonate water snakes. By the system of sizing prey detailed in Chapter II, the mosquito fish were Size 1 prey for the neonates, and the minnows were Size 2 prey. Thus, no Size 3 prey were available in this test. Additionally, 3-4 floating dead minnows were available in the cage during each trial. Since the fish were floating, their position changed throughout the trial, except for an occasional fish which became trapped in the crevices and vegetation. Live fish were added between trials as needed to maintain prey densities.

Data analysis. Data analysis was as described in Chapter I for the primary test pool with the exception that litter effects were examined. There was no pooling of information on individuals because each individual was tested only once.

Results. The water snakes generally hurled themselves into the water without hesitation, although some individuals of litter 2443 litter were slow to move into the water. The behavior of the neonates was similar to the adults although they appeared to be a bit more buoyant (*i.e.*, getting from the surface to the bottom seemed to take longer). They also moved fairly quickly from one area to another in short bursts. The neonates spent much of their immobile time in a crane-cruise posture at the surface (CCS), whether in the open or in cover areas.

Habitat use: Habitat use is summarized in Table V-1 below. The neonates were out of cover very little. They were never scored as using the narrow bare edge. They were in the shallow open water little (litter M=.0-.04) and in the deep water somewhat more (litter M=.0-.18). Recall that the shallow water was extremely shallow and the deep water was still shallow compared to the primary test pool. In looking at use of the open water in general (OWS+OWD), litter 2443 spent significantly less time there (M=0) than did the other litters (litter 2444 M=.41, litter 2447 M=.11; overall H=6.88, p=.03; 2443 v. 2444 and 2447 H=6.21, p=.01). The proportion of time spent in both open water areas was less than would be expected for all litters given the proportion of the habitat that each area comprised (OWS M=.0 v. .258, Z=3.94, p<.0002; OWD M=.06 v. .302, Z=3.94, p<.0002, Wilcoxon signed rank tests, one-tailed).

TABLE V-1

SUMMARY OF HABITAT USE BY FORAGING NAIVE *NERODIA RHOMBIFERA* (N= 20) IN THE SMALL TEST TANKS

Habitat Area	Proportion of Observations[a]	Proportion of Tank	Litter Differences
Edge***	.00	.03	
Vegetation***	.60	.18	
Wood**	.00	.10	
Crevices	.16	.13	
OWS[b]***	.00	.26	OWS+OWD[c]
OWD[b]***	.06	.30	H=6.88, p<.04

[a]The proportion of observations was the median value of the median values of the proportions for each subject (N=20) during foraging trials.

[b]OWS=open shallow water; OWD=open deep water.

***p<.001; **p<.01, one-tailed probability of a significant difference between the proportion of observations and the proportion of the test tank for a given habitat area using the Wilcoxon one sample singed rank test.

[c]A Kruskal-Wallis ANOVA of litter differences in use of the open water (OWS+OWD) was performed (overall H=6.88, p=.03; 2443 v. 2444 and 2447 H=6.21, p=.01).

Clearly, neonates spent most of their time in the cover areas. The most used area was the vegetation (M=.50-.82 per litter), both just at the edge and deep inside, next to the wall of the tank. The proportion of time spent in the vegetation was significantly higher than what would be expected given the proportion of the habitat area that it comprised (M=.60 v. .178, Z=3.75, p<.0001, Wilcoxon one sample signed rank test, one-tailed). Litter differences were not significant (H=4.44, p=.11), and even differences between the litters using the vegetation least and most did not quite achieve were almost significance (2444 v. 2443 H=3.52, p=.06). The next most used area was the crevices (M=.02-.23 per litter). Crevice use did not differ from the expected (M=.16 v. .133, Z=1.43, p<.15, Wilcoxon signed rank test, two-tailed). Litter differences were again not significant (H=3.65, p=.16), nor were the differences between litters using the crevices least and most (2443 v. 2444 H=3.47, p=.06). Use of the wood was lower than expected (M=.0 v. .10, Z=2.89, p<.01), Wilcoxon signed rank test, one-tailed), and was used at a uniformly low rate by all litters (litter M=.0=.02; overall H=.78, p=.78).

Foraging behavior: Foraging behavior is summarized in Table V-2 below. The neonates were in motion varying amounts of time. Litter differences were extreme (H=10.55, p<.0001), with litter 2443 moving much less than the other two (litter 2443 M=.23, litter 2444 M=.71, litter 2447 M=.61; 2443 v. 2444 and 2447 H= 8.08, p<.005; 2444 v. 2447 H=1.35, p>.20). The litters did not otherwise differ in the proportion of time spent in various behaviors. The neonates' heads were above the surface, actually at the surface, about as often (M=.47-.56) as they were under (M=.41-.50). These rates are not significantly different (Wilcoxon signed rank test

TABLE V-2

PROPORTION OF FORAGING TIME SPENT BY NAIVE NEONATE *NERODIA RHOMBIFERA* IN SELECTED BEHAVIORS IN THE SMALL TEST TANKS

Behavior[a]	Proportion of Foraging Time[b]	Litter Differences[c]
Moving	.56	H = 10.55, p < .0001
Swimming	.00	
Diving	.03	
Substrate crawling	.04	
Submergent cruise	.39	
Non-capture attacking	.00	
Above water	.53	
Below water	.45	

[a]Behaviors are described fully in Chapter II. Moving = proportion of foraging time spent moving; the time spent moving was not statistically different than the time spent not moving (Wilcoxon signed rank test, Z = .423, p = .67, two-tailed probability); substrate crawling = crawling prone on the underwater substrate; submergent cruise posture (CCD): the body is on the underwater substrate with the head and neck raised up, but the head still underwater; non-capture attacking = attacking, but not capturing prey; above water = the snake is in a water covered area with the head at or above the surface of the water; below water = the snake is in a water covered area with the head below the surface of the water. The difference in the proportions for above and below the water was not significant (Wilcoxon signed rank test, Z = 1.25, p > .20, two-tailed probability).

[b]Proportion of foraging time is the median of the median values for the proportion of foraging time for each subject (N = 20).

[c]A Kruskal-Wallis ANOVA of litter differences in the proportion of time spent moving was performed (overall H = 10.55, p < .0001; 2443 v. 2444 and 2447 H = 8.08, p < .005).

$Z = 1.25$, $p > .20$, two-tailed). In terms of underwater behaviors, the young snakes dived some (litter M=.01-.06); substrate crawled some (litter M=0-.04); and swam little (M=0 for all litters).

Predatory behavior: Predatory behavior accounted for 11-13% (litter medians) of the foraging time. The attack rate was low in that there were few unsuccessful attacks: 41 of the 57 attacks (72%) resulted in capture. Litter 2447, in fact, made no unsuccessful attacks.

Most attacks were made at the surface from a cruise posture. While some attacks were made with the entire head above the surface, these were rare and were not differentially analyzed. Attacks are summarized in Table V-3 below. A surprising number (5) of attacks, all successful, were made from midwater and anterior dives. Some individuals in each litter engaged in CCS, CCD, and anterior diving in that order of occurrence. Litter 2444, which made the most attacks, also was the only litter to engage in each attack type. One attack listed here was of a type not recorded in the adults: an attack from a craning posture from on top of the vegetation. Open-mouthed (OM) attacks are listed separately here because they were so rare in the juveniles: 4 attacks were made by 3 individuals, 2 in litter 2443 and one in litter 2444. Surprisingly, 3/4 of these OM attacks, and the only successful one, were made at the surface.

The naive neonates exhibited prey selection as only the Size 2 minnows were captured, although the Size 1 mosquito fish were present in equal numbers and are frequently consumed by this species in the wild. Over 70% of the prey were captured head first. Live prey were reacted to more frequently than dead. Five of the 6 times in which a snake made accidental contact with a dead fish, no capture was attempted. Nevertheless, 7 dead fish were captured. Of these, 3 were ultimately lost.

TABLE V-3

SUMMARY OF ATTACKS MADE BY NAIVE NEONATE *NERODIA RHOMBIFERA* (N=20) IN THE SMALL TEST TANKS

	Postures[a]					
Attacks (N=57)	**CRL**	**DIV**	**CCD**	**CCS**	**CRN**	**Open Mouth[b]**
Unsuccessful (16)	.00	.00	.06	.75	.00	.19
Successful (41)	.02	.12	.27	.54	.02	.02
Sucess rate[c]			**.85**	**.65**		**.25**

[a]Postures: CRL=substrate crawling; DIV=diving; CCD=submergent cruise posture and crevice probing; CCS=cruise posture with the head at the surface; CRN=craning over the water from an emergent structure.

[b]Open-mouthed attacks occurred at the surface (N=3) in the CCS posture, and (N=1) underwater in the CCD posture. The only successful open-mouthed attack in this experiment was made at the surface.

[c]Success rate=successful attacks/successful + unsuccessful attacks for each behavior. Success rates are given only for categories in which there were unsuccessful attacks.

Interestingly, these 3 dead fish comprised the sole prey captured by an individual (in litter 2447).

A total of nine fish were lost after capture. The loss rate for dead fish, then, was 43%, while the loss rate for live fish was only 18%.

The 3 dead fish had been captured by the head but were released in 1-2 intervals. Two of the lost fish had been captured by the tail, but the remainder had been captured by the head. Four of the losses were clearly escapes. However, one fish captured by the tail simply seemed to have been released after 2 intervals of attempted manipulation.

All but one fish were ingested head first; that one fish was ingested tail first. Most prey (27/32=84%) were ingested underwater. Ten fish were converted to a head first position before ingestion, and another was converted but subsequently lost. All but one of the prey conversions took place underwater. While total handling times were longer for converted prey than for prey grasped head first ($H=5.93$, $p=.01$), total handling times were still surprisingly short (M=2 intervals for total handling time for converted and unconverted prey). No litter differences in the direction in which fish were initially grasped ($H=2.05$, $p=.35$) or total handling time ($H=.866$, $p=.65$) were found.

Discussion. *Habitat use*: The neonates, like the adults, avoided the edge area. They also used cover much more than did the adults (compare Table V-1, p. 161 to Table III-1, p.83), although the choice of cover areas differed somewhat, with the neonates using the vegetation more than the crevices. Since the vegetation area in the small test tank was the largest and most dense cover area, it is difficult to know

how significant this preference difference is. In comparing usage of the deep and shallow water, one must remember that deep water in the test tank is still within the range of shallow water in the primary test pool. The neonates did use the deeper water more than the shallower. The deeper water formed a larger coherent pool compared to the shallow water areas which were smaller and bounded by cover areas. Given the tendency of the snakes to use cover, this differential use may be accounted for by the neonates seeking contact with the cover areas in the immediate vicinity. Such contact with the cover would have resulted in their being scored as using cover. Indeed, much of the cover use involved the snakes cruising out from cover areas into the more open water.

Foraging behavior: In terms of behavior, the neonates exhibited rates for the listed behaviors similar to those of the adults (compare Table V-2 to Table III-2 p. 89). In contrast to predictions, the neonates moved more than the adults; indeed, they were in motion as frequently as they were still. However, their movement was not vigorous and exhaustion was thus not a problem. In addition, aquatic locomotion is relatively cheap (Jayne et al., 1988). As in the adults, the neonates were above water as much as below. The rates of these two behaviors were higher in the neonates, however, because there was no out of the water area in which to spend time.

Prey capture: The neonates favored different tactics for capturing prey than the adults. Most interestingly, they used very little OM searching from any posture, and were more likely to engage in this behavior at the surface (CCS-OM) than below. Adults, in contrast, used OM attacks almost 50% of the time, and almost exclusively under water. Even the CCS-OM searching was extremely abbreviated, amounting to a single OM sideways sweep at the prey rather than the usual multiple side-to-side

sweeps. Craning over the water was also used once by the neonates. This behavior was never seen in the adults but is commonly used by the generalist natricines and *Nerodia sipedon* (see Drummond, 1980, 1983). Most of the captures (80%) were made from a cruise posture in the water (CCS), more often at the surface than below (CCD). Interestingly, these postures were two of the three most successful postures in terms of capture success for the adults. Additionally, the attacks used by the neonates were largely inactive sit-and-wait type attacks. The neonates, then, used the tactics that were most optimal for energy intake.

Another notable difference between adults and these naive neonates was the much lower attack rate of the neonates, for whom the successful attacks accounted for the bulk of the attacks. In contrast, successful attacks accounted for a fraction of the total attacks in the adults. Thus, the neonates actually had a higher success rate in terms of the ratio of successful to unsuccessful attacks. The low attack rate would serve to conserve energy.

The neonates further optimized energy gain by capturing only the larger Size 2 minnows. The median meal size was 2 fish, the same as for the adults, for whom the median prey size was also Size 2.

The neonates did lose more fish than did the adults. Like the adults, the neonates lost relatively fewer of the live fish than the dead fish. The neonates otherwise had handling times the same as the adults (for Size 2 prey), M=2 intervals. The neonates captured fish by the head, converted prey underwater and ingested prey underwater at rates similar to those of the adults. In contrast to the adults, the neonates converted all fish not grasped by the head to head first ingestions, thereby avoiding difficult folded or tail first ingestions. This, too, is the more optimal behavior.

Conclusion. Many of the expected behavioral differences between neonates and adults were confirmed. Neonate water snakes used cover areas more than did adults. While they moved more than adults, their overall rates of aquatic behaviors were similar to those of adults. They did use less energetically demanding attacking behaviors than did the adults, and tended to use behaviors which optimize energy intake relative to energy expenditure. Litter 2443 in particular confirmed my expectations neatly by being less active than the other litters, and using open water less than the other litters.

The neonates also used some attack behaviors not seen in the adults that are more typical of aquatic generalists than specialists. The OM behavior was not seen in all naive neonates, and was generally not used underwater in the manner typical of larger conspecifics. This behavior, then, would seem to be subject to developmental, and possibly, experiential processes. The naive neonates did, however, exhibit very well developed prey handling capabilities from the beginning, a phenomenon reported for other natricine aquatic specialists (Halloy and Burghardt, in press).

Experiment 2

Introduction. Experiment 1 showed that the predatory behavior and habitat use of neonate water snakes in the small square test tank differed from that of the adults in the primary test pool. These differences could be due either to the different testing environments or to true ontogenetic differences. Therefore, a second group of neonates was repeatedly tested in the same test tanks as in Experiment 1 over a period of a year. These subjects were about 2 weeks older than the previous subjects

and had some experience with the prey but not the habitat prior to the beginning of testing. In order to minimize habituation to the environment or or other experiential effects, the subjects were tested only a few times at widespread intervals. Two alternative hypotheses were made: 1) if the predatory behavior of these snakes changes over the course of the year to more closely resemble that of the adults in the test pool, then the changes could be related to ontogenetic changes; or 2) if there were no changes over time, or if the behavioral alterations did not result in increasing similarity to the adults, then the differences could be related to the testing environment. The behaviors of interest and the expected changes for hypothesis 1 were as follows: 1) use of open water areas should increase; 2) open-mouthed searching should increase and should take place mostly underwater; 3) underwater attack behaviors in general should increase; 4) predatory behaviors should become more active; 5) overall movement should decrease over time.

Subjects. The 8 subjects tested were born in the laboratory to dam 2419 shortly after her capture at Reelfoot Lake. The neonates were weighed, measured, and housed as for Experiment 1. The snakes were offered live fish in the home cage at weekly intervals from about one week of age. All had eaten prior to the beginning of testing. Weight and length measurements are in Appendix A.

Methods. Snakes were tested 5 times each: the first time at 4-5 weeks of age; the 2nd-4th times at 7-8 months, and the last time at 1 year of age. Since the snakes did not forage during each trial, data from 5 snakes which fed at least during the first, last, and one of the middle trials was used for this analysis. For the first 4 trials, the

prey were the same as in Experiment 1. For the last trial, small and medium size minnows *Pimephales promelas* were used. Thus, Size 1 and 2 prey were available in all trials. In all cases, the snakes had been previously fed the test prey. The snakes had had no experience with the test environment or the natural environment, or with freely swimming fish before the first trial. The methods were otherwise as in Experiment 1.

Data analysis. Data analysis was as in Experiment 1 with the following exceptions. Because ontogenetic changes were the focus of this study, data was analyzed in terms of time periods: time 1 was the first trial; time 2 was the middle trials; and time 3 was the last trial. Since data on more than one trial from time 2 was available for 3 of the snakes, there is pooling (*sensu* Machlis et al., 1985) of data for time 2. This pooling does not seriously inflate the sample size, however.

Results. The habitat-naive but prey-experienced neonates in this study in general behaved similarly to the neonates in the last study, particularly in Time 1. As noted before, the neonates did seem to be somewhat more buoyant than the adults, although the neonates appeared to achieve negative buoyancy easily.

Habitat use: In Time 1, the 2419 neonates used the cover areas, particularly the vegetation and crevices, at a high rate, and used the open water areas less. The 2419 neonates, however, used the vegetation much less (M=.07 v. M=.60), and the crevices much more (M=.46 v. M=.16), than did the litters in Experiment 1 (see Table V-1, p. 161, for habitat use by the subjects in Experiment 1). The wood was used at a similarly low rate by both sets of subjects. The 2419 neonates used the open

shallow water more than did the Experiment 1 subjects, and used the open deep water at a slightly higher but similar rate.

As can be seen in Table V-4, utilization of the crevices dropped sharply over time. Use of the crevices during Times 2 and 3 were similar and lower than in Time 1 (overall $H=4.56$, $p=.10$; Time 1 v. Times 2 and 3 $H=4.55$, $p=.03$). To some degree, the neonates switched to the vegetation, as evidenced by by the increase in utilization over time. Utilization of the vegetation was higher, but not significantly so, in Times 2 and 3 than in Time 1 (overall $H=3.27$, $p=.20$; Time 1 v. Times 2 and 3 $H=2.78$, $p<.10$). Utilization of the wood increased over time also, but later in time. Utilization in Times 1 and 2 were similar and lower than in Time 3 (overall $H=4.80$, $p=.09$; Times 1 and 2 v. Time 3 $H=4.12$, $p=.04$). Utilization of the open shallow water dropped consistently but not significantly over time ($H=.71$, $p=.70$). In contrast, utilization of the deep water increased significantly over time. Rates of utilization during Times 2 and 3 were similar and higher (but not quite significantly) than during Time 1 (overall $H=4.46$, $p=.10$; Time 1 v. Times 2 and 3 $H=3.60$, $p=.06$).

Activity rates as measured by movement changed significantly over time (overall $H=7.83$, $p<.02$), increasing in Time 1 (Time 1 v. Time 2 $H=6.76$, $p<.01$), but dropping somewhat, although not significantly in Time 3 (Time 1 v. Times 2 and 3 $H=6.26$, $p<.01$). Substrate crawling increased significantly over time (overall $H=5.49$, $p=.06$) so that the rates in Times 2 and 3 were higher than in Time 1 ($H=5.41$, $p=.02$). The snakes, in general, were more often under water over time (overall $H=6.68$, $p<.04$; Time 1 v. Times 2 and 3 $H=6.25$, $p<.02$).

TABLE V-4

SUMMARY OF HABITAT USE[a] IN THE HABITAT-NAIVE NEONATE *NERODIA RHOMBIFERA* (N=5) IN THE SMALL TEST TANK OVER TIME[b]

	Proportion of Foraging Time			
Habitat Area	**Time 1**	**Time 2**	**Time 3**	**Significant Comparisons[c]**
Edge	.00	.00	.00	
Vegetation	.07	.31	.38	*1 < 2+3
Wood	.00	.00	.20	**1+2 < 3
Crevices	.46	.19	.18	**1 > 2+3
OWS[d]	.12	.10	.04	
OWD[d]	.07	.16	.15	*1 < 2+3

[a]Habitat use is given as the median of the proportion of time spent in each habitat area by each snake.

[b]The time periods represent trials run at different times during the first year of the snakes' lives. Time 1=4-5 weeks of age; Time 2=7-8 months of age; data for this age represents 1-3 trials; Time 3=1 year of age.

[c]Kruskal-Wallis non-parametric ANOVA were performed on the data; *=.10<p<.05, **=p<.05.

[d]OWS=open shallow water; OWD=open deep water.

Foraging behavior: Foraging behaviors for the 3 Times are summarized in Table V-5 below. The Experiment 2, Time 1 neonates moved at a rate that fell within the range of the Experiment 1 neonates (M=.33 v. M=.23-.70). Additionally, as in Experiment 1, the Experiment 2, Time 1 neonates had their heads above and below the water at similar rates (Wilcoxon two sample signed rank test Z=.81, p=.42, two-tailed test). Other behaviors during Time 1 occurred at rates very similar to those of Experiment 1 neonates as can be seen by comparing Table V-5, Time 1 with Table V-2, p. .

Predatory behavior: While the total amount of time spent on predatory behavior increased over time, the increase was not significant (H=2.58, p=.27). Most of the increase in predatory behavior was due to the rate of attacks, which increased significantly over time, but not until Time 3 (overall H=7.53, p<.03; Time 1 v. Times 2 and 3 H=7.41, p<.01).

As with Experiment 1 neonates, more of the Time 1 attacks were aerial attacks made from the surface, with fewer made from below the surface. Underwater attacks consisted of primarily immobile CCD attacks, with few dive attacks, and no attacks made while substrate crawling. By one year of age, however, the snakes were using more attack postures and predominately attacking from below the surface. Attacking from the substrate crawl did not occur until one year of age. Attacks are summarized in Table V-6.

As in Experiment 1, the Experiment 2, Time 1 neonates engaged in very little open-mouthed searching behavior, and again did so in an atypical manner. Only one individual in this experiment performed this behavior during Time 1. Unlike the

Experiment 1 neonates, however, this individual did have its head at the surface so that his open mouth at least raked the surface. Nevertheless, the attacks

TABLE V-5

PROPORTION OF FORAGING TIME SPENT BY YOUNG *NERODIA RHOMBIFERA* (N=5) IN SELECTED BEHAVIORS IN THE SMALL TEST TANK OVER TIME[a]

	Proportion of Foraging Time[b]			
Behavior[d]	**Time 1**	**Time 2**	**Time 3**	**Significant Comparisons[c]**
Moving	.33	.57	.47	**2+3 > 1
Swimming	.00	.00	.00	
Diving	.03	.00	.00	
Crawling	.02	.12	.07	**2+3 > 1
CCD	.35	.52	.44	
Attacking	.03	.03	.11	***3 > 1+2
Above water	.53	.40	.40	
Below water	.39	.58	.60	**2+3 > 1

[a]The time span is the first year of life for the water snakes divided into 3 time periods. Time 1=4-5 weeks of age; Time 2=7-8 months of age; Time 3=1 year of age. See text for details on testing.

[b]Proportion of foraging time is the median of the median values for the proportion of foraging time for each subject.

[c]Sig. Comp.=statistically significant comparisons ($p<.05$) using Kruskal-Wallis ANOVAs; *** <.001; ** <.01.

[d]Behaviors are fully described in Chapter II. Crawling=crawling prone on the underwater substrate. CCD=underwater cruise posture: the body is on the underwater substrate with the head and neck raised up, but the head is still underwater. Above water=the snake is in a water covered area with the head at or above the surface of the water; below the water= the snake is in a water covered area with the head below the surface of the water.

TABLE V-6

ATTACKS MADE BY YOUNG *NERODIA RHOMBIFERA* (N=5) FROM VARIOUS POSTURES IN THE SMALL TEST TANK OVER TIME[a]

	Postures[b]					
	CRL	DIVM	CCD	CCS	CR-DA	Open-Mouth[c]
Attacks	Time 1-2-3	Time 1-2-3	Time 1-2-3	Time 1-2-3	Time 1-2-3	Time 1-2-3
Unsuccessful (N=32)	0-0-2	0-0-0	4-3-12	6-2-7	0-0-1	2-2-9
Successful (N=65)	0-0-4	2-1-1	2-15-16	2-5-11	1-4-1	0-1-5
Total	0-2-6	2-1-1	6-18-28	8-7-18	1-4-2	2-3-14

[a]The time span is the first year of life for the water snakes divided into 3 time periods. Time 1=4-5 weeks of age; Time 2=7-8 months of age; Time 3=1 year of age. See text for details on testing.

[b]Postures: CRL=substrate crawling; DIVM=mid-water diving; CCD=submergent cruise posture and crevice probing; CCS=cruise posture with the head at the surface; CR-DA=craning over the water from an emergent structure and anterior diving, in which the head is below the surface and the rear of the body is on an emergent structure.

[c]Open-mouthed attacks occurred in various postures over time: during Time 1, at the surface in the CCS posture; during Time 2, from underwater in the CCD posture (N=2, 1 successful) and and from a substrate crawl (N=1); during Time 3, from underwater in a mid-water dive (N=1, successful), underwater in the CCD posture (N=11, 4 successful), and from a substrate crawl (N=2, all unsuccessful).

were unsuccessful. The rate of OM searching increased over time and was performed correctly the next time the snakes were tested. Only one subject captured a fish using this tactic in Time 2, but by Time 3 all subjects had successfully used this tactic. All OM attacks in Times 2 and 3 were made well below the surface. In Time 3, some of the OM attacks were made from while substrate crawling.

The Experiment 2, Time 1 neonates captured all but 1 fish by the head. The sole fish not captured by the head was lost as the snake attempted to reorient it. Thus, over 80% of the Time 1 fish were grasped by the head. The snakes were less careful in the following time periods, with only 54% of the fish being captured by the head. The trend to grasp fish other than by the head was not significant, however (overall $H=2.86$, $p=.24$; Time 1 [N=1/6] v. Time 2 [N=13/25] and 3 [N=13/32] $H=2.33$, $p=.13$).

Only one dead fish was captured in Time 1, and that was released after being held 3 intervals. The Time 1 neonates, then, were more successful with live (6/7= 86% successful) than dead fish (0/1= 0% successful). No dead fish were taken in the later time periods. The neonates exhibited prey size selection, taking predominately Size 2 prey (61/64 fish of known size). Relative prey size did not change over time (M=2 for all time periods).

Looking at the neonates ability to handle fish, it is most interesting that all misgrasped prey were converted to head first ingestions until the later Time 2 feedings when a few conversions were to a tail first rather than head first orientation. During Time 2, 4/8= 50% of the tail first captures were converted, all to head first grasps, and 2 were lost. During Time 3, 4/9= 44% of the tail first captures were converted to head first grasps, and 0 were lost.

As has been previously found for both neonates and adults, handling times for converted prey were longer ($H=5.50$, $p<.02$). Handling times for Time 2 tail first ingestions ($N=3$) were long ($M=5$), whereas handling times for the Time 3 tail first ingestions ($N=7$) were shorter ($M=2$). Overall, total handling times decreased over time, but not significantly until Time 3 (overall $H=23.04$, $p<.0001$; Time 3 v. Time 1 and 2 $H=22.99$, $p>.0001$), so that handling times dropped from $M=3$ intervals to $M=1$ interval.

The neonates ingested most of the prey underwater (76%), and the rate of underwater ingestions did not change significantly over time ($H=2.67$, $p=.26$).

The number of prey captured per trial increased over time from $M=1$ in Time 1, to $M=2$ in Time 2, to $M=4$ in Time 3. This increase was significant (overall $H=15.5$, $p<.0001$); the number of fish captured in Time 1 was significantly less than the number of fish captured in Times 2 and 3 ($H=41.4$, $p<.0001$). The difference between meal size in Times 1 and 2 were not quite significant ($H=2.92$, $p=.09$).

Discussion. Habitat use for Time 1 neonates in this study differed from the neonates in Experiment 1 in terms of use of the vegetation and crevices (compare Tables V-1, p. 161 and Table V-4, p. 173). This difference can be interpreted as a difference in choice of cover area. Time 1 neonates used the OWS more than did the Experiment 1 neonates. The two groups of neonates utilized the edge, wood, and OWD at very similar rates, however. Slight changes in the arrangement of the tank, particularly the vegetation, which was completely changed between experiments, may have led to a shift in preference between the two experimental groups. Litter differences alone probably do not account for the differences because the difference

in utilization of these areas between experimental groups is vastly greater than the differences among litters in Experiment 1. This illustrates the importance of slight differences in habitat structure.

The neonates in Experiment 2 exhibited significant changes in habitat use and behavior during the first year of their life. In general, most of the changes in habitat use occurred early, with the second trial. There was a shift to using deep open water more and the vegetation more, and the crevices less. An increase in the use of the wood did not occur until Time 3. Whether use of the wood should be construed as use of cover or the open is debatable because of the very open nature of the wood in the test tank. The snakes were completely visible while in the wood, but were often quite hidden while in the crevices and vegetation. What was clear, however, based on the use of the vegetation, crevices, wood, and deep open water, and my testing notes, was that the neonates tended to spend more time in the front tank in later trials. This is where the wood and open, deep water were located. The snakes also used the vegetation at that end of the tank, cruising out from it over the open area of the tank. The snakes rarely moved across the front of the tank in the first trial, but were noted spending much time at the front in the last trial. The front of the tank undoubtedly had a more open appearance to the neonates in the tank as it faced the darkened room. It may be argued, then, that the neonates spent even more time in open areas later than is indicated by use of the open water area.

The Time 1 neonates exhibited rates of behavior very similar to those of Experiment 1. The two week difference in age between the two groups and such habitat differences as may have existed, then, probably was inconsequential. The low rates of attack and of OM attacks, in particular, in Time 1 were consistent with the results of Experiment 1.

The rates of change were not uniform over time. The changes in behaviors not specifically associated with predation (*i.e.*, moving, substrate crawling and head below water) were apparent by Time 2 so that Times 2 and 3 were statistically similar and different from Time 1. The rates for the various behaviors in Table V-7 below show a general trend toward rising to a peak in the 7-8 month old snakes and dropping after that. While the changes are surprisingly uniform across time, I can offer no satisfactory explanation for this curvilinear change as it may result from any of a variety of causes ranging from laboratory artifacts to natural changes in the rate of growth.

Predatory behaviors changed over time in a more linear manner. The increase in general predatory behavior, *i.e.*, rate of attacking and large increase in OM attacking, did not occur until Time 3. The shift to underwater attacks, that is, from CCS to CCD attacks, was apparent in Time 2. Attacks made from mid-water dives, anterior dives, and craning did not change over time. It can be argued, then, that ontogenetic changes in 1) the rate of attacking, 2) the rate of underwater attacking 3) the rate of OM attacking, and 4) the rate of attacking while substrate crawling appear to have occurred during Experiment 2. The direction of change for the predatory behaviors is consistent with ontogenetic change as the rates of Time 3 animals are more similar to those of adults as can be seen in Table V-8 for attack types. As can be see in Table V-9, however, both meal size and the ratio of captures to total attacks follow the same curvilinear change over time, suggesting that the these changes in non-predatory behaviors are associated with changes in feeding.

All but the last predicted change in behavior were met for the first of the alternative hypotheses to be accepted. The most important predictions, those concerning qualitative and quantitative changes in predatory behavior were

TABLE V-7

PROPORTION OF FORAGING TIME SPENT BY THE VARIOUS AGE GROUPS OF *NERODIA RHOMBIFERA* IN SELECTED BEHAVIORS

Behavior[b]	Proportion of Foraging Time[a]				
	Prey-naive Neonates[c] (N=20)	4-5 Weeks[c] (N=5)	7-8 Months[c] (N=5)	One year[c] (N=5)	>Two year[c] (N=21)
Moving	.56	.33	.57	.47	.34
Swimming	.00	.00	.00	.00	.00
Diving	.03	.03	.00	.00	.00
Crawling	.04	.02	.12	.07	.05
CCD	.39	.35	.52	.44	.28
Attacking	.00	.00	.03	.13	.03
Above/below water	1.18	1.36	.69	.67	.97

[a]Proportion of foraging time is the median of the median values for the proportion of foraging time for each subject.

[b]Behaviors are fully described in Chapter 2. Moving = being in motion; diving = mid-water or anterior diving; crawling = crawling prone on the underwater substrate; attacking = engaging in non-capture attack; above/below water = the ratio of time the snakes spent above and below the water; above water = the snake is in a water covered area with the head at or above the surface of the water; below water = the snake is in a water covered area with the head below the surface of the water.

[c]Prey-naive neonates = Experiment 1 subjects; 4-5 weeks = Experiment 2, Time 1 subjects; 7-8 months = Experiment 2, Time 2 subjects; one year = Experiment 2, Time 3 subjects; >2 year = primary test pool subjects.

TABLE V-8

SUMMARY OF ATTACKS MADE BY THE VARIOUS AGE GROUPS OF *NERODIA RHOMBIFERA*

	Postures[a]					
Group[b]	**CRL**	**DIVM**	**CCD**	**CCS-A**	**CR-DA**	**Open Mouth**
Neonates	.02	.02	.25	.63	.08	.07[c]
4-5 Weeks	.00	.12	.35	.47	.06	.12[c]
7-8 Months	.06	.03	.56	.22	.06	.09
1 Year	.11	.02	.51	.33	.11	.24
>2 Years	.27	.08	.48	.11	.27	.49

[a]Postures: CRL = substrate crawling; DIVM = mid-water diving; CCD = submergent cruise posture and crevice probing; CCS-A = cruise posture with the head at or above the surface; CR-DA = craning over the water from an emergent structure and anterior diving, in which the head is below the surface and the rear of the body is on an emergent structure.

[b]Groups are defined as follows: neonates = Experiment 1 subjects; 4-5 weeks = Experiment 2, Time 1 subjects; 7-8 months = Experiment 2, Time 2 subjects; one year = Experiment 2, Time 3 subjects; >2 year = primary test pool subjects.

[c]Open-mouthed attacks tended were made at the surface or above, rather than below the surface as in older snakes.

TABLE V-9

SUMMARY OF SELECTED MEASURES OF PREY HANDLING IN THE VARIOUS AGE GROUPS OF *NERODIA RHOMBIFERA*

Measure of Prey Handling[b]	Age Group[a]				
	Prey-naive Neonates (N=20)	4-5 Weeks (N=5)	7-8 Months (N=5)	One year (N=5)	>Two years (N=21)
Captures/Total attacks	.72	.41	.83	.66	.34
Prey loss after capture	.18	.17	.08	.00	.07
Head 1st grasps	.71	.86	.45	.50	.72
Head 1st ingestions	.97	1.00	.87	.81	.45
Underwater ingestions	.84	.60	.78	.79	.74
Total handling time	2	3	3	1	2
Meal size	2	1	2	4	2
Prey size	2	2	2	2	2

[a]Age groups are defined as follows: prey-naive neonates = Experiment 1 subjects; 4-5 weeks = Experiment 2, Time 1 subjects; 7-8 months = Experiment 2, Time 2 subjects; one year = Experiment 2, Time 3 subjects; all of these were tested in the small square tanks; >2 year = primary test pool subjects of various ages and sizes.

[b]These measures of prey handling are fully described above and Chapters III and IV. All values are the median of the median value for each subject. Total handling time is given in terms of 30 sec intervals. Prey size is relative to the snake which preyed upon it; table values for the adults are for Size 2 fish only. Size 2 prey are approximately equal in maximum width the maximum width of the snake's head. See Chapter II for details. Median values are used for total handling time, meal size, and prey size.

confirmed. An important exception is the unexpected large effect from slight differences in the vegetation. The snakes in this study were sensitive to the amount of cover, but not the nature of the cover. Nevertheless, it would seem safe to accept the first hypothesis: the changes are accepted as true ontogenetic changes.

General discussion

Experience v. maturational processes. It is difficult to know whether experience or maturational processes or both are important here. Since there are differences in the onset of changes, and many of the changes are qualitative rather than just quantitative, maturational processes would seem to be the more likely explanation. This seems especially so for the onset of OM attacks. An experiential component is suggested by the fact that OM attacks improved gradually over time. However, more experience did not lead to more OM attacks, as the 3 snakes who captured fish in more than 3 trials did not exhibit the higher rates of OM searching. Furthermore, the only snake who OM attacked in the first trial did not exhibit the highest success rate at one year of age, but did consistently exhibit a high attack rate. As was found for the adults in the primary test pool, the rate of OM attacks are correlated with the rate of other kinds of attacks.

Experience seemed to play a role in prey handling and ingestion. Here, the reduction in handling time was steady across time. This steady reduction is hardly surprising since the snakes had experience in these behaviors between trials. This improvement in performance has has been found to occur during the first feedings in other natricine snakes (Burghardt, 1978; Halloy and Burghardt, in press). What is

particularly interesting here is that the snakes became less careful in grasping fish by the head and by Time 2 did not always convert to head first ingestions. This result is at odds with the increase in head first grasps which occur in other natricines, including the aquatic specialist, *Thamnophis melanogaster* from birth to maturity (Halloy and Burghardt, in press). The snakes, by Time 3, did not lose prey grasped by the tail, but were able either to convert or swallow tail first. No snakes in this study swallowed prey folded (mid-body first) in the first year of life. Nevertheless, grasping by the head would be the more optimal behavior in terms of preventing loss of the fish and in terms of reduced handling time.

Comments on the role of experiential or maturational processes in prey handling capabilities. Conversion of prey, *per se*, however, required no experience as the neonates did it quite well the first time it was attempted. The ability of neonatal snakes to convert to a head first grasp seems to vary among natricine groups, with the more highly piscivorous species exhibiting such an ability (Halloy and Burghardt, in press). Some expertise was gained in terms of a reduction in prey loss during conversion. What the snakes appeared to learn, was *not* to convert prey to head first, but simply to ingest tail first, even though tail first ingestions required more time.

The snakes also captured and ingested a greater range of prey with age, taking more small fish later and more dead fish. (The adults ate enough larger [Size 3] fish also, so that median prey size remained the same; juveniles were not offered larger fish.)

The snakes, then, as they matured 1) exhibited a greater range of prey attack and handling tactics, and 2) tended to use tactics which were more costly in terms of

time and, probably, in terms of energy expended. The character of the observed changes in prey handling tactics is similar to the observed changes in prey capture tactics. While the possible selective value of these changes is not apparent, these changes are in accord with the known physiological differences between neonate and adult water snakes. That is, juvenile snakes have less aerobic scope than do adults and consequently tire faster (Pough, 1977, 1978). The behavioral patterns exhibited by the youngest snakes would also keep them in the more predator-free areas where small minnows and juvenile fish are available as food. These small fish proved to be readily catchable at the surface by the neonates in their CCS or CCA posture. As the snakes grow, their risk of predation is reduced, they can then safely afford to be underwater in more open, deeper water. With less predation risk and relaxed need for the fastest growth rate possible, there is less pressure to optimize food intake in terms of time or energy expended.

Problems of inference in this study. It is important to bear in mind that the youngest age groups in this study were laboratory born and reared, and had never been exposed to predatory, climatic, or social pressures. Therefore, any alteration of the direction of changes from the one year olds to the last group may reflect the role of "real world" experience. The prey handling characteristics which changed (see Table V-9 above) are the capture to attack ratio, the rate of head first grasps, meal size and total handling time. All but the changes in meal size and handling time are an improvement in predatory performance. While the lower capture/attack ratio can be interpreted as a decrease in the success rate, it might best be interpreted as an increase in the attack rate. A higher attack rate was found in the specialist garter

snakes than in the generalists (Drummond, 1980, 1983). The changes in total handling time and meal size are not easily explainable, but may reflect the decreased energy needs of older snakes. While this study did not involve exposure to predators, the fairly steady rate of underwater ingestions in all groups may be pertinent in this regard.

3. FIELD DATA

Introduction and Methods

Introduction. The results of field work to be presented here will attempt to address the question of external validity: Do water snakes of various size (age) classes behave in the in the field as in the testing environments? Specifically, this analysis will address the question of changes in habitat use, *i.e.*, cover, open water, and depth of water as a function of snake size and sex, and changes in foraging behavior, *i.e.*, substrate crawling, open mouth searching, and passive (CCS or CCA posture) foraging versus active foraging as a function of snake size. Additionally, the behavior of gravid females will also be addressed as the tests in the primary test pool showed that foraging gravid females used the beach more than did the non-gravid snakes. Finally, field data to be presented here will be used to address the question of where larger snakes capture larger prey.

Data collection. Methods of data collection are discussed in Chapter II.

Data analysis. Data presented here has been analyzed in the same manner as the test pool studies. Since the water level in the three study grids dropped through the summer and utilization of the study grids changed accordingly, differences in the study grids will not be considered here. Instead, habitat use will be related only to the variables discussed above. Data on snakes found in other areas along the lake will be pooled with information taken from the study grids.

To ease recording and analysis of data, water depth was recorded as categories spanning 15 mm. For some analyses, snake sizes (SVL) were lumped into categories spanning 100 mm, except that the categories for the smallest and largest snakes spanned a greater size range.

Results

General information. Information was collected on over 130 different snakes. Since not all types of information (*e.g.*, sex, stomach contents) was available for each sighted snake, each analysis has a different sample size. The water snakes were quite nocturnal at Reelfoot Lake, but were often seen swimming parallel to and near shore during the day. Snakes were also seen moving around in the large clumps of the "cut-grass" *Zizaniopsis miliacea* in several of the "pocket" marshes at Reelfoot Lake. Some daytime activity by very large snakes (over 800 mm SVL) was observed in isolated sloughs. Basking by snakes in the 500-700 mm SVL size range on cypress limbs and snags near shore in the open lake during the day was common in areas

where stands of small cypress trees or button bushes occurred near shore in shallow water. Very small snakes (<400 mm SVL) were seen only at one fishing camp in a shallow area choked with water lilies. Gravid snakes were seen basking on snags and sea walls occasionally. Some snakes appeared to reside in the covelets in cavities within the cypress trees, as water snake heads were occasionally seen peering out from the base of trees during the day and at dusk.

I only saw one snake feeding during the day. That was an individual, at least a meter SVL, attempting to ingest a large dead carp that it found (I had reviously seen the fish there) on the edge of a man-made canal called Donaldson Ditch. The typical pattern was for foraging to begin almost immediately at dark as the snakes swam into the covelets. Unless disturbed, snakes could be seen swimming individually parallel to shore without pausing. The first snakes out at night were usually seen to pause at the mouth of the covelet in a cruise posture before entering. The snakes tended to stay close to structures such as docks, seawalls, and cypress trunks, knees and roots. Later in the evening, entrance into the covelets was less frequently witnessed, and the snakes were discovered in the covelets in a variety of activities.

Habitat use: Foraging began almost immediately at dark with the movement of snakes into the covelets. Unless disturbed, the snakes swam parallel to shore and near shore into the mouth of the covelet without pause. Upon reaching the covelet, the snakes usually paused in a cruise posture with the head out of the water (CCA posture). The snakes course generally kept them close to structures such as docks, seawalls, and cypress trunks, knees, or roots. The association with structures was pronounced. The snakes were sighted near (<1 m) some sort of structure 82 % of

the time, the snakes seen in open water (18%) were either in water < 15 cm deep, were at the water's edge, or were swimming to another area. Small snakes (<400 mm) were especially likely to be found in, or in contact with, cypress knees, exposed tree roots, logs, and stumps: 82 % of the snakes of this size were in contact with wood. The favored habitat areas were not used randomly as snakes, although usually found alone, were cited in the same locations repeatedly as can be seen in Figure V-1. (All snakes were sighted next to different grass clumps or wood in Study Grid III.) Multiple sightings (4-6) were made at some structures: in particular, repeated sightings were made at one log and one clump of smartweed in Study Grid I (definitely different snakes) and one knee in Study Grid II (probably repeated sightings of the same snake).

Snakes were in water 7-30 cm deep in 81% of the nighttime sightings, and only the larger snakes were in deeper water; this differential use of water depths was statistically significant (Kruskal-Wallis ANOVA, $N = 133$, $H = 12.97$, $p = .043$). The average rank for each size range showed a smooth increase in rank, or increasing depth of water, with each size category until the >900 mm category, whose rank was similar to that of the 401-600 mm SVL snakes. Inspection of the data for these snakes showed that all but one snake in this category was a gravid female. Therefore, another analysis of water depth and SVL was made, using only data from non-gravid snakes. This analysis produced similar ($N = 128$, $H = 16.77$, $p < .02$) but clearer results, with the rank of the largest size category being much higher than that of the lower size categories, although only one snake was now in this category. Table V-10 summarizes this test and shows the median water depth in which the snakes of each size category were found. As would be expected, the gravid snakes used significantly shallower water than did the non-gravid snakes in the two larger size categories

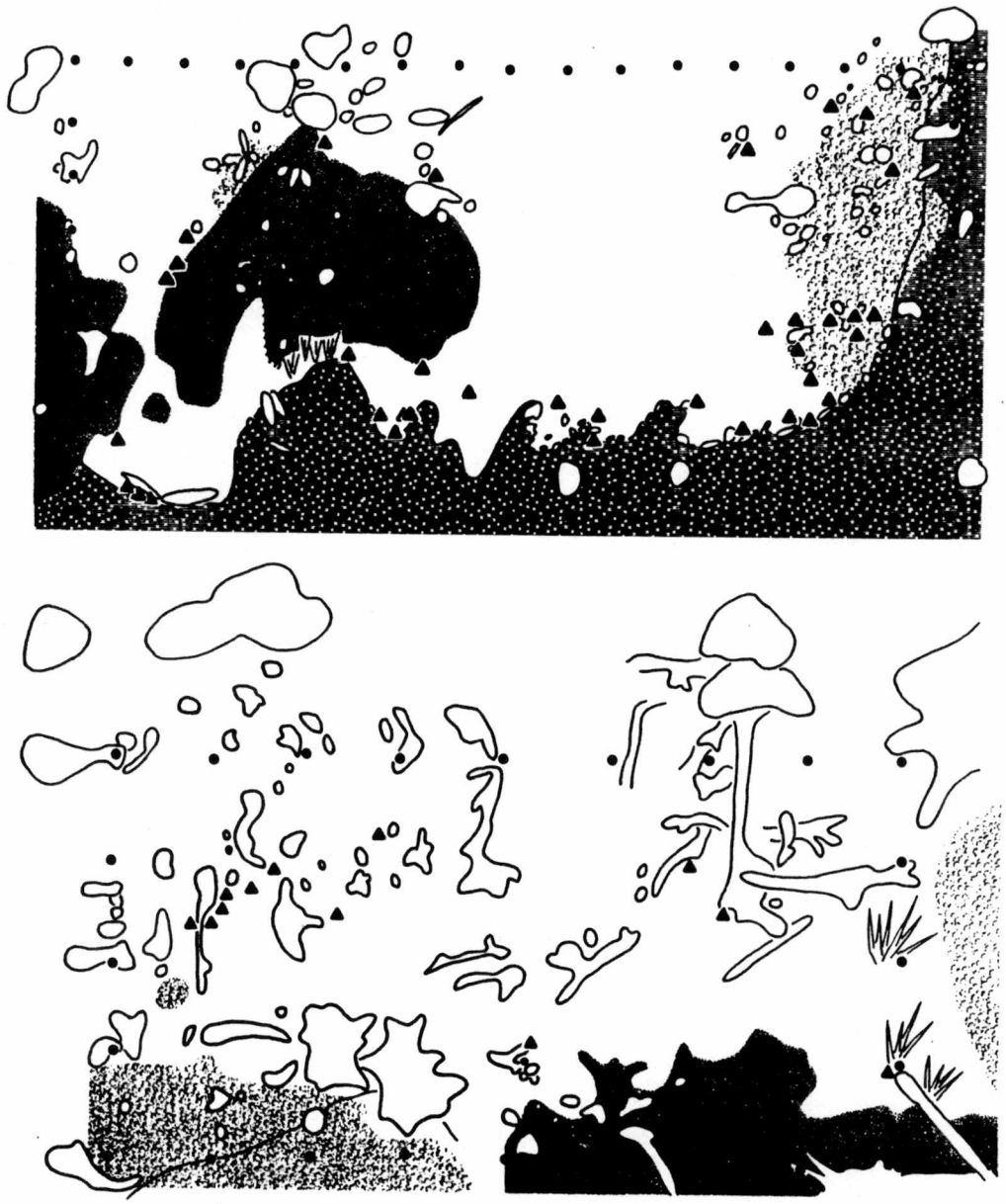


Figure V-1. Maps of Study Grids I and II at Reelfoot Lake, Tennessee showing the sightings of *Nerodia rhombifera* in June and July. Maps are not drawn to the same scale. The circles in each map represent flagged stakes spaced 2 m apart used to mark the quadrats; only stakes around the perimeter are shown. In Study Grid I (at the top of the page), the broken hatching represents dry grass-covered land. Study Grid II (at the bottom of the page) had no dry land, only a small area of moist ground covered by varying amounts of vegetation. The edge is represented by the curved line near the bottom of the map. In both maps, the dark stippling represents thick vegetation; the lighter pattern represents sparse vegetation; the open circular and large, open irregular shapes represent wood such as cypress trees, knees, and stumps; the open elongate shapes represent exposed cypress roots; and The triangles represent sightings of snakes.

TABLE V-10

WATER DEPTHS IN WHICH NON-GRAVID *NERODIA RHOMBIFERA* OF VARIOUS SIZES WERE FOUND AT REELFOOT LAKE, TENNESSEE

Size Category (mm)	Number[a] of Snakes	K-W ANOVA[b] Rank	Median Water Depth (cm)
<400	12(9)	33.67	<15
401-500	34(33)	65.07	15-30
501-600	22(20)	58.45	<15
601-700	29(28)	68.81	15-30
701-800	13	71.35	15-30
801-900	13	83.04	15-30
>901	1	113.00	30-45

[a]The number of snakes represents the number of sightings, some of which were the same individuals. The known or probable number of individuals is given in parentheses.

[b]Kruskal-Wallis ANOVA was performed on the data, $H = 16.77$, $p < .02$. The analysis also included another category of 4 snakes whose size could not be determined because they were not captured or were not visible long enough. Their rank was 59.5, and median water depth was 15-30 cm.

(H=4.64, p<.03). Median water depth for gravid snakes (size categories 801-900mm and >901 mm SVL) was <15 mm, whereas median water depth for non-gravid snakes of the same size was 30-45 cm. Although sex and size covary, an ANCOVA showed that the sexes did not differ significantly in water depth (covariate SVL $F_{1,66}=6.39$, p=.014, main factor sex $F_{1,66}=2.32$, p=.13).

While the larger non-gravid snakes were found in deeper water than the smaller snakes, the larger snakes were also found in a greater range of depths, so that the distribution of water depths was broader and flatter in shape as illustrated in Figure V-2. As can be seen from this figure, the smallest size class of snakes was found only in water at the edge and water up to 30 cm deep, whereas the largest snakes were found rather evenly distributed from shore to the 60-75 mm depth.

Few snakes were found out of the water. Only two snakes were found active on shore; the smaller of the two was 762 mm SVL. Both snakes on shore were attempting to ingest very large dead fish. In past years of work at Reelfoot, only 2 other snakes were found on shore, and they, too, were large (>700 mm SVL) snakes attempting to ingest very large fish. In all cases, however, the snakes were within 2 m of the edge of the lake on open grass. Two snakes were found resting on shore, both stretched out on limbs over water. Both individuals were very large (>985 mm) and gravid.

Contrary to expectation, the proportion of snakes using cover (vegetation or wood) as compared to being in the open was similar for all size categories (G=2.48, df = 2, p>.05) as shown in Fig. V-2. However, when only the use of truly open water is considered, only snakes larger than 500 mm SVL were ever found in open water, and the utilization of open water by the smallest snakes differed statistically from that of the larger snakes (G=166.32, 2 df, p<.001). Additionally, large snakes associated

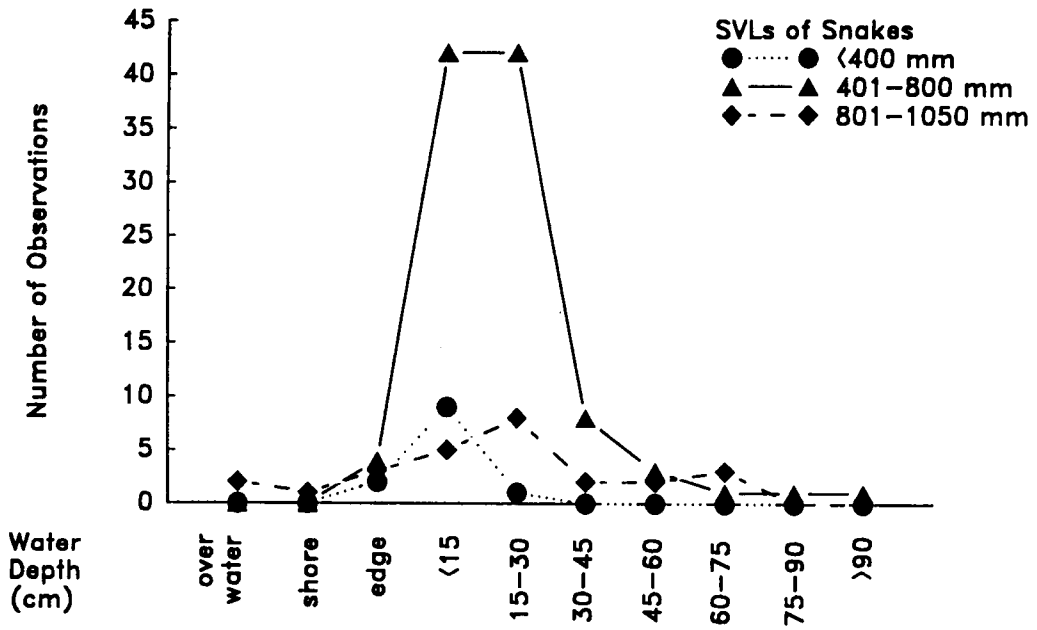


Figure V-2. Water depths at which *Nerodia rhombifera* of different size classes were found at Reelfoot Lake, Tennessee.

with structures tended to be on top of rather than in or beside such structures, thus placing them in the open. Thus, only relatively large snakes were in open water, and the largest snakes were more likely to be found in very exposed positions than the smaller snakes.

As shown in Fig. V-3, utilization of particular cover areas changed with snake size, also. Applying the categories of snake size which were found to be similar in the analysis of the water above, association with wood was significantly more common in the smaller snakes ($G=6.84$, $df=2$, $p<.05$), 73% (<401 MM) of which were associated with wood, than in the larger snakes, 26% (401-800 mm) and 21% (>800 mm) of which were associated with wood. In contrast, association with vegetation was significantly higher in the larger snakes ($G=159.1$, 2 df, $p<.0001$),with only 9% of the smallest snakes (<401 mm) being found in association with vegetation and 29% and 42% of the larger snakes (401-800mm and >800 mm respectively) being associated with vegetation.

Foraging behavior: Marked behavioral differences were seen in the various size categories. The smaller snakes were behaviorally cryptic. No snakes under 500 mm SVL were seen swimming in the open; only one, on a bush in 15-30 cm of water at night was found resting (stretched out prone or in a coil) in the open. The proportion of snakes resting in the open differed significantly among the size groups ($G=7.12$, $df=2$, $p<.05$). Most (58%) of the smallest size group were in a stationary CCS-A posture in shallow water. None of the smallest snakes substrate crawled, although diving was observed. The medium sized snakes were found in the widest variety of behaviors, including CCS-A (45%), resting (11%), substrate crawling (8%),

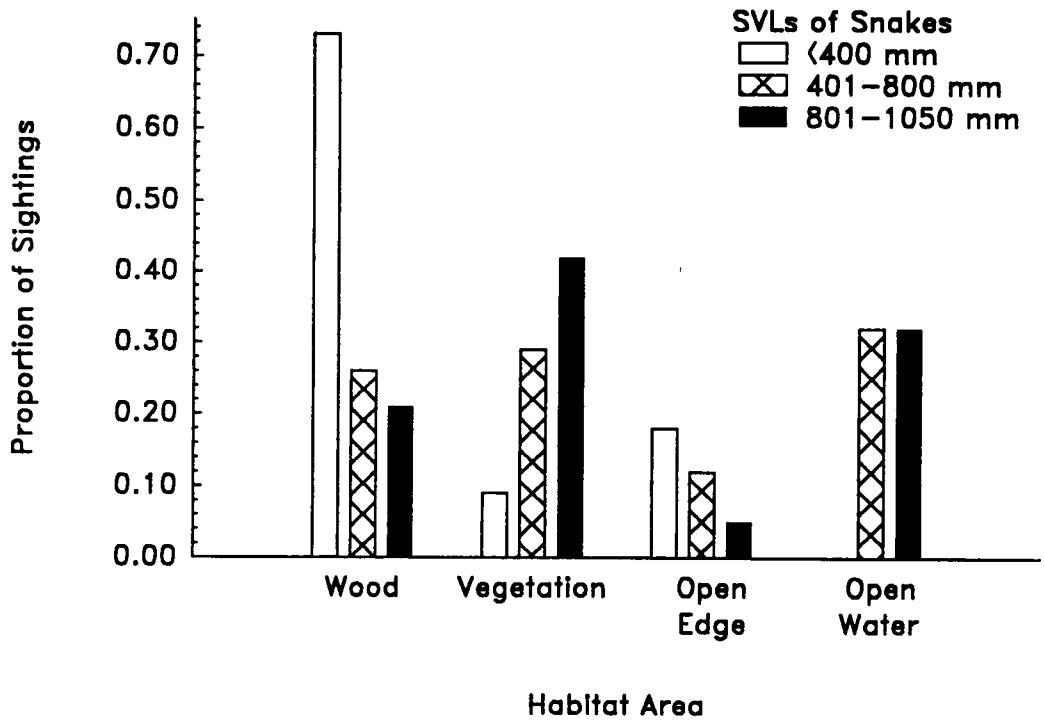


Figure V-3. Proportion of different size classes of *Nerodia rhombifera* sighted at Reelfoot Lake, Tennessee in relation to various structures and open water. Only non-resting snakes were used in this analysis because some large snakes rested on wood in open water, which confuses issues. Habitat areas are defined as follows: Wood = any type of wooden structure in the water such as cypress roots, knees, and diving (19%), trunks, logs; Vegetation = any kind of emergent plant in the water such as cut grass, smartweed, lotus, lizard tail; Open edge = edge area not protected by wood or vegetation such as boat ramp or sandy edge; Open water = open water away not in contact with the edge or a structure of any kind.

and swimming, probing in rock crevices and vegetation and eating occasionally. The largest snakes were found resting in the open 36% of the time, probing in the vegetation (14%), in a stationary CCS-A posture (32%), and swimming and diving occasionally. Interestingly, these snakes were not observed substrate crawling. The proportion of snakes found in the CCS-A posture in water dropped consistently across size categories, but the change in proportions was not statistically significant due to the small sample sizes in some size categories ($G=3.16$, 2 df, $p>.1$)
Snakes in water over 30 cm deep (all >400 mm SVL) were engaged in a limited range of behaviors: swimming ($N=3$), resting on floating limbs ($N=6$), or maintaining a CCS-A posture while attached to a cypress knee ($N=5$), probing on top of emergent vegetation ($N=4$), and diving ($N=1$). Behavioral data, including predatory behavior, is summarized below in Table V-11.

Predatory behavior: As happens in most field studies of snakes, very few prey captures were witnessed. Twenty-nine percent of the snakes sighted were foraging, however, using the observation of attacks as the criterion for foraging. The smallest size snakes were foraging actively, although many were observed in the stationary posture. The low attack rate of smaller snakes makes it likely that more of these snakes were foraging than was apparent (25%). The medium size snakes again engaged in the widest variety of predatory behaviors. The OM circling was seen only in these snakes. All OM searching occurred in water shallower than 30 cm, and most (70%) in water less than 15 cm deep. Substrate crawling followed a similar pattern.

TABLE V-11

PROPORTION OF DIFFERENT SIZE CLASSES OF *NERODIA RHOMBIFERA* SIGHTED IN VARIOUS BEHAVIORS AT REELFOOT LAKE, TENNESSEE

Behavior[a]	Size Classes (mm)		
	<400 N=12	401-800 N=93	>800 N=22
Resting in open	.08	.11	.32
Emergent cruise + OM	.58	.45	.32
Swimming in open	.00	.08	.04
Substrate crawling	.00	.08	.00
Diving + submergent OM	.25[b]	.19	.04
Crevice/vegetation probing	.08	.06	.14
Eating/food stealing	.00	.03[c]	.09

[a]Resting in open = lying coiled or stretched out with the body completely exposed; emergent cruise + OM = sitting still in an emergent cruise posture and/or open-mouthed attacking just below the surface with the eyes at the surface at least some of the time; swimming in the open = swimming in open water; substrate crawling = crawling submerged on the bottom; diving + submergent OM = mid-water diving and/or open-mouthed searching while diving or circling underwater; crevice/vegetation probing = probing in underwater rock or concrete crevices or probing at the base of emergent vegetation at or below the surface; eating/food stealing = found in the process of ingesting food or attempting to steal food from another snake.

[b]No snakes in this size class engaged in highly active OM searching; the sole observation of OM searching took place while the snake was attached to a cypress root.

[c]Only eating was observed in this size class.

All observations of feeding were in water less than 30 cm deep, although 2 snakes were observed attacking in water 30-45 cm deep.

All OM circling, which was qualitatively similar to that seen in the test pool, was done in very shallow water over smooth, sandy substrate in covelets. This observation was also made in previous years, because the OM circling was seen only in certain locations during each visit. While very shallow water and the nature of the bottom seemed to be requirements, some other factors must be important because the behavior was not seen in many areas which met the stated requirements. OM circling was not stereotyped, and did not result in further concentrating or entrapping prey.

The largest snakes were not seen attacking prey although large snakes, including gravid females, were found to have food in the guts about as often as smaller snakes (all captures, divided into five size classes, $N=79$, $X^2=5.59$, $df=4$, $p=.23$; captures >800 mm SVL, gravid [$N=13$] v. nongravid [$N=4$], ANOVA $F_{(1,16)}=1.005$, $p=.33$). A snake (male) in this size class, however, was observed consuming a large fish, and another (female) was seen attempting to steal a large dead fish (kleptoparasitism) from another snake (male) on shore. The would-be thief was first observed at the edge, about to approach the snake on shore attempting to ingest a very large fish that was clearly carrion. The other observations of large snakes foraging were of a gravid snake orienting toward fish from a CCA posture, and another diving in a manner generally associated with OM foraging.

Since so few large snakes were actually seen foraging, gut content analysis was helpful in determining the diet of the large snakes relative to the small snakes, and simultaneously checking for sex differences. Generally, rather small amounts of food were present in the stomach, and most had been eaten within hours of capture

judging by the minimal amount of digestion. Total prey weight was only $\bar{x}=16.92+31.7$ g, and the number of items ranged from 1-35, $\bar{x}=5.2+7.3$. An ANCOVA of total weight of the stomach contents, with SVL as the covariate and sex as the main factor indicated that sex was not an important factor ($F_{1,24}=.257$, $p=<.62$), but that SVL was ($F=_{1,24}=11.08$, $p<.03$). Fig. V-4 below illustrates the relationship among sex, SVL and weight of stomach contents. Since most stomachs which had large food items also had only one item, the results of an ANCOVA relating the weight of the largest item to SVL and sex gave almost identical results: (covariate SVL $F_{1,24}=8.31$, $p<.01$; main factor sex $F_{1,24}=.390$, $p=.55$). The number of items in the stomach was related to neither SVL or sex, however (ANCOVA SVL $F_{1,24}=.388$, $p=.55$, sex $F_{1,24}=1.04$, $p=.32$). Most prey items were the fry of sunfish *Lepomis* species, or of Mississippi silversides (*Menidia audens*) and weighed about .35 g (based on the mean prey weight of 5 snakes 427-1005 mm SVL). Larger prey (> 5 g weight) consisted of basses (*Micropterus* spp.) and shad (*Dorosoma cepedianum*), and bullhead catfish (*Ictalurus* species). The three largest items (75-162 g) were shad, and two were definitely carrion. The third, palpated from a gravid female, appeared to have been dead when eaten because one eye was sunken into the socket. While only the largest snakes ate very large prey (>25 g), large snakes also ate very small prey, and the mean prey size was less than 1 g. Gut contents were similar to the samples of fish seined from the study grids in terms of sizes and types of fish although no shad were seined. Large dead shad were often seen on shore or caught in tree roots, however. Basses and bream were seen becoming trapped in tree roots and were captured after becoming so entrapped.

Most stomachs were empty until the July-August visit when most all stomachs contained food. Water temperatures at this point were always above 29.5 °, ranging

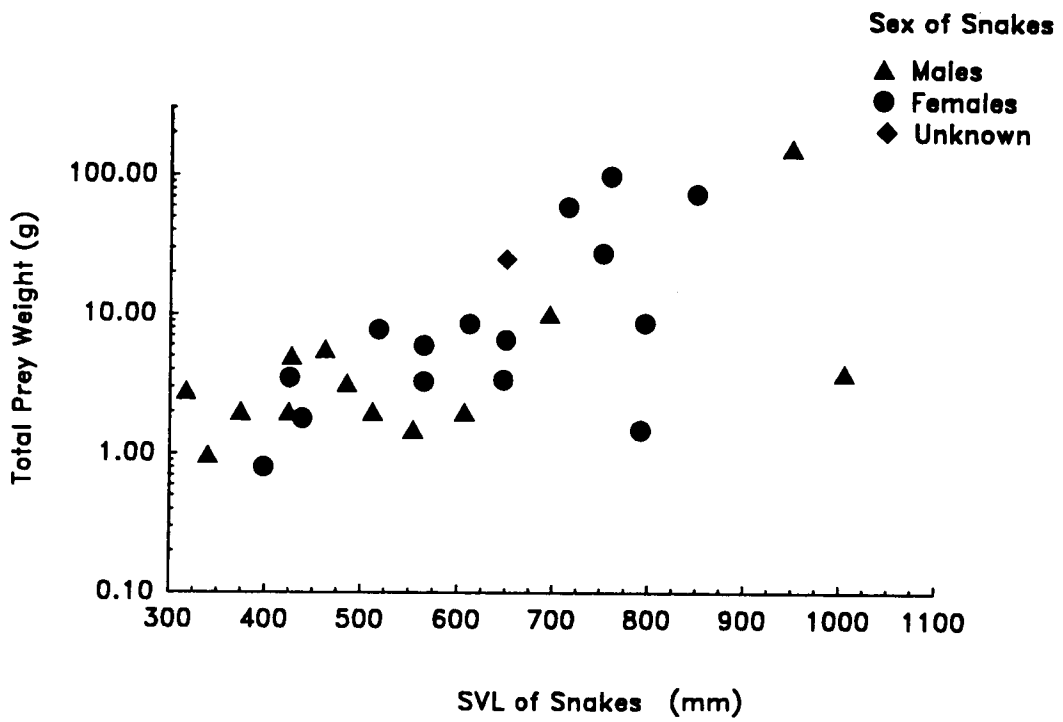


Figure V-4. Plot of the log of the weight of the stomach contents for the different size classes and both sexes of *Nerodia rhombifera* at Reelfoot Lake. An ANCOVA of the total weight of the stomach contents, with SVL as the covariate and sex as the main factor indicated that sex was not an important factor ($F_{1,24}$ = .257, p = < .62), but that SVL was ($F_{1,24}$ = 11.08, p < .03)

up to 36°. Water temperatures were lowest at shore and were 1-2.5 degrees C higher at the deeper open water in the study grids. Open lake temperatures were reported to be as high as, or higher than the study grid temperatures (Dr. W. Smith, University of Tennessee, Martin, pers. comm.).

Discussion

Comparing field to laboratory data. Overall, the habitat use and behavior of the snakes in the field were qualitatively and quantitively similar to the behaviors of the snakes in the test pools. Additionally, the ontogenetic changes in utilization of deep water, open water, the CCS-A posture, and substrate crawling seen in the testing environments were well corroborated by the field work. The predatory behaviors observed in the test pool were also qualitatively and quantitively similar to those seen in the field with the exception that the largest snakes in the field (>801 mm SVL) were not observed OM searching, or substrate crawling. The lack of sexual differentiation in prey utilization found by Mushinsky et al. (1982) is interesting, but not surprising since other studies (Hess, 1966; Plummer and Goy, 1984) on *Nerodia rhombifera* have failed to find such a differentiation. A possible reason for the discrepancy is that the population studied by Mushinsky et al. (1982) has larger females or smaller males than the other populations studied. This would be easy enough to verify by comparing data on snake sizes. Other possibilities, such as differences in the location of structural features in relation to water depth are possibilities, but are less easily explored.

The change in utilization of cover. The change in utilization of cover with size in the field may be associated with movement away from the edge toward deeper water, as the clumps of vegetation, especially the saw-grass, tended to extend out into deep water, whereas the cypress trees, knees, and exposed roots used by the smaller snakes tended to be clustered along the shoreline of the covelets. Since very small snakes were never seen swimming into the covelets, it is quite possible that these snakes remain hidden in the covelet where foraging occurs during the day rather than moving in and out of the covelet to forage. The three snakes captured more than once (SVLs 512-650 mm) were all found in different covelets, or, in one case, different parks. While no very small snakes were recaptured, repeated sightings which did not result in captures at a log in Study Grid 1 and a cypress knee in Study Grid III appeared to be the same snake because the animal was found in exactly the same location and posture on repeated sightings over several nights in July.

Predation by snakes >800 cm SVL. Based on field observations, the largest snakes in the field appeared to prey upon carrion on shore, to steal food from each other, and to capture larger fish in water less than 45 cm deep. Sampling biases are, of course, always a potential problem, and might be particularly so if the largest snakes foraged under water in water over 30 cm deep, because the turbidity of the water would have made observation impossible. There was, however, no indication that such foraging occurs. First of all, in the test pool, even large water snakes foraged underwater less than 3 min continuously, and usually much less, returning to the surface between bouts of attacking. Such underwater activity should have been apparent at the surface, if only when the snake returned to the surface between bouts

of attacking. No such activity was seen in the course of hundreds of hours of nighttime observation.

All available evidence suggests that the water snakes larger than 800 mm SVL forage in water that is deeper than that used by the smallest snakes, but is still relatively shallow (30-45 cm deep); most foraging took place in water <30 cm deep. In fact, the largest snakes found in the field (>900 mm SVL), the gravid females, utilized very shallow water (<15 mm deep) and the shore. Most importantly, the large fish were available there: observation and collection of fish at Reelfoot Lake indicated that relatively large bass and bream, pike, and bullhead catfish frequented very shallow water in June and July. Some were apparently there for breeding, and some were there for unknown reasons, possibly avoidance of the predatory gars that are very common at Reelfoot Lake (Petit, 1984; Trapido, 1943). On the other hand, they could be avoiding the high water temperatures, low dissolved oxygen, and high biochemical oxygen demand (BOD) present in the more open water (see Denton, 1987). Freshly dead fish of these species, as well as shad, frequently floated into the shallow covelets and up to shore. Dead fish were almost always present along shore in numbers, particularly during hot weather and after violent storms (wave action is extreme on the large shallow lake). Fish die-offs due to low oxygen concentrations and high BOD at night are common at Reelfoot Lake. This lake is so hypereutrophic and warm (water temperatures were frequently above 30.5° C during my study), that, by Environmental Protection Agency and Tennessee state water quality standards, water quality is not adquate to support aquatic life. Water quality was particularly bad at the monitoring station closest to my study area (Denton, 1987; Petit, 1984). Such die-offs occurred during my field study (pers. comm. W. Smith, UT Martin). In short, dying and dead fish as well as live fish in shallow water appear to offer an

abundant supply of food for large snakes in shallow water at Reelfoot Lake. There is no support at Reelfoot Lake for the hypothesis (Mushinsky et al., 1982) that large water snakes forage in either deep or open water, although Mushinsky et al. (op. cit.) did not define "deep" water. While the manner in which those prey are captured is not resolved, laboratory observations indicate that the largest snakes forage in the same manner as medium sized conspecifics while field observations indicate only an increase in the opportunistic utilization of carrion. Opportunistically encountered large prey are probably important for the large water snakes, as the small size of most of the prey taken would not seem adequate to sustain these animals, even assuming nightly foraging.

4. LABORATORY STUDIES ON ONTOGENETIC CHANGES IN *AGKISTRODON PISCIVORUS*

Experiment 3

Introduction. The goal of this first experiment, carried out in the late summer and early autumn of 1986 was to observe foraging neonate-sized *Agkistrodon piscivorus* in a setting free from the dangers of larger conspecifics. Predictions about foraging in cottonmouth were discussed at the beginning of Chapter V. Since this was a replication of the concurrent large pool study, this experiment was similar to that as well as Experiments 1 and 2.

Subjects. Four juvenile snakes were available for this study, but only 3 provided usable data: 2501, 2507, and 2517. The first snake was rather large, but still had a sulfur-tipped tail. Data from two trials was obtained from 2507 and 2517, and from one trial for 2501. Snake 2507 was the sole neonate tested in the primary test pool. All snakes had extensive experience with fish prey in the laboratory. For the duration of the study, the subjects were housed in ventilated wooden cages attached to the test tanks.

Methods. Methods and prey were the same as in Experiments 1 and 2 except that the subjects were admitted to the test tank by raising an opaque plexiglas divider separating the snake's home cage from the test tank. The floor of the home cage was flush with the top of the rocks. If the snake did not move from the rest coil within 5 min, it was aroused by opening the top of the test tank and moving the snake forward to the front of the home cage with a snake hook. The snake was considered to be foraging only after leaving the rest coil and at least extending the snout over the test tank. The onset of foraging was clear-cut. Trials lasted 45 min to accommodate the foraging of these snakes.

Data analysis. Data was analyzed as in Experiments 1 and 2 except that the habitat area had to include the home cage. When the snake's head was at the front of the home cage facing the test tank, the snake was scored as being at the edge. Most "edge" observations were this sort. Time spent in the home cage in any other orientation or posture was considered non-search time, and was not included in the data analysis.

Results. The behavior of the juvenile snakes in this study was qualitatively similar to that seen in the large pool, although the snakes did venture into the water more in this study than did the sole juvenile tested in the large test pool.

Habitat use: Habitat use and behavior are summarized in Table V-12. As can be seen, the snakes largely utilized the home cage "edge" and the top of the rock, although they made brief forays to other areas throughout the trials. The snakes were in a water covered area M=.23 of the time, most of the time with the head above water. Only 2517 utilized the vegetation or crevices at all; this snake utilized the vegetation heavily in both trials ($\bar{x}$=.32). Open water was utilized to a small degree, but the proportion of time spent under water in open water was negligible (M=0).

Foraging behavior: The snakes moved slowly in a manner similar to that of the adults. The juveniles were mostly in a crane or cruise posture. While these postures were not differentially analyzed, testing notes and drawings indicate that craning from the home cage edge was the most common behavior. The snakes occasionally craned halfway across the cage to watch fish rather than enter the water. The snakes did enter the water, however, swimming a little, especially 2517, who swam x=.07 of the time. No midwater diving was observed, and anterior diving and substrate crawling were rare occurrences (M=0 for both).

Predatory behavior: The juveniles spent quite a bit of time engaging in predatory behavior, mostly handling prey after capture. The attack rates were extremely variable, with (non-capture) attacks ranging from .00-.17 of the foraging time. Snake 2507 was responsible for the maximal rate of attacking, but had only one non-capture attack during the next trial 2 weeks later. Dead fish (2-4 per trial) were ignored by these cottonmouths.

TABLE V-12

SUMMARY OF HABITAT USE AND BEHAVIOR BY THREE YOUNG *AGKISTRODON PISCIVORUS* IN THE SMALL TEST TANK

	Proportion of Habitat Area[a]	Proportion of Foraging Time
	Edge	.40
	Top of rock	.20
	Open shallow water	.03
	Open deep water	.03
	Vegetation	.00
	Wood	.00
	Crevices	.00
	Behavior	
	In water, head out	.20
	In water, head under	.03
	Swimming	.04
	Substrate crawling	.00
	Diving	.00
	Prey	.22

All of the 31 attacks were made at live fish from a craning posture on the edge or top of the rock, usually after a period of obvious observation and orientation. The snake's body tended to form a perfect sine wave behind the extended neck.

As Table V-12 shows, most (61%) of the attacks were aerial attacks, directed either forward or laterally. The remainder were underwater attacks made from an anterior dive when the craning snake lowered its head into the water from the crane posture. These underwater attacks were sometimes OM attacks, although all of the OM attacks were made by 2507 as part of the very high attack rate discussed above. The OM attacks were very abbreviated and involved turning the head from side to side rather than lateral sweeps of the neck and head seen in the water snakes. The underwater attacks, OM or not, were usually preceded by aerial attacks, successful and unsuccessful. The OM attacks suggested a high rate of motivation, even frustration. As shown in Table V-13, these neonates made relatively few types of attacks and were more successful attacking above the surface (AAW) than below (AUW) (AAW v. AUW $G=7.06$, $df=1$, $p<.01$).

At the time of this study, I was not able to assess the occurrence of envenomation. However, all of the 14 captured fish, except for the one lost immediately, were held for some period before ingestion, and none were dropped prior to ingestion. The longest ingestion time recorded was 4 intervals, and the median ingestion time was 2 intervals. Since the median total handling time was 6 intervals, fish were held about 4 intervals before ingestion.

Some of this time was spent manipulating rather than envenomating prey, however. Extensive manipulation was necessary because 62% of the retained fish were captured by the mid-body. Two of these 8 fish were converted to a tail first ingestion and the remainder were ingested mid-body first by folding. Two (15%) of

TABLE V-13

SUMMARY OF ATTACKS MADE BY THE YOUNG *AGKISTRODON PISCIVORUS* IN THE SMALL TEST TANK

Attacks[a]	Number of Fish Captured	Number of Unsuccessful Attacks	Calculated Success Rate[b]
Above water			
AAW-Crane	11	8	.58
Below water			
AUW-Divea	2	6	.25
AUW-OM1	1[b]	3	.25
Total	14	17	

[a]AAW = attack on live prey from above water; crane = craning neck and head over the water from the edge or shore; AUW = attack on live prey from under water; divea = diving in which only the anterior portion of the body is under water; OM1 = under water open-mouthed searching, done only from an anterior dive in this study.

[b]The success rate for AAW attacks and AUW attacks was significantly different ($G = 7.06$, $df = 1$, $p < .01$, with Yates' correction).

[c]The sole fish captured by OM attacking was lost immediately after capture. The success rate listed for OM attacks might therefore be considered to be .00.

fish were captured tail first; one of these was converted to a head first ingestion. Only 3 (23%) of the fish were captured by the head. As can be seen in Table V-14, prey handling times were more variable depending on how the fish was initially grasped. Grasping by the head resulted in a shorter handling time. Handling times for the different directions of ingestion did not markedly differ, and the median time for fish ingested mid-body first was actually shorter than for fish ingested head or tail first. Handling times for the three prey converted to a different orientation were relatively long 6-8 intervals, M=7), with the time required for conversion from a mid-body to tail first ingestion being slightly shorter (M=6.5). Handling times tended to decrease during the trials, so that handling times for each first item were lower than the handling times for the last item in a trial.

While sample sizes are too low to justify further statistical treatment of these data, it is clear that the juvenile snakes did not preferentially grasp fish head first, and exhibited no preference in the direction in which prey were ingested, although fewer were ingested mid-body first than were captured by the mid-body. Conversion from a mid-body grasp to another orientation did not reduce total handling time, although the folding of prey for mid-body ingestion appeared to be very laborious, requiring extensive jaw activity. The fangs were often erected when the maxillae were moved, and appeared to assist in pushing the prey into the mouth.

Discussion. The juvenile and neonate snakes in this study behaved in a similar but more varied manner than did 2507 in the large pool study, using more habitat area and engaging in more types of attack behavior, including OM searching in the small test tank. Perhaps 2507 was constrained by the odor of the larger conspecifics

in the large test pool when he was tested there the following spring. There was otherwise nothing to suggest that any neonates were minimizing exposure. Attacks were made from a crane rather than a cruise posture in this study because of the elevation of the rock and home cage which constituted most of the edge in this study. Nevertheless, the tendency of the juvenile snakes to attack live fish regardless of the season, and primarily to employ the tactic of aerially attacking fish near the edge were verified. The OM attacks, while less advanced in form than those of the water snakes was somewhat similar to those reported for the generalist natricines (see Drummond, 1980, 1983), and represent a tactic not employed by the adult cottonmouths in the test pool. It is telling, however, that the only fish lost during this study escaped immediately from its captors' jaws after being captured by an OM attack.

Experiment 4

Introduction. Since the juvenile snake, 2501, had refused to capture fish during trials, no information was available on juvenile cottonmouths. Additionally, since neonates foraged differently from adults, it was expected that some sort of progression in foraging should occur with age in the cottonmouths. By 1988, snakes in this size class (over 1 year of age, no sulfur-tipped tail) were available, as were 4 more neonate cottonmouths. Therefore, this study of foraging by young cottonmouths was conducted with the expectation of finding differences between the neonates and juveniles in attacking and handling fish prey. Such between-group differences would be assumed to represent ontogenetic change. This experiment was

TABLE V-14

SUMMARY OF PREY HANDLING BY NEONATE *AGKISTRODON PISCIVORUS* (N=3) IN THE SMALL TEST TANK

Factor	Median Handling Time[a] (Number)	
Direction Grasped[b]		
H	5.0 (3)	Handling times were statistically
M	6.5 (8)	similar (Kruskal-Wallis ANOVA
T	7.0 (2)	H=.26, p=.88)
Direction Ingested[b]		
H	6.5 (4)	Handling times were statistically
M	6.0 (5)	similar (Kruskal-Wallis ANOVA
T	6.5 (4)	H=.007, p=.99

[a]Handling time is in terms of 30 sec intervals. Because behaviors were instaneously sampled at the beginning of an interval, handling time intervals represent times between interval/2-.5 min, and interval/2 min.

[b]H=head first; M=mid-body first or folded; T=tail first.

also carried out in the small square tanks, but with the simplified environment described in Chapter II and illustrated in Fig. II-3. A suspected difference was that the neonates utilized the sinuous attack posture almost exclusively, whereas the older juveniles seemed to use a greater variety of postures. It was desirable to establish this difference quantitatively. Since I was by this point able to diagnose envenomation and was aware that the cottonmouths did not always envenomate live fish, ontogenetic changes in the rate of envenomation were considered possible.

Subjects. The juveniles were 2507, 2531, and 2532. The latter two snakes were captured at Reelfoot Lake the preceding summer, and 2507 had by now lost its sulfur-tipped tail. The neonates were AHS-SC 1-4 which had been born at Savannah River Ecology Laboratory and were donated to Old Dominion University shortly after birth.

Snakes were individually housed in standard plastic reptile cages with a newspaper substrate and a water bowl. The snakes were maintained at 30°C on a 12:12 light:dark cycle. Prior to the study and between trials during the study, snakes were fed weekly, either minnows (*Notemigonos crysoleucus*) in their water bowl or "pinkie" mice (*Mus musculus*) on the cage substrate. Both types of prey were accepted readily at every offering although fish were not offered until the neonates were 3 months old.

Methods. Four of the small test tanks were set up as illustrated in Fig. II-4, **p.** with only a gravel beach, edge, and sloping bottom. Water occupied about 3/4 of the surface of the tank. The tanks were lined up together on a shelf at eye level with

opaque dividers between them to aid observation by me and prevent the snakes from observing each other. The snakes were housed individually in the test tanks from 1-2 days prior to feeding until 4-5 days post-feeding. The snakes were fed by dropping 4-6 live fish into the water from the top of the cage. Invariably, 1-2 fish died rather quickly while the other fish survived for days in the unaerated water. Feeding always occurred on one of two particular days a week for each animal. Thus, the animal was given the cues necessary to anticipate feeding.

Pre-feeding observations: After the first feeding in the test tank, the snakes frequently adopted a feeding posture next to the water before fish were added. In order to determine the frequency and time of day for this behavior, apparently a sit-and-wait posture, the snakes were observed at intervals throughout the day, from shortly before lights came on until after lights were off at night. Their location in relation to the water, posture, and activity were recorded. Posture included 1) head position: elevated or resting on body or substrate; 2) shape: coil or sinuous "S"; 3) neck: extended away from the body or not; and 4) head in relation to water: over water or not, regardless of other aspects of posture.

Feeding observations: Fish were always added to the tanks during the early afternoon hours. Three or four snakes were observed at once: two neonates and one or two juveniles. (Snakes that were not tested were fed in their home cages at the same time). The snakes were then continuously observed for an hour by me and one other trained observer. All attacks and captures were noted (all occurrence sampled) and prey handling was timed. Information collected included whether the prey was live or dead, posture (coil, crane, stalk, anterior dive), location in relation to the edge of the water (beach, edge, water), attack type (AAW or AUW), whether

envenomation appeared to have occurred, time prey was held without manipulation, time required for manipulation, and time required for ingestion.

After the period of continuous observation, the snakes were checked at 1-2 h intervals until lights were out; posture, behavior, and the number of live and dead fish left were noted. For most feedings, observations were made after dark at about 1930 and 2130 in order to ascertain the occurrence of foraging after-dark.

Results. In general, foraging began with minutes of the addition of fish, although the juveniles tended to wait longer to begin foraging, possibly because of the presence of the observers. With the exception of the first trial for AHS-SC1, who took dead fish as the first two prey in the first trial (but after the observation period), live fish were always consumed before dead fish. Dead fish were taken as the last fish during the period of observation or long after the observation period. Only three of the 85 (<4%) witnessed captures were of dead fish, one by a neonate and two by juveniles. The neonate dropped the fish almost immediately and made no attempt to retrieve it. The juveniles, on the other hand, ate the dead fish. Both groups of snakes ate similar numbers of live and dead fish after the observation period.

Attacks: Most of the observed attacks at live fish (145/220 = 65%) were aerial attacks (AAW), most which were made while the snakes were craning from the edge or shore. The neonates all craned over the water, mostly immobile from the sinuous posture with neck and head stretched out straight ahead over the water about 2 cm above the surface of the water, keeping the axis of the body at an angle 90° to the edge. This posture was rather stereotyped in the neonates. One neonate did strike from a coil on the beach at the beginning of two trials, and thereafter assumed

the sinuous posture. The neonates rarely ventured into the water during the observation period, although some attacks were so violent that the neonate was thrown into the water. The snakes usually returned immediately to the edge and resumed the stereotyped posture. Attacks are summarized in Table V-15.

The juveniles also attacked in this manner, but additionally engaged in frequent movement across the edge and into the water and underwater, and stalked prey across the surface before attacking more frequently. The stereotyped posture was not maintained as much, the body often forming irregular curves, particularly

open loops which kept only the neck oriented at 90° angles to the edge. One of the aberrant above water OM attacks seen in 2 adults in the primary test pool was made by a juvenile (2532).

The remainder of the attacks were underwater attacks at live fish (AUW), most of which were made from an anterior dive posture. The frequency of above and below the water attacks were different for the two groups of snakes ($G = 60.24$, $df = 1$, $p < .005$, with Yates' correction). Since the frequencies of underwater attacks were different and most were made from anterior dives, it is not surprising that the rates of anterior diving were different for the two groups ($G = 21.82$, $df = 1$, $p < .005$, with Yates' correction). No underwater OM attacks were made by either group.

As mentioned earlier, the snakes sometimes followed a fish swimming by from above, a behavior which I termed "stalking". Stalking was followed by either AAW or AUW attacks, or no attack. While the juveniles performed this behavior earlier in the trials than did the neonates, and one neonate did not engage in this behavior at all, both groups performed it at similar rates ($16/105 = .15$ attacks for the neonates and $27/115 = .23$ attacks for the juveniles.

TABLE V-15

SUMMARY OF ATTACKS MADE BY NEONATE AND JUVENILE *AGKISTRODON PISCIVORUS* IN THE MODIFIED SMALL TEST TANK

	Neonates (N=4)		Juveniles (N=3)		
	Number of Fish Captured	Number of Unsuccessful Attacks	Number of Fish Captured	Number of Unsuccessful Attacks	Calc. Success Rate[b]
					N J
From underwater					
AUW[b]-Divea	0	0	10	32	.20
AUW[b]-OM1	0	0	0	7	
AUW[b]-Crane	0	0	0	10	.00
AUW[b]-Divem	0	0	0	1	
DUW[b]-Divea	0	0	1	0	
From above water					
AAW[b]-Crane	42	49	15	13	.46 .54
AAW[b]-Stalk	5	12	11	10	.29 .52
AAW[b]-OM2	0	0	0	1	
DAW[b]-Crane	0	0	1	0	
DF[b]-Crane	0	1	0	0	
Totals	47	62	36	74	

[a]AUW = attack on live fish from underwater; divea = anterior diving; crane = craning over the water; divem = mid-water diving; DUW = attack on dead fish from underwater; stalk = following fish from above the water as they swim below the surface; OM2 = open-mouthed attack above water; DAW = sunken dead fish attacked from above the surface; DF = floating dead fish.

Foraging occurred after dark as evidences by the disappearance of fish during the dark hours and occasionally finding both neonates and juveniles with prey at the 1930 and 2130 after-dark checks. The snakes were found with both live and dead prey. The position of the snake and dry skin on all but its head and neck suggested that fish were caught out of the water as during the day.

Prey capture and handling: This group was fairly good at capturing prey by the head (or snout): 67% of the neonates' captures and 57% of the juveniles' captures were by the head; the rates of head first capture did not differ between groups ($G = .04$, $df = 1$, $p > .05$, with Yates' correction). The remainder of the neonates' captures were by the mid-body, and most of the remainder of the juveniles' captures were also, except that 2531 captured 3 fish by the tail. All live fish were held after capture for varying lengths of time, ranging from 0-790 sec. The grasp site made a difference in the hold time to some degree, with fish grasped by the snout being held the shortest amount of time for both groups although the hold times were not significantly different even in the neonates where the effect was most pronounced ($N = 4$, $H = 5.65$, $p = .06$). Otherwise, the numbers were not consistent between groups, although they were consistent within groups as can be seen from Table V-16 below. The juveniles did have shorter hold times than the neonates.

Envenomation was diagnosable in many of the captures using the following criteria: 1) how far back the prey were in the jaws as prey too far back could not be in contact with the fangs; 2) amount of flaring of the labial scales along the maxilla during the hold phase as the erected fangs caused flaring of the labial margin; and 3) how the jaws were moved at the beginning of manipulation as removal of the fangs required protraction and elevation of the maxilla. The duration of the hold was useful to some degree, but fish were often not envenomated until dead, so that

holding times were often short although visible puncture wounds on the prey all but ensured envenomation. Nevertheless, I could not ascertain the occurrence or non-occurrence of envenomation in all captures. Of the captures that I felt confident of diagnosing, envenomation occurred in .40-.82 of the neonates' captures, and in .33-.80 of the juveniles' captures. These proportions are very similar, with the within-group variance exceeding the between-group variance as shown in Table V-15.

As summarized in Table V-16, the manipulation times were clearly affected by the direction in which the prey were grasped, with prey grasped by the snout, head, and tail requiring less manipulation time than prey grasped by the mid-body. For the juveniles, in fact, no manipulation was required for prey grasped by the snout. Manipulation times were also shorter for the juveniles than for the neonates. Again, the fangs appeared to assist in the manipulation process. Some individuals of both groups (one neonate, two juveniles) resorted to dropping prey, even still living prey, during the manipulation process (N=5). This led to short manipulation times in 2 instances, but did not in the other three instances.

Prey ingestion: Most ingestions occurred high on the beach, at the back of the tank. As noted before, most ingestions ended with the snakes' head and neck stretched high. As indicated by Table V-16, the direction of ingestion had no effect on the ingestion time for the neonates. It must be noted, however, that only two neonates made mid-body first ingestions, and only 1 made a tail-first ingestion. For the juveniles, however, the effect of direction of ingestion was similar to that seen in the adults, with head first ingestions requiring the least time and mid-body first ingestions the most time. All juveniles made at least one of each type of ingestion. Ingestion times were consistently shorter for the juveniles than the neonates.

TABLE V-16

SUMMARY OF PREY HANDLING IN THE NEONATE AND JUVENILE *AGKISTRODON PISCIVORUS* IN THE MODIFIED SMALL TEST TANK

Group	Where Grasped				Percent Enven.[a]
	Snout	Head	Mid-body	Tail	
			Holding Time in Sec[b] (N)		
Neonates	233 (12)	508 (20)	318 (15)	----	.60+.20
Juveniles	123 (3)	128 (17)	184 (12)	56 (3)	.50+.23
			Manipulation Time in Sec[c]		
Neonates	58	72	161	----	
Juveniles	00	14	107	00	
			Ingestion Time in Sec[d] (N)		
Neonates		75 (31)	77 (5)	78 (1)	
Juveniles		49 (22)	113 (9)	79 (5)	

[a]Percent enven. = percent of prey envenomated, using only those observations where envenomation could be diagnosed. The values are the x and s.d.

[b]Holding Time = median duration of time the prey were held in the mouth without jaw movement. The number of observations is given in brackets after the time.

[c]Manipulation Time = median duration of time required to manipulate the prey after holding and before ingestion.

[d]Ingestion Time = median time required to ingest prey. The number of observations is given in brackets after the time.

Pre-feeding observations. As noted above, the neonates maintained a more stereotyped posture during feeding than did the juveniles. It was very difficult to quantify this during feeding, however, because of other data recording requirements. The pre-feeding observations were therefore relied upon for this information.The fully developed or stereotyped form of this posture consisted of the sinuous "S" shape with the head elevated, neck extended and over the water. Using only observations taken between 0900 and 1700, the neonates maintained this position significantly more frequently ($G=23.14$, $df=1$, $p<.005$). The juveniles often remained in a rest coil at the water's edge during the day, although a variety of postures were observed. Both groups were most often near the water during the day, and were more likely to be active after 1700 and before 0900.

Discussion. The two groups of young cottonmouths in this study differed in their aquatic foraging behaviors, with the older snakes utilizing a wider variety of attack types, somewhat more active foraging tactics, and attacking more underwater. The older snakes also had reduced handling times. These improvements mirrored the types of improvements found in the water snakes. Another concordance between the two species was the increasing tendency with time to capture and ingest dead fish. Additionally, no improvement in grasping prey by the head occurred in either species. This finding is somewhat at odds with the work of Halloy and Burghardt (in press), at least as far as the cottonmouth is concerned. Phylogenetic differences are probably responsible for this finding as the cottonmouth, as a pit viper, is adapted for manipulating dead prey.

These differences seem to be true ontogenetic changes as the neonates in Experiments 3 and 4 used a similar limited range of attack types, although no OM attacking was seen in Experiment 4 neonates and no stalking was seen in the Experiment 3 neonates. The lack of stalking in Experiment 3 was probably due to the high prey concentration which made stalking unnecessary. The habitat layout also would have interfered with it. Both groups of young in this study were markedly slower in prey handling than were the neonates in Experiment 3. This is probably because the fish were a different species and were slightly larger in this study, although they were still Size 2 prey.

Both groups of cottonmouth young were similar to conspecific adults in 1) habitat use, in that they primarily foraged along the edge and tended to ingest on shore, 2) the tendency to attack live fish from above the water (AAW), 3) the limited ability to manipulate prey, sometimes resorting to dropping prey to correct orientations, and 4) possessing a compensatory ability to swallow prey in any orientation. The types of similarities between cottonmouth young and adults in terms of habitat use, attack strategy, and prey handling abilities were also true of the water snakes. Both species increased their underwater attacking, used more of the habitat, and were similar in prey handling abilities and limitations. The young watersnakes and the young cottonmouths became better aquatic foragers with time, although the water snakes were clearly more aquatic in habits at all stages of development.

Unlike the adults, however, the young cottonmouths showed a strong preference for live fish, almost always taking live fish first. Since one neonate had eaten dead fish first in the first feeding trial and had been presented with no more dead fish during trials, I checked this preference by offering the neonates, juveniles, and 6 adults equal numbers of dead and live minnows (*Notemigonos crysoleucas*) in

their home cage water bowl, 4 fish for each of the neonates and juveniles, and 6 fish for adults, and noted which prey type was selected first. (Additional prey was given to the adults after the trial). Each snake was observed weekly on the regular feeding day. During some observations, the snakes would not feed in my presence, and sometimes an individual grasped prey that did not appear to be the original target. I repeated the weekly offerings until I had two clear-cut choices for each subject. The 4 neonates and 2/3 of the juveniles consistently chose live fish first, but the adults were inconsistent: sometimes they carefully picked up dead floaters, and sometimes they pursued live fish until seized. Although only the first choice of the trial was scored, the second choice generally followed the first choice. Live fish which jumped out of the bowl onto the substrate were almost invariably pursued, however, even though such pursuits were time and energy consuming. The adult cottonmouths thus appear to maintain adequate interest in ingesting fish, live or dead, but appear to lose interest in capturing live fish in water, except in the spring. Cottonmouths, then, undergo even more profound ontogenetic changes in foraging at a later stage in development.

The timing of this change is uncertain. It may be relevant that one juvenile in this study did not exhibit a preference for live fish, and that the other 2 juveniles had both taken dead fish during the observation period of Experiment 4. The neonates, in contrast, were slow to recognize dead fish as prey in the open water, although all had eaten dead fish from their home cage water bowl previously. Of special interest in this regard is the fact that 2507 did not engage in any OM searching as a "juvenile" but had as a "neonate". Two juveniles did OM search underwater, but 2532 also engaged in one bout of the aberrant above water OM foraging seen in two adults in

the primary test pool. Additionally, the juveniles engaged in more prey dropping during manipulation, a common practice of the adults.

Determining the onset in the ontogenetic shift away from live fish may prove difficult. At the very least, it will be necessary to test in a large body of open water as all adult cottonmouths in the laboratory respond eagerly to live fish in water bowls, and most will pursue live fish in a 10 gal aquarium if they respond at all in a test situation.

The apparent degeneration of OM searching discussed above also suggests that juvenile cottonmouths switch away from OM searching. This contrasts with the water snakes which switch toward OM searching as juveniles. While the data in this series of studies support this premise, the sample sizes are still too small to justify acceptance of this premise. Nevertheless, my laboratory and field observations (albeit limited) of the cottonmouths lead me to hypothesize that the juvenile cottonmouth is primarily a sit-and-wait predator, preying heavily on live fish or other aquatic prey such as tadpoles from the water's edge, possibly in very small pools of water. With increasing size, the cottonmouth becomes more of a cruise forager moving from patch to patch, utilizing a wide variety of prey. The adult cottonmouth, then, is probably more of a generalist than is the juvenile.

5. CONCLUSION

The results of my field and laboratory studies have documented the existence and nature of ontogenetic changes in foraging in both species. The changes seem to be more extreme in the cottonmouth. Nevertheless, the concordance in the

ontogenetic changes observed in these independently evolved species as well as the ontogenetic changes discussed in Chapter I suggest some general hypotheses which could be applied to the study of the ontogeny of foraging in any species of snake: 1) juvenile snakes are more limited in habitat use than adults and possibly exhibit less vagility than adults; 2) juvenile snakes utilize a more limited range of predatory tactics and utilize less active tactics than adults.

CHAPTER VI

DISCUSSION AND CONCLUSION

1. COMPARISON OF THE TWO SPECIES AS AQUATIC FORAGERS

An Overview of the Laboratory and Field Observations

Introduction. *Agkistrodon piscivorus* and *Nerodia rhombifera* differed radically in their approach to piscivory. In fact, while the cottonmouth may be a significant piscivore, it really was not an aquatic forager. The diamond back water snake, in contrast, proved to be a competent aquatic forager. Two factors in large measure differentiate the two species: the response to live fish and habitat use. These factors will be discussed in qualitative terms first, and then will be quantitatively analyzed.

The consumption of carrion fish. While the cottonmouth adults exhibited very little aquatic foraging, the juvenile cottonmouth, and, to a lesser degree, the spring-time adult, engaged in a limited range of aquatic foraging in the test pool. In particular, they readily attacked live fish. Even the spring-time adults, however, still attacked dead fish more readily. Nevertheless, adult cottonmouths at all times of the year were attracted to live fish and readily accepted live fish in bowls in the home cage. In contrast, diamond back water snakes of all sizes readily attacked live fish in any situation and at any time.

Interestingly, compared to conspecific adults, the neonates of both species more readily attacked live fish than dead fish. Although very large adult water snakes still foraged more readily on live than dead fish, these snakes took some dead fish in the pool. Many dead fish were ignored, however. At Reelfoot Lake, large water snakes (>800 mm SVL) even appeared to seek dead fish, since the only snakes found active on land were approaching or handling dead fish. All of the dead fish on land were very large relative to most of the live prey available in the covelets where they foraged. Large dead fish offer such large energy gains relative to costs of attainment that utilization of this resource may be important to large adults of both species.

Habitat utilization. While both species are found in a variety of lentic aquatic habitats, they seemed to have fairly specific habitat requirements for foraging. Given the cottonmouths' buoyancy and the infrequent submersion of their head, it would appear that the cottonmouths must have a suitable edge area in which to attack live fish near the surface or where dead fish will accumulate. While floating dead fish would also be an option, the cottonmouths' attempts to grasp such fish were clumsy at best and often insuccessful. The cottonmouths never handled fish underwater or ingested underwater either, and probably cannot handle any but small prey successfully in water.

The diamond back water snakes appear to require shallow, smooth-bottomed areas for active open-mouthed foraging, but also prefer to be near or in contact with structures such as plants or wood. Although the water snakes can attack from the open water substrate, the fish are associated with structures which provide cover and/or are the location of fish prey. The water snakes prefer patchy cover, however,

as they were always found in areas where there is more open water than cover. Furthermore, they always foraged from the edge of cover. These snakes were capable of handling and swallowing fish in the water and underwater, rarely moving to either shallower water or shore for manipulation or ingestion.

Quantitative Comparisons Using Only Large Test Pool Data

Habitat use. Differences between the two species may be argued to begin with habitat use. The specifies-specific pattern of habitat use played an important role in prey selection in both species in the test pool and almost certainly would be an important proximate determinant of diet in the field. One-tailed Mann-Whitney signed rank tests for independent samples were performed on the medians for individual snakes of each species to test the differences in habitat use. There was surprisingly little overlap in habitat use in the large test pool. As can be seen in Table VI-1, the cottonmouth primarily used the edge areas for foraging, and used these areas significantly more than did the water snakes ($M=.51$ v. $M=.04$, $Z=-4.68$, $p<.0001$).

The cottonmouths also spent significantly more time than the water snakes on shore ($M=.08$ v. $M=.00$, $Z=-4.77$, $p<.0001$). While the cottonmouth is clearly more terrestrial than the water snake, neither species spent much foraging time on the beach, and utilization of this area was the same for the 2 species ($M=.00$ for both, $Z=-1.32$, $p=.19$). The water snakes primarily used water covered portions of the crevices and deep open water (OWD), using these areas significantly more than did the cottonmouths (crevices $M=.23$ v. $M=.04$, $Z=3.84$, $p<.005$, OWD $M=.13$ v.

TABLE VI-1

COMPARISON OF FORAGING *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS* IN THE LARGE TEST POOL

	N. rhombifera	*A. piscivorus*	Significance[a] of Comparison
Habitat Use[b]			
Beach	.00	.00	----
Shore	.00	.08	<.0001
Edge	.04	.51	<.0001
Vegetation	.06	.33	<.06
Wood	.06	.08	----
Crevices	.23	.04	<.005
OWS	.03	.02	----
OWD	.13	.00	<.0001
Behavior[b]			
Moving	.34	.58	<.005
Swimming	.00	.11	<.0001
Diving	.00	.02	----
Crawling	.05	.00	<.0001
CCD	.28	.01	<.0001
Above water	.37	.35	----
Below water	.38	.02	<.0001

[a]Only significance levels less than .10, one-tailed tests, are given here. Tests were Mann-Whitney signed rank tests for independent data, using the medians for individual snakes.

[b]OWS = open shallow water; OWD = open deep water; moving = proportion of time spent in movement other than just movement of the head; diving = mid-water and anterior diving; crawling = crawling on the underwater substrate; above water = in the water, head above or at the surface; below water = in the water, head below the surface. Habitat areas, behaviors, and statistical analyses are described in detail in Chapter II.

M=.00, Z= 4.04, p<.005). (At Reelfoot Lake, crevices were used by the water snakes where available, but most foraging took place in the vicinity of wood or vegetation in water approximately the depth of the deep water in the test pool). Foraging cottonmouths and water snakes used the wood and vegetation at statistically similar rates although utilization of the vegetation by the cottonmouths came close to being significantly different from that of the water snakes (wood M=.08 v. M=.06, p=.23, vegetation M=.33 v. M=.06, .06>p>.05). Both species used the shallow open water (OWS) at statistically similar low rates (M=.02 v. M=.03, Z=.098, p=.92). Thus, habitat use was similar for the two species in the OWS, wood, and beach areas. Foraging cottonmouths and water snakes each spent a total of 9-10% of the time in the habitat areas where habitat use did not differ.

Basking and resting snakes of both species, on the other hand, used the vegetation and wood along the edge and the beach in similar manners. (Both species were observed using the edge, shore, and vegetation overhanging the shore at Reelfoot Lake. The two species were, in fact, observed resting within meters of each other on the edge of a slough on one occasion although, overall, the species were not highly syntopic at Reelfoot Lake. The effects of habitat selection and human interference are probably inseparably linked causes of limited syntopy at Reelfoot Lake.)

Comment on habitat use and the consumption of frogs. While not tested here, the tendency of the cottonmouth to utilize the edge may well account for the difference between the species in the consumption of frogs. Both species in this study readily eat frogs as well as fish, but the cottonmouth consumes frogs more frequently

and reliably than do the diamond back water snakes, although some populations of water snakes do consume large numbers of frogs (Bowers, 1966). Frogs seem to be most readily captured by snakes at the edge as suggested by descriptions of foraging for frogs (*e.g.* Evans, 1942; Wendelken, 1978). The utilization of the edge by the cottonmouth, then, almost certainly is a more important factor in the consumption of frogs than is prey preference or phylogenetic constraints on prey capture abilities, as many natricines other than *Nerodia rhombifera* prey heavily on frogs. Bowers (op. cit.) in fact hypothesized that one population of *N. rhombifera* (in commercial minnow ponds) that he studied consumed more frogs than did another (in a natural lake) because the steep banks of the minnow ponds minimized the amount of relatively shallow water present. Water snakes were thus forced to forage near the edge where the frogs were.

Foraging behavior. Differences in foraging behaviors (enumerated in Table VI-1), of course, also produced differences in prey utilization (enumerated in Table VI-2). Behavioral differences were tested using the Mann-Whitney test as described above, the method of Fleiss as described in Chapter II, and the G test. As noted, behavioral differences were most obvious in the adult cottonmouths' limited tendency to capture live fish. The difference in the proportion of live fish attacked by each species was statistically significant (water snakes = .92 v. cottonmouths = .09, $p < .0001$). Nevertheless, change in use of the habitat preceded behavioral change ontogenetically in the diamond back water snake (this study), and evolutionarily at the micro-evolutionary level in other natricines (Arnold, 1981; Drummond and

TABLE VI-2

COMPARISON OF PREDATORY BEHAVIOR IN *NERODIA RHOMBIFERA* AND *AGKISTRODON PISCIVORUS* IN THE LARGE TEST POOL

Behavior	*N. rhombifera*	*A. piscivorus*	Significance[a] of Comparison
Attacks			
Non-capture	.03	.02	----
Underwater	.90	.12	<.0001
Surface	.09	.19	<.05
Out-of-water[b]	.02	.58	<.0001
Captures			
Shore	.02	.02	----
Edge	.12	.29	<.0001
Cover,in water	.36	.25	<.10
Crevices	.24	.05	<.0001
OWS[c]	.06	.06	----
OWD[c]	.46	.07	<.0001
Live prey[d]	.92	.09	<.0001
Prey size[e]	Size 2	Size 2	----
Meal size[f]	4	4	----
Head 1st Grasp[g]	.72	.39	<.005
Manipulation			
Phase present[h]	.30	.88	<.0001
by Dropping	.01	.12	<.0001
Under water	.73	.00	<.0001
Time[i]	0-0-0	1-1-2	<.01
Habitat change during manipulation[j]	no	yes, shoreward	----
Ingestion			
Head 1st	.88	.79	<.10
Under water	.74	.00	<.0001
Time[i]	1-1.5-2.0	1-1.5-5.5	
Total prey time[k]	.07	.22	<.02

[a]Only significance levels less than .10, one-tailed tests, are given here. Tests were either the Mann-Whitney signed rank tests for independent data, using the medians for individual snakes, or the method of Fleiss (1979) for comparing two proportions.

[b]Out-of-water attacks are those made at or from the edge and shore.

[c]OWS = open shallow water; OWD = open deep water.

[d]Live prey = proportion of fish attacked that were alive.

[e]Prey size = size of fish relative to the snake; see Chapter II for details of determining fish size.

[f]Meal size = number of items eaten during a trial.

[g]Head 1st grasp = proportion of fish initially picked up by the head.

[h]Manipulation phase present = a period of manipulation was required between the grasping and swallowing of fish. See text above for details.

[i]Time = number of 30 sec intervals during which a behavior occurred. Numbers separated by hyphens refer to Size 1, 2, and 3 fish respectively.

[j]Habitat change during manipulation = the snake moved during manipulation from the area where the fish was captured to another area, resulting in statistically different habitat use for capture and ingestion as described in Chapters III and IV.

[k]Total prey time = proportion of the foraging time spent on attacking, capturing, manipulating, and swallowing prey, based on the individual medians as described in chapter II.

Burghardt, 1983). The limited tendency to capture live fish certainly in part results from utilization of the edge.

Statistical comparisons of the behavioral variables measured in the large pool showed just how dissimilar the species were. The proportion of time spent moving can beused as a measure of activity level in order to categorize the snakes as sit-and-wait, cruise, or intensive foragers (Regal, 1978). While these foraging strategies have not been quantitatively defined in terms of the proportion of time spent in motion, comparing the proportion of time spent in motion by different species has been used for ranking species along a continuum (Regal, 1978). As discussed in Chapters III and IV, the water snakes were moving significantly less than they were still. The cottonmouths were moving as often as they were still. Neither species would thus appear to be an intensive forager. The cottonmouths moved significantly more than did the water snakes in (based on individual medians, cottonmouths moving $M=.58$, water snakes moving $M=.34$, $Z=-3.41$, $p<.005$, Mann-Whitnesy signed rank test, one-tailed test). Since many crotalines are sit-and-wait foragers (Fitch, 1960; Reinert, et al., 1984; Greene, 1986b), and diamond back water snakes have been characterized as active foragers (Mushinsky and Hebrard, 1977a), it was surprising to find that the cottonmouth was more active than the water snakes. Although both species tended to move at a leisurely pace with only brief bouts of intensive movement, the water snakes did engage in more extended bouts of intensive activity. Some snakes attacked while moving continuously for 4 intervals. Such intensive activity was rare, however: only 3 such bouts were recorded. Since no measures of energy expenditure were made, nothing can be said about the relative energetic costs of feeding except that neither species seemed to approach the

limits of a snake's limited aerobic scope (Gratz and Hutchison, 1977; Pough, 1977, 1978).

Another surprising difference was in the proportion of time spent swimming and diving: the cottonmouths spent significantly more time swimming than did the water snakes ($M=.11$ v. $M=.00$, $Z=-4.86$, $p<.0001$) and dived at similar rates ($M=.02$ v. $.00$, $Z=-1.44$, $p=.16$). This is undoubtedly related more to the buoyancy of the cottonmouths than to aquatic predilections, as the water snakes engaged in other aquatic activities significantly more than the cottonmouths. The water snakes were more often (1) in water with the head out, although not significantly so ($M=.37$ v. $M=.35$, $.Z=1.24$, $p=.22$), (2) under water ($M=.38$ v. $M=.02$, $.Z=4.9$, $p<.0001$), (3) sitting in a submergent cruise posture ($M=.28$ v. $M=.01$, $Z=5.04$, $p<.0001$), and (4) substrate crawling ($M=.05$ v. $M=.00$, $Z=4.27$, $p<.0001$). The species differed most radically in the time spent in the most aquatic behaviors (Drummond, 1980, 1983a), *i.e.*, total underwater time, substrate crawling and submergent cruising.

Predatory behavior. Since the cottonmouths spent so little time in the water and underwater, it is not surprising that the water snakes made more attacks underwater (AAW and DUW attacks, water snakes = .90 v. cottonmouths = .12 of all attacks) such as while substrate crawling (.27 v. .0, $p<.0001$), and while submergent cruising (.48 v. 105, $p<.005$). The cottonmouths attacked at the surface more than did the adult water snakes (.15 v .07, $p<.05$). This type of attack in the cottonmouths was directed only at dead fish (DF or DAW attacks), whereas it was also directed at live fish (AAW attacks in CCS posture) in the water snakes. Attacks from out of the water (edge + shore) were the least common type of attacks for the water snakes (2%

of the total attacks) and the most common for the cottonmouths (58% of the total attacks). The rate of these attacks was, of course, significantly different for the 2 species (.02 v. .58, $p < .0001$). Again, the species differed most radically in the behaviors that were the most aquatic, *i.e.*, underwater attacks. They also differed radically in the behavior that was the least aquatic, *i.e.*, out-of-water attacks.

The water snakes were more proficient than the cottonmouths at handling prey. The proficiency was evident in all phases of the handling process. At all ages, they began the handling process by grasping prey, live or dead, by the head more reliably than the cottonmouths. The adult water snakes initially grasped about 72% of the prey by the head, whereas the adult cottonmouths grasped only about 39% of the prey by the head, even though most of these fish were dead and some time was taken to examine fish before grasping. This difference is highly significant ($G = 23.4$, $df = 1$, $p < .0005$, with Yates' correction).

The cottonmouths were then faced with the problem of either reorienting the fish for a head first ingestion, ingesting tail first, or folding the fish for a mid-body first ingestion. For the adults, prey handling times for the cottonmouths were very long (Size 1, $M = 1$; Size 2, $M = 1$; Size 3, $M = 2$) and usually consisted of a distinct manipulation phase (88% of the ingestions) followed by the swallowing phase. Manipulation often involved dropping the fish (12% of the ingestions) and regrasping it. Manipulation always took place above water, and the cottonmouths often moved shoreward during the manipulation process so that ingestion took place shoreward of prey capture. Even after regrasping or reorientation, fish were not always in a head-first orientation.

In contrast, the water snakes required a period of manipulation before beginning ingestion in only 30% of the prey captures. Even with very large fish

required very little manipulation, and the median manipulation time was still M=0 intervals. With the exception of one reorientation (<1% of ingestions), the water snakes reoriented fish by jaw movements rather than by dropping and re-grasping. All reorienations were to a head-first position. Although the water snakes ingested more prey head first than did the cottonmouths, the difference was not quite statistically significant (88% v. 79% G=3.0, df=1, .10>p>.05, with Yates' correction). The water snakes manipulated fish under water 74% of the time, and showed no tendency to move shoreward during manipulation.

The water snakes and cottonmouths had similar swallowing times for Size 1 and 2 fish (M=1 and M=1.5 respectively). The cottonmouths, however, had much longer swallowing times for Size 3 fish (M=5.5 v. M=2 for the water snakes). Since there was no upper limit on the range of Size 3 fish, and some were quite large relative to the snakes, it is possible that the cottonmouths ate more of the extremely large fish. In fact, I believe this to be true. Nevertheless, methodological limitations of this study make it impossible to address this question further. Nevertheless, the total time spent on prey per trial was higher for the cottonmouths than for the water snakes (M=.22 v. M=.07, Z=-2.55, p<.02), although both species had similar median prey sizes (M= Size 2) and similar meal sizes (M=4 items).

Morphological differences. As discussed in Chapter I, the water snake possesses many fairly long recurved teeth of the sort typically found in piscivores. These may help maintain a firm grip on wriggling fish. Additionally, the snake has the hingelike supralabial groove found in many piscivores. This hinge is most visible when the maxilla is moved out laterally during prey manipulation. The maxillae of

these snakes are highly mobile and capable of wide lateral excursion. The hinge appears to be associated with this mobility.

Cottonmouths, as discussed in Chapter I, although bearing large mobile front fangs, otherwise have an overall reduction of tooth number and size. They are not adapted for gripping wriggling prey. The cottonmouths were at no disadvantage during ingestion, however, as even juveniles were able to ingest all but the large (Size 3) fish mid-body first. While jaw kinetics were important in getting folded fish into the mouth, the neck took over the swallowing process before all of the prey had been taken into the mouth. Extreme elevation of the head generally accompanied swallowing. The role of the neck muscles in swallowing in snakes has been ignored to date.

The differences in prey handling abilities are very much in line with the differences in jaw structure and function in the species. Morphological differences would not seem to account for the lack of underwater ingestion in the cottonmouth, although staying underwater may involve some muscular activity (in order to squeeze air from the lung) incompatible with swallowing.

The obvious differences in buoyancy between the species may result from differences in lung volume as the cottonmouth lung extends quite far back in the body, and the more aquatic natricines have somewhat less lung volume than do less aquatic snakes (Baeyens et al., 1980). Differences in the ability to alter lung volume behaviorally may also be present. This is suggested by differences in the submersion process: submersion in the cottonmouth is slow and accompanied by the expulsion of a large mass of air bubbles, whereas submersion in the water snake is a rapid plunge accompanied by the expulsion of few visible bubbles.

Ontogenetic changes. The ontogenetic changes in the cottonmouths were complex and even a bit bizarre. The young cottonmouths exhibited some lability in foraging behaviors as there were ontogenetic increases in time spent foraging underwater. Foraging by the young cottonmouths resembled that of the young diamond back water snakes to the extent that the young of both species attacked more from above the surface than from below. The young water snakes, however, were in the water most of the time, and were in cover most of the time, whereas the cottonmouth young were on the edge in the open most of the time (see Chapter V for details). The predatory lability described is apparently short-lived during the life of the cottonmouth as the adults exhibited an interest in attacking live fish in the pool only during the spring. No increase in the types of attacks used occurred after the juvenile phase. In fact, the adults did not use the anterior dive attacks attacks which the juveniles used with some success. The prey handling abilities of the young snakes of both species were very similar to those of the adults. The water snakes were proficient at handling fish from the very beginning of life, exhibiting the ability to capture fish by the head, and then manipulate and swallow underwater. The fish which were not grasped by the head were easily manipulated to a head first position. Even when prey required reorientation, handling times were relatively short (1-2 intervals). These snakes were more adept at handling live fish than dead fish from the beginning. Like the adults, the juvenile cottonmouths (1) captured relatively few of the fish by the head (23% in Experiment 3, 25% in Experiment 4, Chapter V), (2) tended to have a long, distinct manipulation phase (5-7 intervals), (3) often dropped fish before swallowing them, and (4) always took the fish to shore before beginning manipulation.

In contrast to the cottonmouths, the ontogenetic changes in attack behaviors in the water snakes were straightforward: the snakes progressively increased usage of active underwater attack types as they grew. The species-characteristic open-mouthed foraging was very weakly developed at birth, and was used only at the surface. Attacks made at the surface, open-mouthed or not, were the most successful type of attack for both juvenile and adult snakes in terms of the attack-to-capture ratio. Nevertheless, open-mouthed attacks were only made underwater, and fewer attacks were made at the surface by older juvenile and adult snakes.

Overall habitat use for the two species was stabile over time. The activities of neonate, juvenile, and adult cottonmouths took place along the water's edge. The water snakes also maintained a very definite aquatic orientation over time, but larger animals moved into deeper water and spent more time underwater whether in shallow or deep water. Larger animals spent less time in cover, also. (Field work, however, showed that even the largest snakes still used relatively shallow water and stayed in the vicinity of cover.)

Discussion of the Cottonmouth's Aquatic Foraging

Envenomation in the consumption of dead fish. Interestingly, although cottonmouth venom is particularly proteolytic and is considered to be an adaptation for the digestion of large prey because of the similarity of the venom to digestive enzymes (Kochva et al., 1983; Savitzky, 1980; Pough and Groves, 1983), large dead prey were not envenomated, and many small live prey were not envenomated. Dead fish, therefore, were handled very much as post-evenomated prey of any type are.

The approach and initial tongue-flicking and probing with the snout were also similar to the treatment given envenomated rodents (Kardong, 1975, 1982; de Cock Buning et al., 1981; Chiszar et al., 1977). No adaptation for the consumption of large dead prey was exhibited. Since large dead fish are more common during the warm summer months as described in the Field Data section of Chapter V, optimal ambient air temperatures for digestion (30° for crotaline digestion (Naulleau, 1983) could easily be achieved. Chemical enhancement of the digestive process would probably not significantly increase the rate of digestion at this time (Thomas and Pough, 1979). It was not uncommon, however, for envenomated small fish to be ingested while still alive (Studies 3 and 4, Chapter V), thus supporting the theory that crotaline venom is primarily for digestion rather than prey control. At any rate, envenomation was not an important factor in cottonmouth piscivory.

The cottonmouth's aquatic foraging: terrestrial foraging moved to the water's edge. The predatory tactics used by the cottonmouths at all ages were basically the same as those used in terrestrial foraging as determined by laboratory observations and as described in the literature (de Cock Buning, 1981; Kardong, 1975, 1977, 1980). The only clear difference was that fish were usually held after striking as has been reported previously (O'Connell et al., 1981). Generally, post-strike retention of prey occurs only when prey are large or dangerous in cottonmouths (Kardong, 1975; 1982) and in other species of *Agkistrodon* (Kardong, 1988).

The stereotyped posture of the neonate cottonmouths was identical to that used when foraging for mice (pre-strike posture) or frogs, except that the tail was never raised and moved in a luring manner in the presence of fish as is done in the

presence of frogs (Allen and Swindell, 1948, photograph, p.128). The caudal luring seen by Allen and Swindell (1948) and Cook (1983) was seen once during the pre-feeding observations described in Chapter V, Experiment 4 (when no fish were present) and once in the home cage (no prey present).

The aquatic foraging and feeding of the cottonmouths as adults and neonates thus indicated no special feeding adaptation to the aquatic environment (see Gould and Lewontin, 1979; Wanntorp, 1983) other than responding to fish in a predatory manner. The tendency of the cottonmouth to utilize the water's edge is required to capture fish, but cannot be considered an adaptation for piscivory as it also facilitates the capture of frogs and other vertebrates which might be at the water's edge. Rather, this habitat use could be better argued to be an adaptation for the prey-generalist predatory strategy of the cottonmouth, as the edge will be visited by terrestrial, amphibious, and aquatic vertebrates. The term adaptation may seem extreme for this habit, but seems warranted (see Dobson, 1985; Wanntorp, 1983) when looking at the crotalines as a whole: no other crotaline is known to be so generalized a feeder or to utilize this microhabitat. Within its lineage, the cottonmouth appears to exhibit unique foraging tactics (Wanntorp, 1983).

The underwater side-to-side OM sweeps exhibited by the water snakes, on the other hand, are more clearly associated with piscivory (see Taylor, 1987, Pritchard, 1984) as they occur in piscivorous members of several snake lineages (see Jayne et al., 1988, Hailey et al., 1982; Hailey and Davies, 1986a,b) as well as in other tetrapod piscivores (Pritchard, 1984; Schaller and Cranshaw, 1982; Taylor, 1987; Williston, 1914) and hence are more readily recognized as adaptive. The proficiency with which the water snakes in this study captured fish head first and manipulated and ingested fish underwater beginning with the first prey encounter would seem to imply

adaptation to piscivory, as similar results were found by Halloy and Burghardt (in press) for the natricine aquatic prey specialists, but not the generalists, tested.

Is the cottonmouth behaviorally adapted for piscivory because it retains fish after striking as suggested by O'Connell et al. (1981) and Chiszar et al. (1985)? The post-strike retention of fish is contrary to the usual post-strike release of prey in this species (Kardong, 1975, 1982; O'Connell et al., 1981), although the cottonmouth, like many crotalines, is variable in this habit (Kardong, 1988). Snakes have been found to vary prey control techniques depending on prey size (Loop and Bailey, 1972) and risk of damage from prey (de Queiroz, 1984). It can then be argued that fish are retained because they cannot inflict the sort of damage that large rodents can, as fish lack claws and teeth capable of harming the snake. Very large sunfish, which have sharp dorsal spines (100g), however, were captured very carefully by the head, anterior to the dorsal spines. The cottonmouths in the pool and in home cage feedings often waited some time before grasping large fish, sometimes following the fish carefully from nearby, apparently waiting to strike until the proper grasp was assured. Such unusually large fish were not retained after capture. As noted above, however, smaller fish were not envenomated by adults during the pool trials or in the home cages, nor were they grasped with obvious caution. Even the juvenile snakes often did not envenomate fish, and even when envenomation was observed, fish were often ingested while still alive. This type of prey handling is common with very helpless prey such as newborn mice or rats (de Queiroz, 1984), regardless of prey size. The dorsal spines of sunfish and even the barbels of catfish are easily overcome even by nonvenomous snakes (see Richmond, 1944) by head-first ingestion. The treatment of fish by the cottonmouth (and other snakes) suggests that all but the largest fish are retained by the cottonmouth because they are not potentially harmful to the snakes.

It does not seem necessary to invoke adaptation to piscivory to explain this generalist predator's ability to gauge the danger of prey.

The Role of Phylogeny in the Predatory Behaviors of the Two Species

Habitat use and aquatic capabilities. While the juvenile cottonmouth was not an outstanding aquatic predator, it performed quite adequately. In addition to its aquatic foraging tactics, the cottonmouth is similar to some populations of the semi-aquatic natricine generalist garter snake, *Thamnophis sirtalis*, in terms of diet and habitat use (see Drummond, 1980, 1983; Carpenter, 1952; White and Kolb, 1974; Catling and Freedman, 1980a,b; Gregory, 1978, 1984; Kephart, 1982, Kephart and Arnold, 1982). Both species exhibit population differences in diet, even utilizing a largely overlapping range of prey, although the cottonmouth eats reptiles and more mammals than does the garter snake, and the garter snake eats earthworms and leeches which the cottonmouth does not. The garter snake, in contrast to the cottonmouth, continues to utilize fish in its diet as an adult (in populations where fish are available). Why should one semi-aquatic generalist essentially give up live fish and the other not? A possible explanation rests on the one advantage which the garter snake has over the cottonmouth: the adult garter snakes achieve negative buoyancy easily enough that substrate crawling is possible (Drummond, 1980). Natricines appear to develop this capability readily, showing great variably among species depending on the degree of association with aquatic habitats (Fleharty, 1967; Drummond, 1980, 1983). Adult cottonmouths, on the other hand, achieve negative buoyancy well enough to coil on the bottom underwater, but apparently not well

enough to substrate crawl. Since no other crotalines are known to be as aquatic as the cottonmouth, it is not surprising that the cottonmouth is unable to develop this capability. This pattern suggests the presence of phylogenetic differences of import (Gould and Lewontin, 1979; Greene, 1986a; Wanntorp, 1983; Dobson, 1985).

While an adult snake may not require as much food per gram of body mass as does a young snake, it does require more food in absolute terms because of increased size (Barnard et al., 1979; Ford, 1974; Gehrmann, 1971). It is quite likely that an adequate supply of live fish cannot be captured from the edge because most fish at the edge are small ("minnow"-sized) and constant foraging would be required to supply the needs of a large cottonmouth. At Reelfoot, large dead fish, however, were frequently seen along Donaldson Ditch and fish certainly became trapped in the drying forest pools. Dead fish were also available in the heron rookery at Reelfoot Lakes. Utilization of these types of habitats as well as the utilization of carrion has been widely reported for other populations of the cottonmouth as detailed in Chapter I. Since cottonmouths usually utilize habitats where such sources of fish carrion abound, there may be selective pressure to favor its use, and favor the loss of foraging for live fish except in late spring when the receding spring flood waters leave many fish trapped in drying pools.

Chemosensory processes in carrion feeding. Other phylogenetic differences make the crotalines pre-adapted for foraging on dead fish. A characteristic of particular importance is the widespread tendency among crotalines to utilize carrion in the wild and in captivity (Klauber, 1956; Patten and Banta, 1980; Gillingham and

Baker, 1981; Lillywhite, 1982), and to exhibit a strong attraction to putrefied animal matter, even putrefied milk (Cowles and Phelan, 1958). Because the feeding of crotalines is organized around envenomation and the subsequent ingestion of envenomated prey (Duvall et al., 1978, 1980; Savitzky, 1980; Pough and Groves, 1983) that contain the chemical products of protein breakdown (see Kochva et al., 1983), it is not surprising that crotalines exhibit not only an acceptance of, but even a fondness for, putrefying flesh (Cowles and Phelan, 1958; Lillywhite, 1982).

Chemosensory stimuli are even more important to the cottonmouth than to rattlesnakes (*Crotalus* spp.) (de Cock Buning et al., 1981), as cottonmouths trail prey-derived chemosensory stimuli whenever present (Chiszar et al., 1979, 1986), in contrast to rattlesnakes which respond to such stimuli much more strongly after striking (Burghardt, 1970; Chiszar et al., 1983; see also Graves and Duvall, 1983). It is not surprising, then, that the cottonmouth should develop a carrion feeding strategy.

The water snakes, in contrast, while ingesting more dead fish over time in the various test situations, still preferred live fish as adults. The rate and minimal amount of change involved in the response to fish carrion suggest that experiential processes similar to other reported experiential changes (Porter and Czaplicki, 1977) were involved. *Nerodia* species, like other natricines respond immediately to prey-derived stimuli so that chemosensory stimuli of prey alone is often sufficient to induce searching or striking (Burghardt, 1968; Dukes, 1983; Drummond, 1979). Visual cues are also important (Burghardt, 1968; Czaplicki and Porter, 1974; Porter and Czaplicki, 1977) and can be sufficient to induce attack also (Drummond, 1985). While sensory control of the predatory process is somewhat different in *Nerodia* and *Agkistrodon*, the strong and immediate reaction to chemosensory stimuli is an

important convergence between these snakes, and appears to be the minimal requirement for the development of piscivory in a lineage of snakes.

2. THE GENERALIST-SPECIALIST CONTINUUM IN AQUATIC FORAGING

Comparisons Between Other Species

Review of Drummond's results. As discussed in Chapter I, Drummond (1980, 1983) found that there were reliable differences between the generalist and specialist aquatic garter snakes, genus *Thamnophis*, as did Halloy and Burghardt (in press) using some of the same species. Drummond (*op. cits.*) found the northern water snake, *Nerodia sipedon*, to be somewhat intermediate in character. Results are summarized in Table VI-3. Like the specialists, the juveniles of this species spent most of their search time in water (77%), exhibited a high attack rate, and captured many fish. Like the generalists, they spent little time underwater (16%), spending most of the time in a crane-cruise posture at the water's edge, and they relied on undirected OM and lateral attacks like the generalists. Underwater attacks most often involved probing in rock crevices (31%). As with the generalists, fish were never pursued through the water. Aerial attacks occurred at a rate (52%) intermediate between that of the generalists (76%) and the specialists (22%).

Comparing *Agkistrodon piscivorus* to the natricine generalists. Can the cottonmouth be considered to be an aquatic generalist? Although the selection of dead fish suggests a carrion feeding strategy more than piscivory, cottonmouths of all

TABLE VI-3

SUMMARY COMPARISON OF GENERALIST AND SPECIALIST AQUATIC SNAKES (JUVENILES) FROM DRUMMOND (1983)[a]

Behavioral Trait	Generalists[b] (Group Mean)	*Nerodia sipedon*	Specialists[c] (Group Mean)
% of Total Search Time spent on Aquatic Search	43%	77%	75%
Time spent underwater	14%	16%	38%
Anterior diving	3%	<1%	4%
Mid-water diving	8%	4%	0%
Crevice crawling	<3%	8%	15%
Attacks			
Overall attack rate	high	high	low
Aerial attacks	76%	52%	22%
Underwater attacks:			
Substrate crawling	1%	4%	27%
Crevice probing	6%	31%	10%
Mid-water pursuit	none	none	frequent
Underwater attack distance (cm)	.34	.42	1.83

[a]Based on calculations derived from Drummond, (1983).
[b]*Thamnophis sirtalis* and *Thamnophis elegans*
[c]*Thamnophis couchi* and *Thamnophis melanogaster*

ages foraged in a manner reminiscent of Drummond's (1980, 1983) natricine generalists, especially the common garter snake, *Thamnophis sirtalis*. As can be seen in Table VI-4, both species spent most of the time out of the water, and submerged very little when in the water. Additionally, most attacks for both species were aerial attacks directed at fish near the surface at the edge, and fish were not pursued underwater (Drummond, 1980, 1983). The other natricine generalist studied by Drummond (*op. cits.*), the western terrestrial garter snake, *T. elegans*, was less buoyant and dived more frequently, thus engaging in more aquatic activity than either the cottonmouth or the common garter snake (Drummond, 1980, 1983).

Common garter snake juveniles were very buoyant like the cottonmouth, which undoubtedly was at least partially responsible for the the lack of substrate crawling in both species. The adult common garter snakes (in the field) were less buoyant than the juveniles, however, which was not true of the adult cottonmouths. Drummond's (1980) description of the common garter snake's behavior suggests that the cottonmouths oriented toward the water and the water's edge more than did the garter snakes. The garter snakes apparently wandered away from the water frequently and seemed to return to it only when attracted by the activity of fish. Additionally, the cottonmouths at least occasionally submerged in apparent pursuit of fleeing fish, and oriented to fish underwater, which the garter snakes did not (Drummond, 1980). The pursuit of adult cottonmouths was so slow, however, that it was not useful. Both snakes are clearly terrestrial snakes which respond to aquatic prey, capturing them at the boundary of the these environments. The cottonmouth would seem, however, to be a habitat edge species rather than a habitat generalist like the common garter snake. Nevertheless, the cottonmouths does seem to qualify as an aquatic generalist.

TABLE VI-4

SUMMARY COMPARISON OF *AGKISTRODON PISCIVORUS*[a] AND *THAMNOPHIS SIRTALIS*[a]

Behavioral Trait	*Agkistrodon piscivorus* **adults/juvs.**	*Thamnophis sirtalis*
%Total Search Time Spent Overland[b]	.59/--	.54
%Total Search Time Spent in Water, Head out	.35/.20	.42
%Total Search Time Spent Underwater	.02/.03	.04
Diving	.02/.00	.04
Substrate crawling	.00/.00	.00
Attacks: Above water	.88[c]/.71	.86

[a]Data are from adult cottonmouths in the large test pool. Habitat use and foraging behavior for juvenile cottonmouths are from Experiment 3 in Chapter V, and attack data are combined from Experiments 3 and 4 in Chapter V.

[b]Time spent overland for the cottonmouths includes time spent on the edge, shore, and beach. Some of this time would have been considered aquatic foraging by Drummond (1980, 1983) as some craning over the water occurred; hence, the reported value is somewhat inflated.

[c]Above water attacks for the cottonmouth adults include edge and shore attacks on dead fish. Such attacks were not possible for the garter snake as no prey were out of water.

Comparing *Nerodia rhombifera* to *N. sipedon*. Since ontogenetic changes in the diamond back water snakes were pronounced, a true comparison between the species would require the comparison of similarly aged juveniles. Drummond's northern water snake juveniles were 117-158 days of age when tested. It would seem best to compare the Experiment 2, Time 2 *Nerodia rhombifera* juveniles to Drummond's *N. sipedon* as these would be the subjects from my study closest in age to Drummond's. Unfortunately, the testing tanks used in Experiment 2 were substantially smaller than Drummond's test pool and have no shore area. Therefore, comparisons will be limited. Some data could not be statistically tested because of Comparisons are summarized in Table VI-5.

The juvenile northern water snakes spent a mean of 77% of the foraging time on aquatic search. The remaining 23% of the time was spent out of the water. Since the juvenile diamond back water snakes had no opportunity to get out of the water, statistical comparisons cannot be made. The adult diamond back water snakes, however, spent a mean of only 4% out of the water, or 96% of the time on aquatic search. Even allowing for an ontogenetic change in the amount of time spent in the water, the numbers suggest that the diamond back water snakes may spend more time in the water. As further evidence of this, the juvenile water snakes in my study rarely used the top of the rock, spending a M=0% of the time on the rock. The rock was used as an out of the water area by the juvenile cottonmouths (Experiment 3, Chapter V). They spent M=20% of the time on top of the rock. The diamond back water snakes thus appear to spend more time in the water than do the northern water snakes.

Comparing time spent underwater, the northern water snakes spent about 16% of the time underwater compared to 58% of the time for the juvenile diamond

TABLE VI-5

SUMMARY COMPARISON OF *NERODIA RHOMBIFERA*[a] AND *N. SIPEDON*[a]

Behavioral Trait	*N. rhombifera*	*N. sipedon*	Significance of Comparison
% of Total Search Time Spent on Aquatic Search	.96[a]	.77	not calculated
Time Spent Underwater	.58	.16	<.0001
Diving	.05	.00	<.01
Crevices[b]	.12	.08	not calculated
Substrate crawling	.12	.03	not calculated
Submergent cruise[c]	.52	--	
Attacks	N=32	N=218	
Aerial attacks	.25	.52	<.0001
Underwater attacks:			
Substrate crawling	.13	.03	>.05
Crevice probing	--[b]	.15	not calculated
Submergent cruise	.67	--[c]	not calculated
Mid-water diving	.03	.28	<.0001

[a]Data for *Nerodia rhombifera* are from Time 2, Experiment 2, in Chapter V, except for total aquatic search time which are large test pool for adults. Data for *N. sipedon* is from Drummond, (1980).

[b]While *N. rhombifera* made 22% of their attacks underwater in the crevices, the behavior was only occasionally describable as crevice probing but was not so recorded.

[c]The submergent cruise posture (CCD) was not described by Drummond (1980, 1983a). It differs from substrate crawling only in that the head is raised off the substrate and the snake may be mobile or motionless.

back water snakes. (Note: Drummond [1980, 1983] uses the term diving for any underwater activity, whereas my definition of diving refers to only mid-water and anterior diving, terms also used by Drummond [*op. cits.*].) Testing values from individual snakes from Drummond (1980) and the Time 2 snakes from this study by means of the Fleiss test used previously, the diamond back water snakes were under water significantly more than the northern water snakes (.58 v. .16, $p < .001$).

Both species of water snake mid-water dived relatively little, although the northern water snakes may have engaged somewhat more in this behavior as 24/102 observations of submersion in the northern water snake consisted of mid-water diving, whereas it occurred generally only once, if at all, during a trial in the diamond back water snakes. Unfortunately, these data are not given in a form suitable for statistical testing. As Table VI-5 shows, the diamond back snakes also spent more time in the crevices and substrate crawled more. (The values were unfortunately not statistically testable, but do not seem to be extremely different.) Both species engaged in undirected OM attacks underwater, and did not engage in underwater pursuit at all. The diamond back snakes, however, oriented to fish across the pool underwater, and responded to fish more than 2 cm away. Both species made some frontal attacks from the substrate and engaged in minimal preparation before attack (*e.g.*, forming the neck into sinuous waves).

The diamond back water snake young were more aquatic than were the northern water snake young as evidenced by 1) the larger amount of time spent underwater (39%-60% in the 1-7 month age groups), 2) the higher rate of underwater attacking (52%-62% in the the 1-7 month age groups), and 3) the smaller amount of mid-water diving (diamond back water snakes did virtually none). The diamond back water snakes young additionally spent much time (35%-52% of the search time) in

the CCD posture underwater, a posture not described by Drummond (1983) for the northern water snakes. The diamond back water snakes also did not probe crevices in the manner described by Drummond (op. cit.). The northern water snakes in his study may have probed crevices *in lieu* of remaining in a CCD posture. While the diamond back water snakes crawled among the rocks, hid in the rocks, and captured some fish in the rocks, they appear not to utilize the crevices in the same manner. Additionally, most of the diamond back water snakes' aerial attacks were made from the water in a cruise posture rather than from out of the water or at the edge in a crane posture as did the northern water snakes. The young diamond back water snakes in my study did not really have the opportunity to crane from the edge to the extent that Drummond's did. However, his descriptions of foraging in the field also indicated considerable wandering along the edge, a behavior not observed in the diamond back water snakes in the test pool or in the field. Drummond did report that the northern snakes frequently sat in crevices in a cruise ("peering" is his term) posture in the field, which sounds very much like the emergent cruise posture seen in both the test pool and in the field in the diamond back water snakes.

It would appear, then, that the diamond back water snakes (1) spend more time in water, (2) wander along the shore less, and (3) spend more time underwater, (4) attack from underwater more, and (5) probe crevices less than do the northern snakes. The species are similar, however, in that both rely on undirected OM attacks at groups of fish and short, directed attacks at individual fish, but do not pursue fish through the water. Diamond back water snakes are more aquatic than the northern snakes, which correlates well with the known diet of the two species (See Chapter I). The apparent qualitative difference in use of the crevices suggests that the two species also have different aquatic strategies. Further study would be required to

resolve that question. Both species would seem to qualify as aquatic specialists, however.

The Characteristics of Aquatic Specialists

Underwater vision and aquatic specialization.. The underwater foraging tactics of the two species of *Nerodia* do not rely on good underwater vision as do the foraging tactics used by the *Thamnophis* specialists (Schaeffel and de Queiroz, submitted). Drummond (1980, 1983) speculated that good underwater vision was of little use to the northern snakes as it foraged primarily at night. The same is true for the diamond back water snakes, as they are generally inhabitants of eutrophic waters, of which Reelfoot Lake is an extreme example. Good underwater vision would probably be of little use even for daytime foraging in such water. Other than eutrophic conditions and darkness, wave action, and suspended soil particles can all nullify the need for good underwater vision in underwater foraging. While good underwater vision would be useful for underwater navigation, the species of *Nerodia* discussed here appear to move along the surface when moving from one location to another (pers. obs.).

Are we dealing with a phenomenon peculiar to the natricines? A review of the literature suggests that, in general, there is no reason to associate the pursuit of individual prey with aquatic specialization as many of the most aquatic forms, the sea snakes, forage by crevice probing (Dunson, 1975; Klemmer, 1967; Voris et al., 1978; Voris and Voris, 1983) or by lying still in ocean slicks and capturing hapless fish which hover under the slick (Kropach, 1975; Voris and Voris, 1983). Open-mouthed

foraging has also been reported for the most aquatic sea snake, *Pelamis platurus* (Kropach, 1975). There is no reason to associate the pursuit of individual prey with aquatic specialization *per se*.

There is good reason, however, as shown by Drummond (*op. cit.*), to associate good underwater vision with long underwater attacks and the pursuit of prey through the water. The active pursuit of fish and good underwater vision most likely are associated with environments where prey are dispersed, and/or fish densities are lower. Lower fish densities and clearer water are characteristic of aquatic environments that are not highly eutrophic. I suggest that aquatic specialists of the type studied by Drummond (1980,1983) are found in less eutrophic aquatic environments whereas aquatic specialists such as *Nerodia rhombifera* and *N. sipedon* are, in general, associated with more eutrophic environments.

Open-mouthed searching. While open-mouthed searching is, in the main, a form of undirected attack because it is directed at groups of prey rather than at individual prey, it is an effective tactic for dealing with aggregated prey. OM attacks range from simple OM stabs at prey to extended bouts of OM sweeps of the head from side-to-side accompanied by circling or figure-eight swimming (Drummond, 1980, 1983; Evans, 1942; Kofron and Dixon, 1980; Mushinsky and Hebrard, 1977a; Hailey and Davies, 1986a; this study). The behavior is seen in some form in Old and New World natricines; the simple stabs made from above, below, or at the surface seem to be more typical of the generalist piscivores (Drummond, 1980; 1983; *Agkistrodon piscivorus*, this study) and the initial efforts of the neonate *Nerodia rhombifera* (this study), whereas the fully developed form has been described only in

aquatic specialists of at least two unrelated colubrid families and a hydrophiid: the natricines (Drummond, 1980, 1983; Evans, 1942; Hailey and Davies, 1986a; Kofron and Dixon, 1980; Mushinsky and Hebrard, 1977a; Stoner, 1941), the homalopsine *Cerberus rhynchops* (Jayne et al., 1988), and the pelagic hydrophiid *Pelamis platurus* (Kropach, 1975).

The fully developed form is effective in dealing with groups of fish because it puts the body of the snake in the path of dispersing fish, forcing the prey against the body or trapping prey in loops of the body. Even when the continuation of movement does not aid in prey entrapment, it would seem to make use of the momentum produced by the lateral thrust of the head and neck. I therefore believe that this tactic deserves more credit than Drummond (1980, 1983) gave it. It does not, however, seem to merit the almost supernatural powers sometimes ascribed to it (*e.g.*, Evans, 1942; Kofron and Dixon, 1980; Stoner, 1941). In particular, it does not really concentrate prey, although, as noted, it does seem to foil the dispersal defense used by schooling fish. It also does not stir up prey hidden in detritus (Stoner, 1941), and, in fact, was not observed over detritus-covered bottoms. Even in *Nerodia rhombifera* it was not a stereotyped behavior, as it was performed in a variety of ways. The fully developed form described by Evans (1942) and Kofron and Dixon (1980) only occasionally occurred, and under certain circumstances (see discussion of Field Data, Chapter V).

The "necessary and sufficient" characteristics of aquatic specialists. Aquatic specialization does seem to be associated with negative buoyancy (Drummond, 1980; 1983; Fleharty, 1967; Seymour, 1982; Zug, 1971). This capability allows the aquatic

predator access to the entire water column as well as the bottom and crevices, although most snakes seem to forage in particular aquatic settings. Aquatic specialists are most easily recognized by the amount of time spent in the water. Aquatic specialists which are piscivore specialists do not remain along the edge much, whereas aquatic specialists which also prey upon anurans can be expected to spend time along the edge in the water. Extensive margin-wandering (Drummond, 1980, 1983), however, is not typical of aquatic specialists. Aquatic specialists seem to be able to handle and ingest prey in the water, although the methods of handling vary considerably (see Taylor, 1987). As discussed in Chapter I, the density of water requires accommodation. Attacks may be lateral (trawling) or forward (spear fishing), and particular head shapes are associated with each type.

Since specialists are undoubtedly as specialized morphologically as behaviorally, head shapes should be correlated with attack type and should be a good clue to the foraging tactics used. (A flat, long, relatively narrow head like that of *Nerodia rhombifera*, however, is useful for both lateral and forward types of attacks, however. Head shapes, like all morphological adaptations, need to be compared to close relatives in order to assess the degree of adaptation (see Dobson, 1985; Wanntorp, 1983). As an example of the use to which this sort of paradigm can be used, I would predict that the narrow-headed garter snake, *Thamnophis rufipunctatus*, is a fish specialist using tactics very similar to those of Drummond's specialists.

3. CONCLUSION

The results of this study greatly extended our knowledge about the foraging and ontogeny of foraging in the cottonmouth and the diamond back water snake as well as largely confirming what was already known about these species. Both species were found to resemble related species in some aspects of their foraging, with the juveniles more closely resembling less specialized members of the respective lineages. The laboratory findings were corroborated by the field work or, in the case of the cottonmouth, were in basic agreement with the literature, although the literature had led me to some contrary expectations. In particular, the use of carrion by the cottonmouth had previously been documented, but was considered to be a peculiarity of a population in a suboptimal environment. Other work corroborating my results remains unpublished (W. Auffenburg, pers. comm.).

The ontogeny of foraging was particularly interesting. Ontogenetic changes of the sort found here had not been documented previously in these or many other species. Both of these precocial species exhibited clear ontogenetic changes over time. The changes in the cottonmouth were especially marked. Unlike the water snake, the color pattern of the juvenile cottonmouth does not closely resemble that of the adult as it has a much more pronounced dorsal pattern. Since snake pattern usually aids crypticity, it would appear that young and adults are adapted for being cryptic in different environments. Given the number of other snakes which exhibit such ontogenetic change in pattern and color, many snakes can be expected to exhibit pronounced ontogenetic changes in foraging. In fact, ontogenetic changes seem to be found whenever looked for (Halloy and Burghardt, in press; Henderson et al., 1988;

Lagler and Salyer, 1945; Macias Garcia and Drummond, 1988; Mushinsky et al., 1982; Mushinsky and Hebrard, 1977a; Plummer and Goy, 1984).

Sex differences of a limited sort were found in the water snake in the pool and field. The difference was not as extreme as those found by Mushinsky et al. (1982), however, because the gravid females in my field study moved back into shallower areas and shore in both the test pool and field. Therefore, food and habitat separation within this sexually dimorphic species was not confirmed by my work.

The taxonomy of both the natricines and crotalines is in a state of rapid change (Cadle, 1987), and little can be said about the evolution of the behaviors within each family. Both of the species studied are generally alleged to be more closely related to New World species than to Old World (Brattstrom, 1964; Cadle, 1987 for the cottonmouth (Cadle, 1987; Dessauer et al., 1987; Lawson, 1987; Rossman and Eberle, 1977 for the water snake). Yet, both species resemble Old World relatives as closely as New World relatives in some ways. However the taxonomic relationships are settled, the foraging tactics of the cottonmouth are ancestral traits, but the habitat use is derived as no other crotaline is known to forage at the water's edge. The aquatic foraging of the water snake seems to resemble both New and Old World natricines. Because of that, and because of the the independent development of open-mouthed searching tactics in several families, it is impossible to resolve the phylogeny of the trait in the natricines. Open-mouthed searching in some form does seem to occur in many natricines, suggesting that the tendency to attack in such a manner is an ancestral trait. The aquatic specialist *Thamnophis*, on the other hand, which pursue individual prey through the water almost certainly are exhibiting derived traits. Such behaviors have evolved at least two times in the Thamnophiini, as the two aquatic specialists which have been studied use different means of focusing

the eyes (Schaeffel and de Queiroz, submitted). Although behavior often correlates well with taxonomic relationships (*e.g.*, Gove, 1979; Greene and Burghardt, 1975), the foraging behaviors used by these species clearly does not. This finding is not unexpected, as food getting behaviors are often analogous rather than homologous (Mayr, 1958).

The generalist-specialist continuum in aquatic foraging as set forth by Drummond (1980, 1983) was somewhat modified by my work. This modification makes the foraging tactics of the northern water snake less problematic as it now fits smoothly into the continuum at the specialist end. The diamond back water snake also fits in well now, just a little farther toward the specialist end. The cottonmouth fits in well at the far generalist end of the continuum.

There are some important issues left unresolved. The ontogeny and rather unusual aspects of the cottonmouth foraging (*e.g.* heavy reliance on carrion) were unanticipated. Since my findings do not conform to known patterns, laboratory replication and further field study are needed before the results will be widely accepted, although I feel secure about the findings. In part, the problem is the limited range of knowledge about snakes: the known patterns are few. Another unsatisfactorily resolved problem is the actual methods used by large water snakes to capture large fish. While I found no evidence that large snakes have any other tactic for capturing large fish, and there was good evidence from the field study that the large fish were available in relatively shallow water, further investigation is warranted. Testing in a very large deep pool in the spring shortly after hibernation might overcome the reluctance of large snakes to forage in captivity that initially plagued this study.

Can snakes be fit into foraging theory? The snakes did exhibit some prey size selection, and other studies have found such size selection (Hailey and Davies, 1986c). Perhaps tests of "risk" theories such as that of Caraco (1981) could be done to gauge the alteration of risk with weight loss. As discussed in Chapter I, snakes have unusual responses to changing food supply, so that metabolic rate changes either must be controlled or must be measured. The young snakes appeared to optimize food intake in accordance with standard models (Schoener, 1971) better than did the older snakes. More could be done with this. In the main, however, new models need to be created for snakes. As a suggestion based on previously published ideas (Gans and Pough, 1982; Greene, 1986b; and Pough, 1980, 1983b), I offer the hypothesis that snakes optimize energy expenditure rather than energy intake. Based on the diamond back water snake, possible behavioral responses to forced energy expenditures might include (1) switching to less active foraging tactics, (2) switching to the tactics that have the highest success rate, (3) selecting larger prey, even prey that are dangerously large (see Hailey and Davies, 1986c), or (4) capturing prey more reliably by the head. Snakes are always going to be difficult to test, however, so that another possibility is to test the hypothesis by comparing strategies of snake species with differing energy expenditure minima and maxima.

In the main, this study was successful at obtaining the desired information. The combination of testing in the large naturalistic pool and a formal field study provided more information than does the usual field study of snake feeding, and appears to be a useful approach to understanding snake foraging.

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APPENDICES

APPENDIX A
SVL AND SEX OF SNAKES

Nerodia r. rhombifera

Snake	Sex	SVL	Snake	Sex	SVL
2410	M	675-700	Time 1		
2418	F	1000-1025	2419A	F	236
2420	F	1000-1025	2419C	F	242
2421	F	1050-1075	2419D	M	235
2422	F	875-900	2419G	F	237
2424	F	675-700	2419J	F	231
2425	F	700-725			
2426	M	700-725	Time 2		
2427	M	675-700	2419A	F	265
2428	F	675-700	2419C	F	261
2429	M	700-725	2419D	M	266
2430	F	900-925	2419G	F	246
2431	F	725-750	2419J	F	258
2437	F	425-450			
2438	M	650-675	Time 3		
2439	M	875-900	2419A	F	287
2440	F	975-1000	2419C	F	284
2441	M	775-800	2419D	M	290
2444	F	960-975	2419G	F	264
2446	M	775-800	2419J	F	278
2447	F	975-1000			
Neonates					
2443B	M	245			
2443C	F	244			
2443E	F	234			
2443F	M	246			
2443G	F	239			
2443J	M	242			
2444A	M	245			
2444B	F	249			
2444D	M	248			
2444H	F	259			
2444I	M	257			
2444J	M	246			
2444M	F	252			
2444Q	M	246			
2447C	F	226			
2447D	M	222			
2447E	M	230			
2447F	F	205			
2447G	M	224			
2447J	M	220			

APPENDIX A (CONT.)

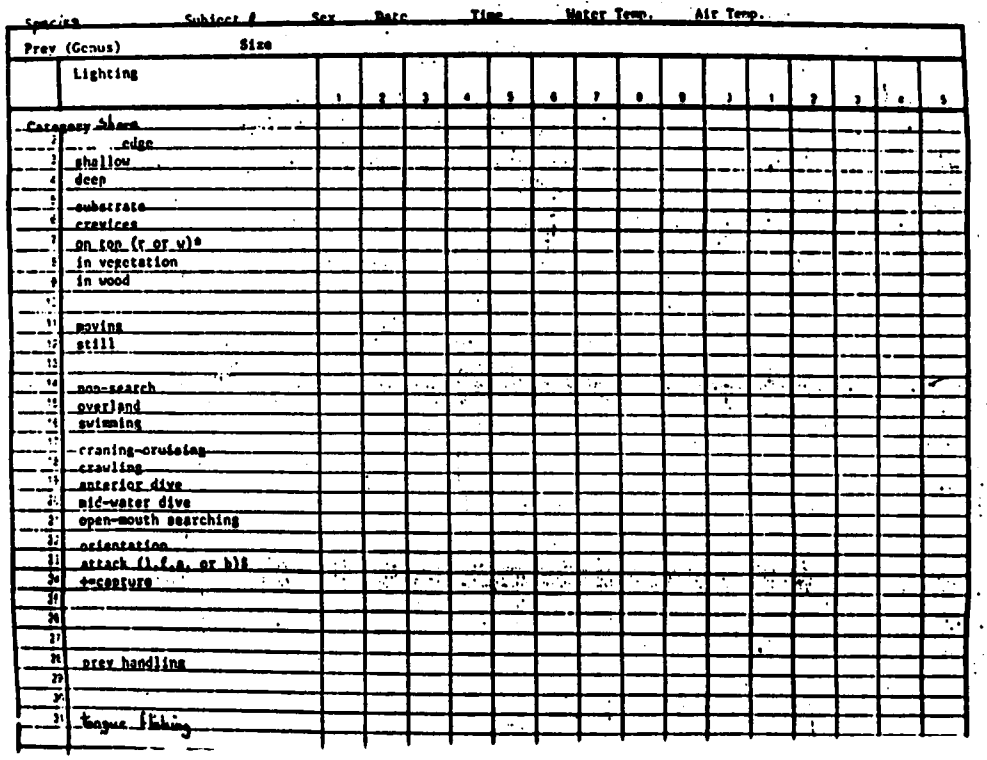
Agkistrodon piscivorus

2501	M	425-450
2502	M	1000-1025
2503	M	900-925
2504	M	975-1000
2505	M	950-975
2506	F	600-625
2507(neonate)		350-375
2507(juvenile)		425-450
2509	M	825-850
2511	M	600-625
2513	M	800-825
2515	M	675-700
2516	M	250-275
2517	M	300-325
2521	F	650-675
2527	M	800-825
2529		550-575
2530	M	675-700
2531(juvenile)		425-450
2532(juvenile)		400-425

Neonates	
AHS-SC1	300-325
AHS-SC2	300-325
AHS-SC3	300-325
AHS-SC4	300-325

APPENDIX B

SAMPLE CHECK SHEET



Species Subject # Sex Date Time Water Temp. Air Temp.

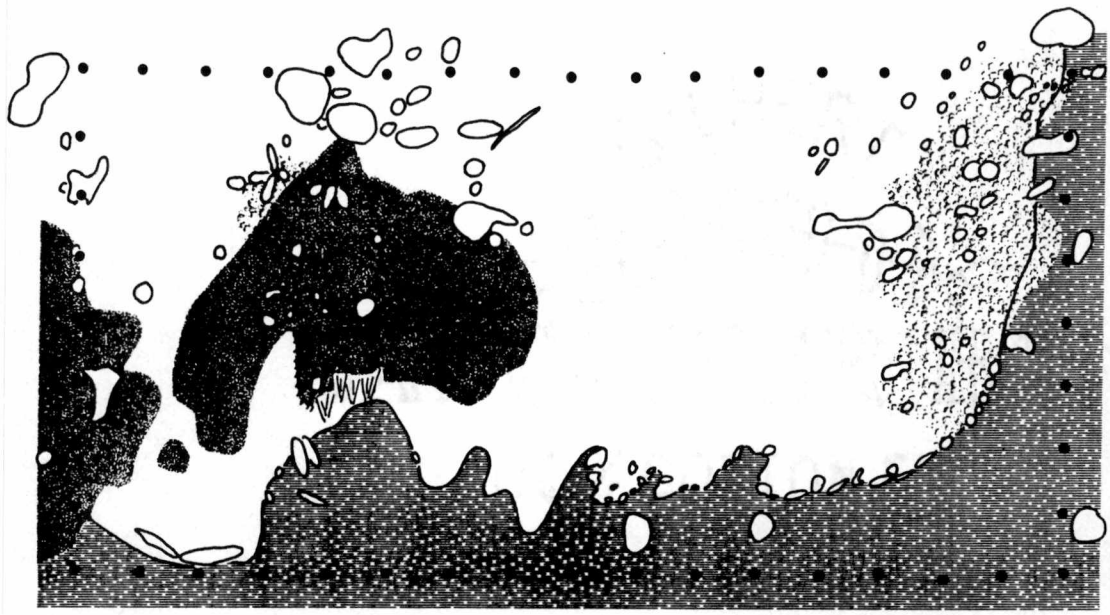
Prey (Genus) Size

	Lighting	1	2	3	4	5	6	7	8	9	1	1	2	3	4	5
	Category Shore															
2	edge															
3	shallow															
4	deep															
5	substrate															
6	crevices															
7	on top (r or w)*															
8	in vegetation															
9	in wood															
10																
11	moving															
12	still															
13																
14	non-search															
15	overland															
16	swimming															
17	craning-cruising															
18	crawling															
19	anterior dive															
20	mid-water dive															
21	open-mouth searching															
22	orientation															
23	attack (l,f,a, or b)§															
24	†capture															
25																
26																
27																
28	prey handling															
29																
30																
31	tongue flicking															

APPENDIX C

STUDY GRID MAPS AND DESCRIPTIONS

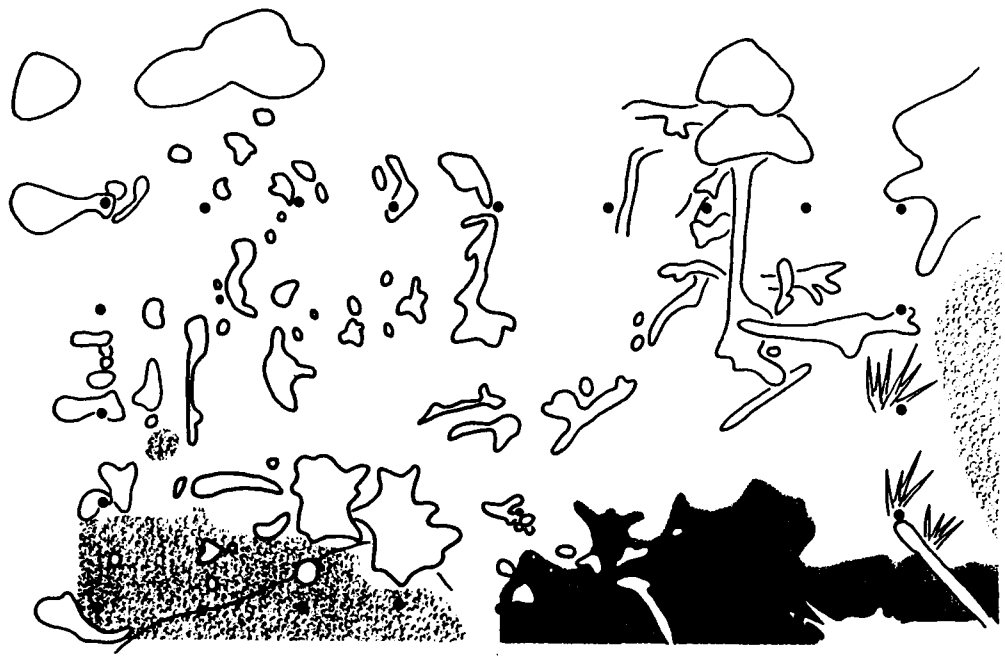
Study Grid I



Map of Study Grid I. Water depths were 0-15 cm at the shore line. Shore was low grass with interspersed cypress trees. The grass is indicated by the broken hatched tone. The water level increased gradually and regularly to 45-60 cm deep. See Chapter II for detailed descriptions of the study grid.

APPENDIX C (CONT.)

Study Grid II



Map of Study Grid II. All but the lower left portion of the grid was covered by water. The shore area was moist and covered with varying amounts of vegetation. Dark stippled areas represent thick vegetation, and the lighter patterned areas represent sparse vegetation. Open circular shapes represent trees, cypress knees, and stumps. Elongate open shapes represent exposed cypress roots.

Study Grid III

Description Only for this Grid. This grid consisted almost entirely of very dense "cut-grass" interspersed with areas of open water with sparse patches of water. Each quadrat is described in terms of the percentage of cover and the range of water depths in 15 cm intervals. Water depths not given as a range measured approximately the stated depth throughout the quadrat. Quadrats are numbered with a letter for the rows and a number for the columns. The columns are numbered from the shore outward, and the rows run parallel to the shore. Abbreviations are as follows: TG = thick tall cut-grass; STG = sparse tall cut-grass; MG = medium cut-grass; DV = dense mixed vegetation; SV = sparse mixed vegetation; L = dry land; OW = open water.

Description of Each Quadrat of Study Grid III.

A1:100% TG; L
A2:100% TG; 0-15 cm
A3:100% TG; 15-30 cm
A4:10% TG, 90% OW;15-30 cm

B1:100% TG;L-15 cm
B2:90% TG, 10% OW;0-15 cm
B3:100% TG; 15-30 cm
B4:100% TG; 15-30 cm

C1:90% TG,90% DV; L-15 cm
C2:100% TG; 0-15 cm
C3:90% DV; 10% OW; 15-30 cm
C4:100% TG; 15-30 cm

D1:75% TG, 25% MG; 0-15 cm
D2:25% TG, 75% OW; 15 cm
D3:25% TG, 75% OW; 15-30 cm
D4:25% TG, 75% OW; 15-30 cm

APPENDIX C (CONT.)

E1:50% TG, 50% MG; 0-15 cm
E2:100% OW; 15 cm
E3:90% OW; 10% TG; 15-30 cm
E4:25% TG, 75% OW; 15-30 cm

F1:50% TG,50% MG; L
F2:80% DV; 20% OW; 15 cm
F3:90% TG, 10% OW; 15 cm
F4:25% TG, 75% OW; 15-30 cm

G1:100% MG; L
G2:25% TG, 75% OW; 0-15 cm
G3:80% TG, 20% OW; 15 cm
G4:90% STG, 10% OW; 15 cm

H1:100% MG; L
H2:90% OW, 10% TG;0-15 cm
H3:90% TG, 10% OW; 15 cm
H4:75% SV, 25% OW; 15 cm

VITA

Barbara Ann Conner Savitzky was born in Bridgeport, Connecticut on August, 7, 1947. She moved to Mansfield, Ohio three years later and attended elementary and junior high school there. She moved to Knoxville, Tennessee in 1961 and attended Bearden High School. In 1964, she was accepted as an early admissions student at The University of Tennessee, Knoxville. After successfully completing her freshman year at the University, she was awarded a diploma from Bearden High School. In June 1968 she received a Bachelor of Science degree in Psychology from the University of Tennessee, Knoxville.

After taking care of the needs of a growing family and working in day care, she returned to the University of Tennessee, Knoxville as an adult special student in 1981. In September 1982 she was accepted into the The Graduate School of The University of Tennessee, Knoxville. She received the Doctor of Philosophy degree with a major in Life Sciences, Ethology in August 1989.

The author is a member of Sigma Xi, the Animal Behavior Society, the American Society for the Study of Amphibians and Reptiles, the Society for the Study of Reptiles and Amphibians, and the Herpetologists' League. Ms. Savitzky is currently employed by the Virginia Zoological Society and Norfolk Public Schools.