ECOLOGY AND LIFE HISTORY OF THE BROWN WATER SNAKE (*NERODIA TAXISPILOTA*)

by

MARK S. MILLS

(Under the direction of Dr. J. Whitfield Gibbons)

ABSTRACT

Population parameters, habitat, diet, reproductive traits, and other natural history characteristics of the brown water snake, *Nerodia taxispilota*, from the Savannah River Site, South Carolina, USA, were determined or estimated using mark-recapture data collected over an 8-yr period (1991-1998). Population size estimates for a 10-km section of the Savannah River ranged from 2782 - 3956 (approximately 0.14 - 0.20 snakes/m of shoreline). Growth was similar in juveniles of both sexes, but adult females grew significantly faster than adult males. Life history traits for this population include: 1) relatively high adult survivorship, 2) estimated ages at maturity of approximately 5-6 years for females and 3 years for males, 3) relatively long-lived (6+yr) individuals, 4) high fecundity (mean litter size =18.2), and 5) annual reproduction by females larger than 115 cm SVL. Litter size was positively correlated with female length and mass. No apparent trade-off exists between litter size and offspring size. Brown water snakes were not randomly distributed and were significantly associated with the steep-banked outer bends of the river and availability of potential perch sites. River sections with the highest number of captures were clustered within 200 m of backwater areas. Most (70%) of 164 recaptured *N. taxispilota* were <250 m from their previous capture site; however, three moved >1 km. Only large (>80 cm snout-vent length) individuals (n = 8) crossed the river (approximately 100 m). I collected foraging and dietary information from 1565 individual captures by using a nonlethal, albeit labor intensive, technique. Of all captures, 257 (16%) had food in their gut, and of the identifiable food items (n=168) all were fish and 63% were catfishes (Ictaluridae). A significant shift to an almost exclusively catfish diet occurred in snakes greater than about 60 cm SVL. Of 814 females captured, 18% had eaten, compared to 15% of 748 males. Feeding frequency (percent captured with food) ranged from 15.8%-20.3% between four general study sites and varied monthly, with peak frequencies in May, July, and October.

INDEX WORDS: *Nerodia taxispilota*, Squamata, Serpentes, Colubridae, Brown water snake, Spatial ecology, Habitat use, Movement, Mark-recapture, Diet, Fish, Ictaluridae, Catfish, Ontogenetic diet shift, Food chain/web, Population size, Growth, Reproduction, Life History

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DEDICATION

I dedicate this dissertation to my wife, Louise, and my children, Jacob and Maria, whom I love with all my heart.

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INTRODUCTION

NATURAL HISTORY OF THE BROWN WATER SNAKE

(*NERODIA TAXISPILOTA*)

A central goal of science is the discovery and documentation of patterns in the natural world, followed by formulation of unifying rules or concepts that underlie and predict these patterns. However, our scant knowledge of many organisms precludes or hinders detection of patterns, let alone formulation of experiments to test theories surrounding the patterns. One of the first topics discussed in introductory biology and other science courses is the Scientific Method.. The first step in this familiar process is observation, and in the field of ecology, observation is natural history. As Greene (1986) stated, “It (natural history) is the ‘idea and induction’ part of ‘the’ scientific method, the *essential* (emphasis added) prelude to formulating hypotheses as well as the raw material for testing them… It inspires theory as well as provides crucial data for answers to comprehensive, synthetic problems in ecology, ethology, evolution, and conservation biology.” Descriptive natural history is vital in comparative studies in evolutionary ecology and creates a basis for subsequent experimental analyses (Huey and Bennett, 1986). Natural history provides the questions that ecology attempts to answer and is the foundation for life history theory.

Several preliminary attempts have been made to summarize and quantify the natural history of snakes (Seigel et al., 1987; Shine, 1991; Seigel and Collins, 1993; Greene, 1997), but the predominant conclusion is that relative to most other major vertebrate groups, little is known about snakes. Studies on snakes often suffer from low sample sizes and lack of long-term observations, and therefore attempts to discern phylogenetic or ecological patterns in snake biology have met with limited success. Multiple authors (e.g., Parker and Plummer, 1987; Seigel and Ford, 1987; Turner, 1977; Dunham et al, 1988) have lamented over the problems associated with field studies used to address issues related to population ecology, foraging ecology, and life history of snakes, leading some snake ecologists to exhibit "Lizard Envy" (Seigel, 1993), the perception that snakes make poor research animals when compared to their squamate relatives. Most of the historic "problems" in studying snakes are related to small sample sizes and low recapture rates, as illustrated in the references listed above. For example, in their review of snake reproductive biology, Seigel and Ford (1987) summarize the relationship between female size and clutch size for snakes. Of the 61 regression equations with sample sizes reported in their Table 8-2, 57% have samples sizes of <25, 89% have sample sizes <50, and 97% have samples of <100, with only two (3%) of 61 studies having sample sizes greater than 100. In Parker and Plummer's (1987) review of snake population ecology, recapture rates for snakes ranged from 0 to 95%, but 28 (62%) of the 45 studies reported in their Table 9-1 had recapture rates of < 20%.

As a group snakes possess traits that make them particularly difficult to study in the field, including: 1) population densities are often low, 2) most snakes are secretive, and 3) snakes often remain inactive for long periods of time, and therefore are difficult to locate and capture. Capture methods (e.g., drift fences and pitfall, funnel, or box traps) and other techniques (e.g., radiotelemetry) have been developed and modified to attempt to solve or address some of these problems, but snake studies continue to be plagued by relatively low sample sizes and low recapture rates.

Brown water snakes, *Nerodia taxispilota*, especially those on the Savannah River Site (SRS), SC, obviate some of the problems associated with snake natural history studies. They occur in high densities compared to other local species and are frequent, conspicuous baskers, making them relatively easy to locate and capture. Adults reach comparatively large body sizes and individuals are hardy, allowing for easy marking and for the use of techniques such as telemetry. Brown water snakes are viviparous and will readily have young in the lab, aiding in the acquisition of reproductive data. Finally, they are non-venomous, thus reducing the capture and handling problems associated with studies of venomous species. Because of these features, *N. taxispilota* seemed to be a model species for study, not only to add to our general knowledge of snake ecology, but also to document the natural history of a common vertebrate. Given how common this animal is in parts of its range, little is known of the ecology of the species (fewer than 10 papers have been published that deal with the natural history of *N. taxispilota* in more than an anecdotal manner).

My intended purpose for this research is to identify and fill in gaps in our knowledge and understanding of this species at the SRS in order to provide the solid background needed for future and ongoing studies in ecology, life history evolution, ecotoxicology, and other areas. This dissertation represents the largest (in terms of sample size and number of years) and most comprehensive study to date on *N. taxispilota*, and is broken into four independent chapters that focus on different aspects of its natural history.

Chapter 1 is a species account and literature review for this species. It was written for the book, “The Natural History of North American Water Snakes” (Gibbons and Dorcas, in press) and follows the specific format designated for species accounts in that book. I describe current knowledge about the biology and ecology of *N. taxispilota* and include a complete literature review and range map for this species.

Chapter 2 is a discussion of the habitat use and general movement patterns of *N. taxispilota* in a 10-km section of the Savannah River adjacent to the SRS and is published in *Herpetologica* (Mills et al., 1995). In addition to an estimate of population size or density, we describe the macro- (e.g., which sections of the river the snakes frequented) and micro-habitat (e.g., basking locations and perch heights) of this population. We also document movement patterns based on recaptures of marked animals.

In Chapter 3, I discuss the foraging ecology and diet of *N. taxispilota*. I use both field and laboratory studies to document the primary prey of this species as well as to assess prey preferences. I then related prey and feeding to aspects of the biology of *N. taxispilota* (e.g., sex, size, and maturity). I also used two data sets to compare my dietary data from non-lethal sampling of snakes to data collected from snakes that were dissected in other studies.

Chapter 4 continues the population studies addressed in Chapter 2, but focuses on reproduction and selected aspects of life history. Using open population size estimation models, I estimate the number and density of *N. taxispilota* living in a 10-km section of the Savannah River. I use a large data set (> 1500 original captures) collected over five years to determine the characteristics of reproductive females and their litters (> 2200 offspring). I then explore the demography and components of the life history of this population using the reproductive characteristics coupled with estimates of survivorship.

Although each of these chapters can stand alone, the topics discussed are united. For example, prey abundance or food intake has been shown to have influences on reproduction, growth rates, and survivorship in snakes (Andren, 1983; Seigel and Ford, 1992; Ford and Seigel, 1994; Plummer, 1997; Madsen and Shine, 2000; Barron and Andraso, 2001). Likewise, relationships exist between habitat use, movement patterns, reproduction, and foraging (see review in Reinert, 1993). Taken together, the four chapters represent a major advance in our understanding of *N. taxispilota*, and offer fruitful research avenues for future work on this and other species of snakes.

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CHAPTER 1

SPECIES ACCOUNT OF THE BROWN WATER SNAKE

(*NERODIA TAXISPILOTA*)

See Appendix 1.1 for synonymy

DESCRIPTION

“Both in appearance and disposition, this is one of the most ugly of the American snakes” -- (Ditmars, 1907). *Nerodia taxispilota* is a large, heavy-bodied water snake with keeled dorsal scales. The head is wide posteriorly, distinct from the neck, and relatively long. The snout is tapered, giving the head a triangular shape. The eyes are high and forward on the head. The dorsum is tan or light brown with a row of 21-29 dark, rectangular blotches down the midline that alternate with similar lateral blotches. Anteriorly, the dorsal blotches usually do not contact those on the sides of the snake, although posteriorly the dorsal blotches of many individuals are “H”-shaped and often connect with the lateral blotches. In some individuals, dorsal blotches connect with one another forming short, longitudinal stripes. Neill (1963) shows a photograph of a completely striped individual. The head is brown and usually unmarked, although the labials have dark, vertical bars (one per scale). The venter is cream to light brown with dark spots, often half-moon shaped or rectangular, that can be scattered or organized as two rows of lateral spots with a thin midventral line. The color pattern of juveniles is similar to adults, although often more bold and distinct. While most individuals retain this pattern throughout life, some take on a rusty appearance and large individuals (usually females) often are dark and seem to lack a pattern when viewed from a distance. The rusty or reddish-brown color probably is the result of a stain acquired in certain habitats. Some *N. taxispilota* at the northern edge of their range exhibit this rusty color when they first emerge from hibernation, subsequently losing it after the first shedding (Charles Blem, pers. comm.). Similar observations have been made in South Carolina and Georgia, although individuals can retain this color throughout the year if they frequent certain habitats (e.g., swamps and backwater areas adjacent to the Savannah River, pers. obs.).

Nerodia taxispilota is distinct throughout its range in color pattern and appearance and is distinguished from other *Nerodia* by usually having 2 anterior temporal scales (although Mount and Schwaner [1970] found 15% to have single anterior temporals) and parietals that become fragmented posteriorly. Males lack chin papillae, which are present on male *N. rhombifer*. “The hemipenes are greatly expanded apically with a simple straight sulcus and with a very extensive nude apical area” (McCranie, 1983). Line drawings of the parietal and basioccipital bones are presented in Rossman (1963) and the scalation patterns for *N. taxispilota* are presented in Appendix 1.2.

TAXONOMY AND SYSTEMATICS

Nerodia rhombifer was first described as a subspecies of *N. taxispilota* by Löding (1922), followed by Haltom (1931) and subsequently by other authors (Cagle, 1952; Cagle, 1968; Cliburn, 1956; Neill, 1954, 1958; Viosca, 1949). Only one author (Cliburn, 1956) provided support for this argument, but his evidence was based on the examination of only two *N. taxispilota* vs. 46 *N. rhombifer*. Using color pattern and squamation, Mount and Schwaner (1970) separated them into two distinct species based on a thorough examination of 53 *N. taxispilota* and 26 *N. rhombifer* from “critical areas” of their range (primarily Alabama, western Georgia, and the panhandle of Florida).

Subsequent studies using allozyme and mtDNA evidence confirm that *N. taxispilota* and *N. rhombifer* are separate but closely related sister taxa, distinct from other *Nerodia* lineages, and probably the result of Pleistocene glaciations that separated them into eastern and western populations (Lawson, 1987; Densmore et al., 1992). While Mount and Schwaner (1970) concluded that their ranges “apparently” do not overlap, the two species may occur together in Alabama, although this remains to be confirmed (Gosser et al., 1996).

ETYMOLOGY

The specific epithet *taxispilota* is derived from the Greek words “taxis,” meaning “arrangement,” and “spilos,” meaning “spot,” apparently in reference to the alternating blotches on the dorsum.

COMMON NAMES

Nerodia taxispilota has many common names, including: aspic, brown water snake, southern water snake, moccasin, water moccasin, pied-bellied water snake, water pilot, and water rattle (or rattler). Few outside the fields of science or amateur herpetology refer to *N. taxispilota* as the brown water snake.

Although *N. taxispilota* is often mistaken for the cottonmouth (*Agkistrodon piscivorus*) and many people believe all water snakes to be venomous, many South Carolinians and Georgians distinguish between *N. taxispilota* and the cottonmouth, usually calling it a moccasin (reserving “cottonmouth” for *A. piscivorus*), water rattler, or water pilot. The name “water rattler” comes from the belief that *N. taxispilota* is a rattlesnake that has lost its rattle because of its aquatic existence. The name “water pilot” originates from the myth that *N. taxispilota* warns venomous snakes of danger and even leads them to safety.

GEOGRAPHIC DISTRIBUTION

Nerodia taxispilota are found throughout the Coastal Plain and into the Piedmont along major rivers from eastern Alabama to eastern Virginia (Fig. 1.1 - Map) and have been reported from salt and brackish waters (Neill, 1951; Neill, 1958), although at least one of Neill’s references (Jobson, 1940) is erroneously used as evidence. Jobson states that two large *N. taxispilota* “...were captured ... in tidal, fresh water creeks.” Neill himself apparently observed *N. taxispilota* “...about salt marshes and mud flats...” and suggested there might be a salt water “race” based on the small size and color (pinkish-brown with X-shaped dorsal spots) of the specimens captured and observed in Beaufort and Colleton Counties, South Carolina (Neill, 1951). In support of Neill’s observations of the coastal habitats of this species, Charles Blem (pers. comm.) states, “Brown water snakes are largely inhabitants of tidal, brackish habitat in most of the species’ range in Virginia” .

Konrad Mebert (Old Dominion University, VA; pers. comm.) has captured *N. taxispilota* north of Manns Harbor, Dare Co., NC, foraging in water with a specific conductivity of 2205 μmho/cm (fresh water usually falls between 50-500 μmho/cm; Brower et al., 1998) and salinity of 1.7 ppt, which qualifies as brackish water (0.5-30 ppt). Using the “Venice System” of classifying marine waters, 1.7 ppt is mixo-oligohaline (0.5-5 ppt), with fresh water being < 0.5 ppt (Reid, 1961).

McCranie (1983) implied the range may be expanding farther south into Florida (based on Schwartz, 1950) and into the Piedmont along the rivers. A locality record for Habersham Co., Georgia (Williamson and Moulis, 1994; Fig. 1.1 – map) is disjunct and almost in the North Georgia mountains, but upon examination of the specimen (a large female in the University of Georgia's museum collected by Carlos Camp near Demorest in 1984) its identity was confirmed as *N. taxispilota*. Whether the range of this species is expanding or contracting in certain areas remains uncertain and in need of further study (see Mitchell, 1994, and discussion below).

FOSSIL HISTORY

Fossil vertebrae of *N. taxispilota* from the Pleistocene have been found in Alachua and Levy Counties, Florida (Auffenberg, 1963). Holman (2000) indicated that the identification of Late Pleistocene or Early Holocene *N. taxispilota* fossils were partially based on present geographic range of the species because the fossil vertebrae of *N. taxispilota* and *N. rhombifer* are indistinguishable.

NATURAL HISTORY AND ECOLOGY

HABITAT

Nerodia taxispilota have the distinction of being described by most authorities as the most aquatic and as the most arboreal of the *Nerodia* species. Their morphology (eyes and nostrils high on the head), physiology (can hold their breath for extended periods of time, constrict peripheral circulation, and are more susceptible to cutaneous evaporative water loss), and other aspects of their biology (e.g., piscivorous, excellent swimmers) support the contention that they are extremely aquatic. (Additionally, using one definition of arboreal snakes (i.e., those that spend at least 50% of their time above the ground; Lillywhite and Henderson, 1993), one could classify *N. taxispilota* as arboreal. Carr (1940) credited them with being “the most arboreal of the Florida watersnakes” and as “probably the swiftest swimmers of all our snakes.” These snakes regularly climb up to 2 m above the water, and have been seen at heights of more than 4 m (pers. obs.; Charles Blem, pers. comm.).

Although *N. taxispilota* can be found in many aquatic habitats, almost all descriptions indicate that they seem to be most abundant in rivers, lakes, large streams, and associated waters (e.g., oxbow lakes, cypress swamps, and beaver ponds). Probably because of their fondness for fish, they are rarely found in ephemeral waters. In the Savannah River, they are more abundant on the outside bends and straight sections of river than on the inside bends (Mills et al., 1995). The observed difference in habitat use in the Savannah River may be a result of fluctuating water levels (the inside bends can be dry) and the availability of prey.

PHYSIOLOGY AND BEHAVIOR

Using “ingested” transmitters, Osgood (1970) observed that gravid females (n=3) emerged from the water to bask, maintaining a body temperature of 26-31^{o}C, then re-entered the water when the air temperature was lower than the water temperature. A similar pattern of leaving the water to warm and then re-entering the water when the air temperature dropped was observed by Goodman (1971). These studies must be viewed with caution as it has been demonstrated that ingested transmitters, similarly to food items, induced snakes to maintain higher body temperatures (Lutterschmidt and Reinert, 1990). Blem and Blem (1990) reported a mean body temperature of 24.8^{o}C (n=68) for field-captured *N. taxispilota* (which they admitted was probably biased because of collecting techniques) and 28.2^{o}C (n=10) for laboratory temperature preferences. The latter figure is near to the mean body temperature observed by Goodman (1971) in an outdoor enclosure (27.1^{o}C, n=7). The above studies on *N. taxispilota* agree with others on *Nerodia* species that indicate a preferred body temperature range of 26-29^{o}C (based on field and laboratory data; Table 14-1 in Lillywhite, 1987).

Under laboratory conditions, brown water snakes maintained at a high temperature (30.6^{o}C) consumed more food and shed more often than those kept at a lower temperature (20.4^{o}C). The individuals kept at a high temperature did not grow faster and all individuals lost weight, probably because of the increased metabolic rate at the higher temperature (Semlitsch, 1979). *Nerodia taxispilota* have the ability to hold their breath for long periods of time. Whether foraging, moving, or inactive, brown water snakes spend much of their time underwater and some hibernate underwater for long periods of time (Mills, unpub. data), a behavior not unique to water snakes (Costanzo, 1989).

In a series of both restrained and unrestrained forced dives, and voluntary and “scare” dives, *N. taxispilota* were able to remain submerged for 30 min. at 25^{o}C with no apparent harm to the animals (Irvine and Prange, 1976). Irvine and Prange also found that *N. taxispilota* have the ability to dive repeatedly without fully recovering (in terms of oxygen debt) before the next dive. Individuals apparently do not rely on anaerobic mechanisms and are probably able to accomplish long dives because their hemoglobin has a very high oxygen affinity (Sullivan, 1967), and they have a relatively large lung volume (Irvine and Prange, 1976). An ability to slow the heart rate and reduce blood-flow to the muscles has been reported for other *Nerodia* (Murdaugh and Jackson, 1962). As in sea snakes, where up to 33% of their total oxygen consumption can be through cutaneous respiration, cutaneous or other non-pulmonary respiration may also play a role in *N. taxispilota*'s ability to remain submerged for long periods (Irvine and Prange, 1976; Seymour, 1982).

In a laboratory experiment, *N. taxispilota* lost about 3.3 times more of its body weight per day than *Pituophis catenifer affinis*. About 88% of the total water loss was through the skin, and the percentage lost cutaneously was about 4.5 times greater in *N. taxispilota* (Prange and Schmidt-Nielsen, 1969). Presumably, cutaneous water loss is greater in juveniles because of their greater surface area to volume ratio.

The process of ecdysis may represent a significant factor in the allocation of energy to growth and maintenance. Semlitsch (1979) found shed skins to be a mean of 3.9% of total dry body masses of 20 large individuals (> 600 mm SVL). Blem and Zimmerman (1986) calculated 21.7 ± 0.3 (N=10) kJ/g of energy in the shed skins of brown water snakes. Using a 600g snake as an example, they estimated that 7.3% of its metabolized energy would be devoted to ecdysis during an activity season and concluded that this was a significant investment and should be included in energy models. They also found that the energetic investment in ecdysis is correlated negatively with temperature and positively with size. Also, the energy content of skin is proportionally higher at any given temperature for heavier snakes and therefore the "energetic impact" of shedding is greater for adults than juveniles.

The usual escape behavior of *N. taxispilota* at the Savannah River Site (SRS) and elsewhere is to drop from a basking site over the water and dive straight to the bottom or to a submerged object (e.g., log or root; pers. obs., > 1300 captures and >1000 escape observations), a behavior also observed in laboratory experiments (Irvine and Prange, 1976). Many an angler has seen this behavior first-hand when a “moccasin” dropped into their boat.

Nerodia taxispilota in Virginia have been reported to exhibit a “playing dead” behavior (Charles Blem, pers. comm.). Blem and his coworkers were able to reach out and touch 71 of 72 basking *N. taxispilota* over a period of several months, with no apparent relationship to temperature. When touched, the snakes stopped breathing and did not attempt to escape. This behavior has been observed on the SRS, but was attributed to sleeping vs. alert individuals (Mills, pers. obs.). The same behavior was also observed independently among all of several basking *N. taxispilota* in Four Hole Swamp, South Carolina, in 1978 by Whit Gibbons who, upon commenting on the phenomenon to a local guide, was told that another herpetologist had noted the same behavior the year before. The other herpetologist was Archie Carr.

ACTIVITY

Nerodia taxispilota have been captured during every month of the year on the SRS, but rarely so from November through February. They are probably active all year in Florida (Ernst and Barbour, 1989) and have been observed year-round in Virginia (Mitchell, 1994). However, museum records for Virginia are available only from 4 April to 9 November (Mitchell, 1994), and Charles Blem (pers. comm) reports that he has not captured *N. taxispilota* in Virginia from December through February. Palmer and Braswell (1995) reported activity from 12 February to 31 December, with most of their records (77% of the captures) from April to June. Except in Florida, reports of winter activity could be incidental occurrences due to changes in water level (e.g., flooding;

Neill, 1948; Ernst and Barbour, 1989). Based on radiotelemetry studies on the SRS, *N. taxispilota* will emerge and sometimes move short distances on warm winter days regardless of water level; but, they do not actively forage, mate, or move longer distances (Mills, unpubl. data).

Some disagreement or confusion exists as to whether *N. taxispilota* is nocturnal, diurnal, or both. Most authorities list this species as diurnal (Allen, 1938; Mount and Schwaner, 1970; Mount, 1975; Ernst and Barbour, 1989; Gibbons and Semlitsch, 1991), but Mitchell (1994) describes them as “usually” diurnal, and nocturnal in midsummer based on the field observations of Blem and Blem (1990). Behler and King (1979) state that they are primarily diurnal but sometimes forage at night. Nocturnal activity in *N. taxispilota* has been supported in laboratory experiments (Blem and Killeen, 1993; Luckeydoo and Blem, 1993), and the only specimens that could be located diurnally during July in Virginia were hidden beneath aquatic debris (Charles Blem, pers. comm.).

Do these observations indicate a geographic difference in daily activity patterns in *N. taxispilota*? Brown water snakes may show increased nocturnal activity in areas devoid of alligators (e.g., Virginia), although these snakes have been observed actively foraging and moving during the day and at night in areas with alligators (pers. obs.). *Nerodia taxispilota* may become more active at night as temperatures warm, but they do not cease diurnal activity. The confusion about when *N. taxispilota* is active arises partially from definitions of “activity.” That is, many authors equate activity with when the snake can be captured, which, in the case of *N. taxispilota*, is usually during the day when they are basking (and inactive).

Circadian metabolic cycles and activity have been documented in *N. taxispilota* (Blem and Killeen, 1993; Luckeydoo and Blem, 1993). Individuals tested in total darkness at high temperatures ($32^{o}C$) showed a significant increase in metabolic rate corresponding to their acclimated dark phase (scotophase). A related experiment using an activity wheel (at $32^{o}C$) confirmed that higher activity levels during the scotophase probably contributed to the rise in metabolic rate (Blem and Killeen, 1993). In other words, *N. taxispilota* showed increased activity and corresponding increases in metabolic rate during the acclimation "dark phase" without any light cues, indicating an intrinsic cycle. In support of these findings, it has been suggested that these circadian cycles of nocturnal activity are temperature dependent, with higher temperatures ($\geq 29^{o}C$) inducing nocturnal activity (Luckeydoo and Blem, 1993). Thus, the reported mid-summer "switch" to nocturnal activity (Blem and Blem, 1990) is supported by laboratory experiments. Nevertheless, individuals have been observed foraging, consuming fish, and moving in the water during the day throughout the summer at the SRS (pers. obs.). During hot summer days, a bimodal basking pattern has been observed on the SRS, with fewer snakes sighted in mid-afternoon. Blem and Blem (1990) reported a similar pattern (i.e., snakes becoming rare in the daytime during midsummer) in a Virginia population. It seems plausible that strong selective pressures would preclude activity at night in certain areas; for example, areas with high numbers of alligators that forage nocturnally. Also, in some habitats (e.g., large rivers) it may be easier to find and capture their prey (catfish) while these fish are inactive (i.e., during the day).

DIET AND FEEDING

All pertinent literature indicates that *N. taxispilota* are piscivorous, eating almost exclusively fish. The most thorough, published study of their diet revealed that in Georgia they ate only fish, with the largest portion of the diet being catfishes (family Ictaluridae; Camp et al., 1980). Data from the Savannah River agree with their findings (Table 1.1). Of the identifiable food items, all were fish and 62% were catfishes (both *Ictalurus* sp. and *Noturus* sp.), with individuals > 600 mm SVL consuming almost exclusively catfish. Although a variety of other non-fish prey have been reported in the diet of *N. taxispilota*, including frogs (Wright and Bishop, 1915), a crayfish and a turtle (Herrington, 1978), and small snakes and lizards (Allen, 1938), these observations are few and some may have been the result of secondarily ingested prey (Neill and Allen, 1956). Most field guides and other accounts of *N. taxispilota* probably base their report of frogs in the diet on Wright and Wright (1957), who in turn based their report on two frogs (Rana sp.) found in one Okefenokee *N. taxispilota* (Wright and Bishop, 1915). In captivity *N. taxispilota* have been reported to accept frogs (Palmer and Braswell, 1995), but most who have kept them find that they refuse anything but fish (Neill and Allen, 1956; Linzey and Clifford, 1981; Ernst and Barbour, 1989; Rossi, 1992).

Nerodia taxispilota seems to use two methods of foraging: sit-and-wait and active. The first method takes the form of the individual wrapping a coil of its body around a stationary object (e.g., branch, root, or rock) with the rest of its body stretched out in the water. Apparently this method is used to capture fish as they swim within striking range, and has been observed in captivity (Scott Pfaff, pers. comm., Riverbanks

Zoo, Columbia, SC,.; Mills, pers, obs.). Ditmars (1907) reported this type of behavior, although he did not associate it with foraging.

The second method, active foraging, is accomplished by moving through the water on or near the bottom, tongue-flicking and probing holes, crevices, and submerged vegetation, presumably in search of prey (pers. obs.). In captivity, some *N. taxispilota* will actively pursue live fish, moving the head rapidly with mouth opened (pers. obs.; Ditmars, 1907). Once the prey has been captured, the snake moves to the shore or shallow water to consume the fish headfirst. Several snakes have been observed swimming mid-channel in the Savannah River with large catfish held in their jaws (pers. obs.). Richmond (1944) described how *N. taxispilota* manipulate and swallow catfishes.

PREDATION, PARASITISM, AND DEFENSE

Predators of snakes are many, although no documented cases of predation on *N. taxispilota* have been reported in the literature. An SRS *N. taxispilota* being tracked with radiotelemetry was eaten by an alligator, and others were presumably killed by birds (Mills, unpubl. data). Nevertheless, authorities report a wide range of potential predators including alligators, fish, raccoons, birds, and other snakes (e.g., cottonmouth, *Agkistrodon piscivorus*). Most authors list humans as their worst enemy.

Spears (1977) measured predation frequency on *N. taxispilota* and other colubrid snakes in Florida by examining the frequency of tail-abbreviation in museum specimens. He found no significant difference between male and female predation rates, but did find that the largest individuals exhibited the highest frequency of tail-loss and that tail loss was absent in specimens less than 340 mm SVL (Table 4 in Spears, 1977). Similarly, White et al. (1982) found that the frequency of broken tails in a Virginia population increased with increasing SVL; equating the high frequency of tail loss or injury (22%) to some measure of predation frequency, and suggesting that freshwater turtles (particularly *Chelydra serpentina*) were the probable predator.

Nerodia taxispilota can get fish spines lodged in their tissues, which can result in death (Carr, 1940), although this is not always the case. A female captured in 1992 had a spine protruding through her body wall, was marked (PIT tag), and subsequently recaptured in 1997 without the spine and no apparent scar (Mills, unpubl. data).

Relatively few published records exist of the parasites infecting brown water snakes, and all were helminths (Wright and Bishop, 1915; Byrd and Roudabush, 1939; Collins, 1969; Camp, 1980;). In a Georgia population of *N. taxispilota*, 92% (N=25) were infected with various helminth worms (12 species) and 72% of these were infected with *Proteocephalus perspicua*, an intestinal Cestoda (Camp, 1980). In North Carolina, Collins (1969) documented 9 species of parasites from 16 *N. taxispilota*, with the most common being *Ophiotaenia perspicua* (56%) and *Ochetosoma aniarum* (44%).

GROWTH AND SIZE PATTERNS

The only published account of growth in *N. taxispilota* (Herrington, 1989) suggests that females mature at 3.5 yr (850-900 mm) and that a 900-mm SVL female is between 4 and 5 years old. Males mature at 2.5 yr (580 mm), and a 750-mm SVL male is about 5 years old (Herrington, 1989). Herrington rather confusingly reports growth rates for different size classes based on a limited number of recaptures (summarized in Table 1.2). Growth in his population was highly variable, but evidently slows in both sexes after reaching sexual maturity, although more so in males than females. Growth rates in an SRS population similarly slowed after reaching maturity, with males growing slower (Table 1.3).

Similarly to other *Nerodia*, brown water snakes are sexually dimorphic with females reaching significantly greater lengths and being heavier than males of similar lengths. Adults range from 460 mm SVL (males) and 730 mm SVL (females) to the maximum reported size of 1766 mm TL (Conant and Collins, 1991). Neonates range from 175 - 270 mm SVL. The average SVL of adults from the Savannah River near the SRS is 663 mm (males, n = 452) and 932 mm (females, n = 292), and neonates range from 127-284 mm (mean = 245 mm, n = 1970; Mills and Arnold, unpublished data). Females have significantly longer heads than males, relative to SVL (Shine, 1991). Males have proportionally longer tails and a correspondingly greater number of subcaudal scales. Males may also have more ventral scales (Mitchell, 1994). The only other reported sexually dimorphic feature is the presence of “supra-anal keels,” which are also present in many other male natricines (Blanchard, 1931; Wright and Wright, 1957).

REPRODUCTION

According to Herrington (1989), males in central Georgia become mature between their second and third years (after their third hibernation) between 500-600 mm SVL, and females become mature during their fourth year at 850-900 mm SVL. In Virginia, males reach maturity at 463 mm SVL and females at 725 mm SVL. (White et al., 1982; Mitchell and Zug, 1984). Sexual maturity in females on the SRS occurs between 725 mm and 800 mm SVL based on follicle length (Table 1.2 in Aldridge, 1982). The smallest confirmed gravid female (i.e., gave birth in captivity) captured on or near the SRS was 800 mm SVL (Mills and Arnold, unpubl. data).

Mating occurs in spring (March-June), although Ashton and Ashton (1981) report, presumably erroneously, mating in mid to late summer. During mating season, a single female is often accompanied by 1-3 males (Mills, pers. obs.) and pairs have been observed copulating in trees overhanging the water (Carr, 1940; Mills, pers. obs.). Ernst and Barbour (1989) also report that they will mate in the branches over water, but state that copulation usually occurs on the ground or in water. However, they provide no reference to support this assertion. As in some other natricines (e.g., *Thamnophis*), copulatory or "sperm" plugs have been observed in female *N. taxispilota* (Devine, 1975; Herrington, 1989). Vitellogenesis occurs in the spring and ovulation occurs in June (Aldridge, 1982; White et al., 1982); although partial yolking of ova has been documented in the fall before hibernation (Blem and Blem, 1990). Spermatogenesis begins in April and ends in November (White et al., 1982; Mitchell and Zug, 1984).

Females can reproduce annually (Semlitsch and Gibbons, 1978; White et al., 1982; Herrington, 1989) and parturition occurs in late summer and fall (August-November). Parturition dates as early as 15 June (Franklin, 1944; Wright and Wright, 1957) may be erroneously based on a report of "advanced" embryos obtained from an Okefenokee specimen on 15 July (Wright and Bishop, 1915). Parturition dates of females captured on the SRS range from 30 August to 21 October, with an average parturition date of 22 September (n= 121; Mills and Arnold, unpubl. data).

The young are born out of the water and usually shed within two days or less (Franklin, 1944; Mills, pers. obs.). Litter size (often based on number of follicles or embryos) ranges from 4 - 61 (see Chapter 4) and is positively correlated with female body size (Semlitsch and Gibbons, 1978; Semlitsch and Gibbons, 1982; White et al., 1982; Herrington, 1989). The mean litter size for SRS *N. taxispilota* is 18 ± 7.6 (range = 4-50).

POPULATION BIOLOGY

Nerodia taxispilota are usually considered locally common to abundant throughout their range in appropriate habitat, but population ecology and demographic studies are lacking. The only published estimate of population size in this species is a linear density of 43 individuals/ km of river or about 0.02 individuals/m of shoreline (Mills et al., 1995) and is probably an underestimate (Mills, unpubl. data).

CAPTIVE MAINTENANCE

Nerodia taxispilota has proven to be difficult to maintain in captivity for long periods of time (Scott Pfaff, pers. comm.; Mills, pers. obs.). Many refuse to eat and those that do eat often slowly lose weight, succumb to various skin problems, and exhibit other health problems. Other authors report similar observations with keeping this species (Ditmars, 1907; Ernst and Barbour, 1989). Rossi (1992) describes *N. taxispilota* as, “...one of the most difficult water snakes to keep in captivity.” He reports further that while some refuse to eat, others will take fish readily, but frogs are usually refused.

Alternatively, *N. taxispilota* has been reported to do well in captivity, even to the point of becoming docile (Ashton and Ashton, 1981; Linzey and Clifford, 1981). One small male was kept for almost a year, being fed minnows (family Cyprinidae) and displaying no apparent problems, but it never became docile (Mills, pers. obs.). In general, water snakes are messy, smelly creatures, and anyone who works with them would surely agree with Breen (1974): “A single water snake will require more attention to the cleanliness of its cage than six or more mouse-eating snakes of the same size.”

CONSERVATION

No published accounts document that *N. taxispilota* is imperiled in any part of its range, but anecdotal evidence suggests that they are heavily persecuted. Most accounts of *N. taxispilota* report them to be mistaken often for the cottonmouth or believed to be venomous and therefore killed (Mount, 1975; Linzey, 1979; Martof et al., 1980; Linzey and Clifford, 1981; Ernst and Barbour, 1989; Mitchell, 1994; Palmer and Braswell, 1995). Mitchell (1994) states that *N. taxispilota* may be declining in Virginia due to the outright killing mentioned above as well as environmental pollution affecting them indirectly via effects on the fish populations. Because almost no information is available on the population ecology of *N. taxispilota*, it is difficult to determine if it is indeed declining in parts of its range. If *N. taxispilota* is declining, it is probably doing so on the edge of its range and in more urban and highly polluted areas, although these animals seem to be able to withstand some radioactive pollutants (Brisbin et al., 1974; Staton et al., 1974; Bagshaw and Brisbin, 1984). Preliminary analyses for mercury in the tissues of *N. taxispilota* from contaminated sections of the Savannah River suggest that the species does not bioaccumulate this potential toxin (C. Jagoe and M. Mills, unpubl. data).

QUESTIONS AND COMMENTS

Many relevant questions about *N. taxispilota* have already been raised in this species account. For example: Is the range expanding? Are they primarily or exclusively diurnal? Some of the following questions, although not exclusive to *N. taxispilota,* are also of interest.

Why does *N. taxispilota* commonly bask in the winter? *N. taxispilota* have been observed to emerge and bask in the cooler months throughout their range. Could this behavior be related to gonadal development, lactic acid buildup, foraging, heavy parasite loads or some combination of these factors? What is the role of parasites in their biology and ecology? Does parasite load affect basking behavior, reproduction, or growth? How are *N. taxispilota* able to survive major injuries (e.g., fish spines through the gut and body wall), and have they evolved physiological or endocrinological traits that are adaptive for a species that preys on animals with venomous spines? What are the primary predators of *N. taxispilota*? This species seems to be more aware of predators from above rather than from below (i.e., avian vs. aquatic predators; pers. obs.). Are predation rates higher in the winter? Does *N. taxispilota* exhibit single or multiple paternity?

Interspecific competition in snakes has never been documented (Reichenbach and Dalrymple, 1980; Toft, 1985), but there seems to be some division in diet and habitat use among the semi-aquatic snakes of the SRS as well as other areas (e.g., Virginia, Charles Blem, pers. comm.). Would this species be suitable for addressing resource competition with other snake species with which it is sympatric?

How do potential aquatic toxins (e.g., mercury, PCB's) affect *N. taxispilota*? Do they bioaccumulate these toxins or are they able to get rid of them? Also, to what extent do *N. taxispilota* use non-pulmonary respiration and how does it vary seasonally and with environmental conditions?

Nerodia taxispilota can be an extremely common snake. Thus, if one wishes to overcome a central obstacle to ecological studies with snakes (i.e., low sample sizes), this is an ideal species to work with.

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Table 1.1 - Percent occurrence* of food items in the diet of a Savannah River population compared with other populations[1] of *Nerodia taxispilota*.

	Savannah River (n=411)	Gibbons[2] (n=135)	Camp et al. (1980) (n=96)	Collins (1980) (n=16)	Wright and Bishop (1915) (n=11)	Herrington (1978) (n=176?)
Prey Items	Percent Occurrence					Number
Ictaluridae	37.0	29.4	32.1	25.0		5-8?
Cyprinidae	6.2		10.7			1
Moronidae	6.2					
Percidae	3.7		7.1			
Lepisosteidae	1.2					
Esocidae		11.8				
Centrarchidae		5.9	19.6	75.0	33.3	2
Unident. Fish	3.7	44.1	5.4		33.3	2
Frog (*Rana* sp.)					33.3	
Frog (*Hyla* sp.)		2.9				
Turtle (*Trionyx* sp.)						1
Crayfish						1
Unidentifiable	42.0	5.9	26.8			
No. w/ food	81	34	56	4	3	11-14?

* Unable to calculate percent occurrence for Herrington (1978)

1 All except the Savannah River study dissected the snakes; and Herrington used data from both dissections and palpations.

2 Unpublished data from snakes collected from various localities throughout the SRS (see Semlitsch and Gibbons 1978, Semlitsch and Gibbons 1982)

Table 1.2 - Growth rates of *Nerodia taxispilota* from Wilkinson Co., GA, expressed as cm/season (season = 240 days) and based on recaptures (N) of marked individuals (Herrington, 1989).

	N	Mean ± SD	Range
1st season	4	9.6 ± 4.1	3.8 - 13.6
2nd season	0		
3rd season	2 M	13.0	4.0 - 19.1
3rd season	2 F	21.7	
4th season	6 M	3.2 ± 1.8	2 - 4
4th season?	3 F	12.2 ± 2.8	
4th season	3 F	11.0 ± 2.4	8.8 - 13.6
5th season?	4 F	5.7 ± 2.0	3.2 - 6.4

Table 1.3 - Growth rates of *Nerodia taxispilota* from the Savannah River, Savannah River Site, South Carolina, based on recaptures (N) of marked individuals over seven years. Mean length (SVL) between the two capture periods was used to classify individuals as juvenile or mature. I assumed no growth for 3 months (120 days) of winter. Means are followed by 2 SE.

Sex and Size Class[1]	N	Mean (mm/d)	Range (mm/d)
Males < 50 cm SVL (juvenile)	3	0.50 ± 0.40	0.29 - 0.90
Males ≥ 50 cm SVL (mature)	38	0.20 ± 0.06	0.0 – 1.01
Females < 79.5 cm SVL (juvenile)	34	0.45 ± 0.08	0.08 – 1.11
Females ≥ 79.5 cm SVL (mature)	32	0.28 ± 0.07	0.0 – 0.71

[1] Size classes based on size at maturity

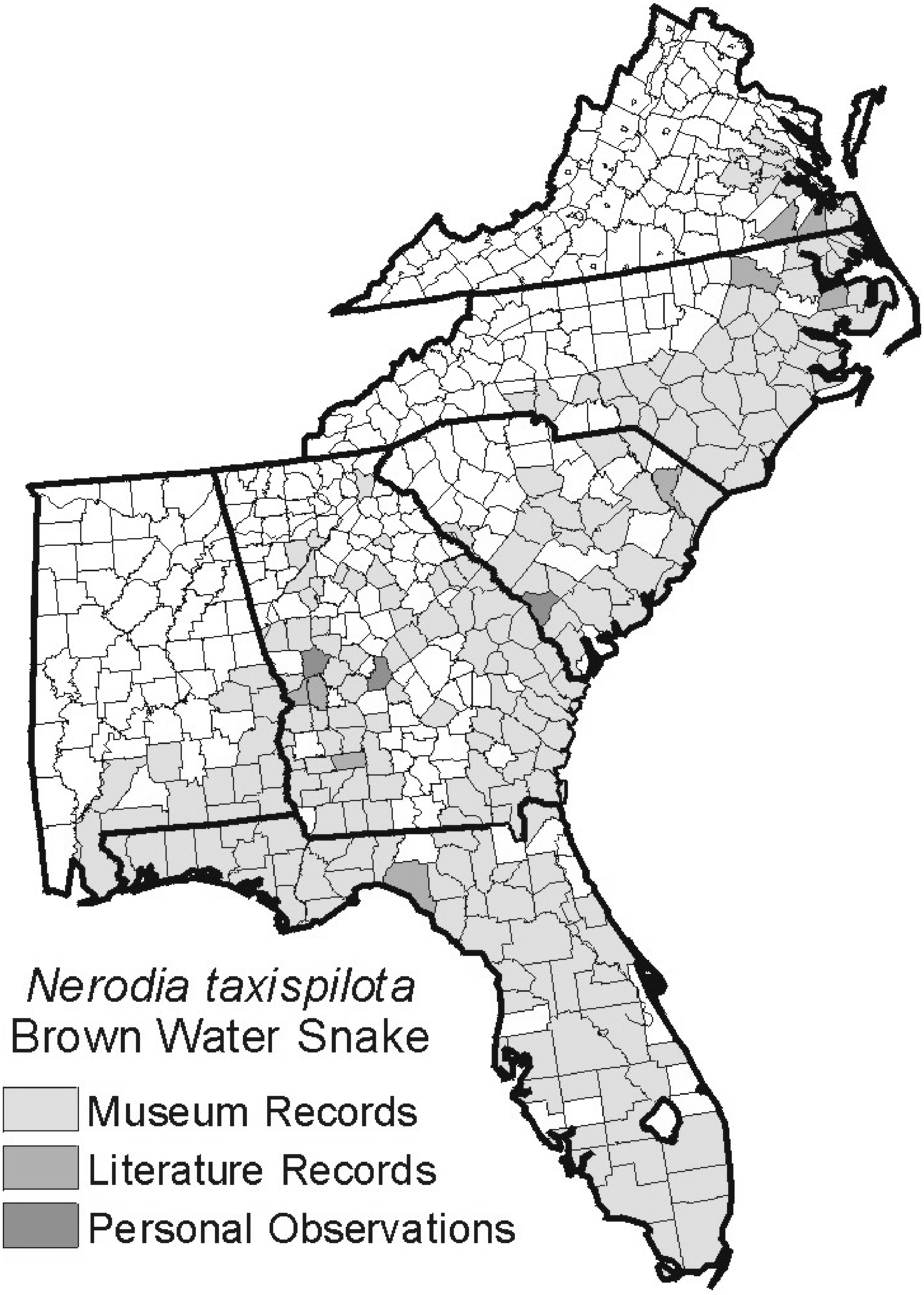

Figure 1.1 – Distribution of the brown water snake, *Nerodia taxispilota*.

APPENDIX 1.1 - SYNONYMY, TYPE AND LOCALITY, TAXONOMY*

Brown water snake, *Nerodia taxispilota*

Coluber taxispilotus Holbrook, 1838: 113. -- Type-locality, “the seaboard of South Carolina...[and] the neighbourhood of the Altamaha river in Georgia.” No holotype designated.

Tropidonotus taxispilotus: Holbrook, 1842: 35.

Nerodia taxispilota: Baird and Girard, 1853: 43.

Tropidonotus taxispilotus var *Brocki* Heilprin, 1887: 129. Type-locality, “Eagle Bay, Lake Okeechobee.” Holotype, Acad. Natur. Sci. Philadelphia 6619, juvenile female, collected early 1886 by Angelo Heilprin.

Natrix taxispilota: Cope, 1889: 392.

[*Natrix taxispilota taxispilota*]: Viosca, 1948: 11. By implication.

Natrix taxispilota taxispilota: Cagle, 1952: 20. First actual use of trinomial.

No subspecies are currently recognized.

*from (McCranie, 1983)

APPENDIX 1.2 – SCUTELLATION OF *NERODIA TAXISPILOTA*

	Nerodia taxispilota
internasals	2
prefrontals	2
suboculars	0
parietals	2, but fragmented (divided) posteriorly
loreal	1-2 (usually 1)
preoculars	1-3 (usually 1)
postoculars	2-4 (usually 2-3)
anterior temporals	1-4 (usually 2)
upper labials	7-11 (usually 8)
lower labials	9-14 (usually 11-12)
dorsal scale rows*	25-34 25-33 (m) 26-33 (f)
ventrals *	128-152 132-152 (m) 128-140 (f)
subcaudals*	59-87 (99)** 59-87 (m) 62-79 (f)
anal plate	divided***

*Measurements that did not delineate sex were not included.

** Wright and Wright (1957) report a maximum of 99 subcaudals, which others (Smith and Brodie, 1982) repeat. This is probably incorrect as most other authors report a maximum in the low-to-mid 80’s.

***Wright and Bishop (1915) collected 2 individuals with undivided anal plates.

CHAPTER 2

SPATIAL ECOLOGY AND MOVEMENTS OF THE BROWN WATER SNAKE (*NERODIA TAXISPILOTA*)[1]

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[1] Mills, M. S., C. J. Hudson, and H. J. Berna. 1995. Herpetologica 51(4):412-423. Reprinted here with permission of publisher.

ABSTRACT

We used mark-recapture techniques from August 1991 through September 1993 (52 sampling days) to study habitat use and movement of *Nerodia taxispilota*. We captured 411 individuals and estimated a linear density of 43 individuals/km of river habitat. River sections exhibiting the highest number of captures were clustered within 200 m of backwater areas; brown water snakes were not randomly distributed and were significantly associated with the steep-banked outer bends of the river and availability of potential perch sites. Recaptured individuals (n = 50) reaffirmed this habitat association by remaining in or moving to straight sections and outside bends of the river (90% of recaptures) with steep banks (88%) and a moderate to abundant concentration of perch sites (86%). Most recaptured *N. taxispilota* (70%) were found <250 m from their previous capture site, but six moved >500 m, and three moved >1 km. Ten of 11 individuals that moved >10 m/day between captures did so from 12 August through 15 October, indicating a possible seasonal movement pattern. Distance moved by individuals was not associated with size, sex, or number of days between captures; however, only large (>80 cm snout-vent length) individuals (n = 8) crossed the river (approximately 100 m). We found significant relationships between snout-vent length of basking individuals and perch height, perch exposure, and perch substrate. This is the first published study of the spatial ecology and movements of *N. taxispilota* in natural populations.

INDEX WORDS: Serpentes, *Nerodia taxispilota*; Brown water snake; Spatial ecology; Habitat use; Movement; Mark-recapture

The distribution of resources influences large- and small-scale patterns of species habitat use. Because resources are spatially and temporally heterogeneous, animals that use them usually are distributed in patches (Andrewartha and Birch, 1984; Forman and Godron, 1986). A population's spatial arrangement is determined in part by differential use of habitats, movement of individuals between habitat patches and colonization of new or unused patches. Knowing the characteristics of a species' habitat and how individuals move within and among habitat patches can lead to a greater understanding of the ecology and evolution of organisms in a patchy environment (Pulliam, et al., 1992; Taylor, et al., 1993).

Despite the long history of snake studies relating movement and dispersal patterns to habitat use and resource availability (e.g., Carpenter, 1952; Fitch and Shirer, 1971; Plummer, 1981; Weatherhead and Hoysak, 1989), many aspects of the spatial ecology of snakes remain poorly understood because of the secretive nature and apparent low population densities of most species (Seigel, 1993). The lack of consistent patterns in snake movements related to habitat has prompted some researchers to suggest the need for long-term studies and standardization of methods (Gregory, et al., 1987; Macartney, et al., 1988).

There are a number of characteristics a species might possess that would facilitate the study of its population ecology, spatial dispersion, and movement patterns (Parker and Plummer, 1987). The brown water snake, *Nerodia taxispilota*, is well suited for spatial-distribution studies because it: 1) is limited to aquatic systems (Ernst and Barbour, 1989; personal observation) and likely has distinct population boundaries, 2) occurs over a wide geographic range (Ernst and Barbour, 1989), thus enabling investigations across geographically varied conditions, and 3) has high local densities and is relatively conspicuous unlike many other species of snakes (personal observation). Furthermore, large body size in *N. taxispilota* enables various intrusive monitoring techniques not possible in smaller species (e.g., radiotransmitters).

Nerodia taxispilota is often one of the most abundant species of snakes in rivers and streams of the southeastern United States, yet many aspects of its natural history remain poorly known (Ernst and Barbour, 1989; Mitchell, 1994). Although movements have been related to thermal ecology in captive *N. taxispilota* (Goodman, 1971; Osgood, 1970), the spatial ecology and movements of individuals in a natural population of this species are unknown. We have three objectives in the present study on *N. taxispilota*: 1) describe spatial distribution and habitat use in this population, 2) describe movement patterns, and 3) to relate movement patterns to distribution and habitat use.

MATERIALS AND METHODS

STUDY AREA

We studied *N. taxispilota* along a 10-km section of the Savannah River adjacent to the Savannah River Site (SRS), South Carolina. The river is bordered by bottom-land hardwood and cypress-tupelo swamp forests. The river channel was modified for navigation but is no longer maintained for this purpose. In our study area, river width is usually >100 m; depth of the channel at base flow is approximately 4.4 m (U.S. Army Corps of Engineers, Savannah District, personal communication). The river's flow (mean discharge and velocity = 316 m^3/s and 0.74 m/s) is variable and largely controlled by a hydroelectric dam upstream of the study site. Peak flow usually occurs in the spring, causing the river to exceed its banks and form an extensive floodplain. Low flows occurring in late summer and autumn may expose sand bars (for a map and more detailed description, see Gibbons and Semlitsch, 1991).

DATA COLLECTION

"...whoever...had experiences with this species in its wild state knows they are vicious and belligerent...The natives were not anxious to help us in the captures of this species." -- (Wright and Bishop, 1915).

We sampled *N. taxispilota* by hand-capture during 52 collecting trips from August 1991 through September 1993: five trips during 23 August to 6 September 1991, 22 trips from 16 May through 15 October 1992, and 25 trips from 22 January through 29 September 1993. Brown water snakes were located visually by 2 to 4 observers during daylight hours (typically between 0900 and 1900 h) from a slow moving boat maneuvered 5 to 15 m from the bank.

For each captured individual we recorded snout-vent length (SVL) to the nearest 1 mm and mass with a Pesola™ spring scale (nearest 10 g or 50 g for snakes <1 kg or >1 kg, respectively). We determined sex (relative length and thickness of tail and occasionally by probing or everting the hemipenes), palpated for the presence of stomach contents and embryos, and noted cloudiness of eyes or sloughing skin as an indication of approaching ecdysis. For each capture we also recorded bank (right or left, facing downstream), perch height (centimeters above water), relative exposure (shade, partial shade, and sun/exposed), and perch substrate (e.g., log, maple tree, grape vines). Each individual of *N. taxispilota* was given a unique mark. In 1991, snakes were marked by conventional scale clipping (Blanchard and Finster, 1933; Brown and Parker, 1976). In 1992 and 1993, each individual was marked by passive integrated transponder (PIT) tags ventrally injected into the body cavity approximately $^2/_3$ of the SVL from the head (Camper and Dixon, 1988) and given a ventral scale clip denoting year of first capture. Because of scale regeneration and the frequency of scale injuries (Keck, 1994), we lacked confidence in our scale clipping methods, and therefore only PIT-tagged individuals were used to calculate estimates of the population size. In 1992 and 1993, we recorded the number of *N. taxispilota* seen but not captured and their exposure (shade, partial shade, sun) to test for possible sampling bias.

We used a map of the study area to divide each bank of the river into 50-m intervals; each section was numbered and marked on the map. Each capture was recorded on the map and after processing, each individual was released at the site of capture. For calculating movement of recaptured *N. taxispilota*, capture locations were assigned to their respective bank (right or left) and 50-m section; "movement" was defined as distance between sections on the map. For example, an individual recorded in section No. 45 on initial capture and section No. 49 (same bank) on a subsequent capture had "moved" 200 m. To standardize movement data, we report movement as meters/day as well as distance between captures (Gregory, et al., 1987; Macartney, et al., 1988).

For the purpose of interpreting spatial patterns, all 50-m sections of each bank in the study site were characterized using three coarse-grained habitat variables: bank type, bank slope, and perch site abundance (Hebrard and Mushinsky, 1978). Bank type was defined as outside, inside, or straight and was determined by map and field surveys. Outside banks are characterized by high water velocities, deep channels, and eroded steep banks. Inside bends are characterized by gradually sloping banks, shallow water with occasionally exposed sandbars, low water velocity, and abundance of willow (*Salix* spp.).

Straight banks are variable sections between river bends with mixed hardwood riparian communities. Bank slopes were divided into gradual slope (< 45°) or steep slope (> 45°). A qualitative assessment of potential perch sites was determined by field surveys and defined as few, moderate, or abundant based on the relative abundance of overhanging branches, vegetation (alive and dead), and other stationary items (Hebrard and Mushinsky, 1978). A section classified as having "few" perch sites had very little or no vegetation and few logs, dead branches, or other debris; those classified as "abundant" had continuous vegetation and/or debris.

To estimate population size we used the triple-catch method (sometimes referred to as Bailey's triple-catch; Begon, 1979; Tanner, 1978). This estimate allows for recruitment and removal and requires the identification of three sampling periods of equal effort. For this analysis, data from 1992 and 1993 were divided into three periods of approximately 15 sampling days each: Period 1 = 16 May to 27 August 1992, Period 2 = 1 September 1992 to 3 June 1993, and Period 3 = 9 June to 29 September 1993. The triple-catch estimate is based on the assumption that all individuals in the population have an equal risk of being captured regardless of sex, age or previous capture history. In order to reduce effects of unequal catchability during a sampling period, each individual was counted only once during a given period regardless of how many times it was captured.

Our statistical tests and interpretation followed Zar (1984) with significance level set at $\alpha = 0.05$. Nonparametric tests were used if the assumptions for parametric tests were seriously violated. Data for mass and SVL were normalized using a log-transformation in order to compare mass between the sexes with SVL as a covariate. Most tests were performed using the statistical software programs StatView® and

SuperANOVA® (Abacus Concepts, Inc., Berkeley, CA) for the Macintosh. Means are reported with one standard deviation unless otherwise noted. Because of the low sample size for January (n = 1), this individual was omitted from analyses when splitting by month. For some analyses, individuals were classified as juvenile or adult based on SVL; males ≥ 46 cm and females ≥ 72 cm were labeled adults (Ernst and Barbour, 1989). To test if the dispersion of capture locations was random, clumped, or uniformly dispersed, we calculated Morisita's index (I_d; Vandermeer, 1981). This index was calculated twice using our mapped captures divided into 1) 50-m sections, and 2) 200-m sections of river bank, giving us two estimates of dispersion for this population. This index ranges from zero (indicating a perfectly uniform pattern) to the number of sections (n = 216, indicating a clumped distribution with all individuals in one section). An I_d = 1 indicates a random distribution. We used Chi-square analysis to test if I_d differed significantly from one (Brower and Zar, 1984). For these analyses, we tested each side of the river separately.

RESULTS

SPATIAL ECOLOGY AND HABITAT USE

From July 1991 through September 1993, we marked 361 individuals of *N. taxispilota* (187 males and 174 females) and obtained 50 recaptures distributed across all size classes (Table 2.1, Fig. 2.1). Mean male SVL (mean ± 1 SD = 60.2 ± 17.8 cm, n = 209) and mass (232 ± 173 g, n = 212) were significantly less than female SVL (67.3 ± 26.3 cm, n = 196) and mass (439 ± 446 g, n = 197; Mann-Whitney *U*-test, SVL: $U_{196,209}$ = 23704, $P = 0.006$; mass: $U_{197,212}$ = 24193, $P = 0.006$). Also, females (5.14 ± 4.14 g/cm, n = 195) were significantly heavier per unit length than males (3.35 ± 1.87 g/cm, n = 209; ANCOVA: SVL as covariate, $F_{1,400} = 9.23$, $P = 0.0025$); this difference was more pronounced in larger individuals. Using the triple-catch method, we estimated 426 ± 227 (SE) individuals of *N. taxispilota* in our study area, a density of approximately 43 individuals per kilometer of river. This is equivalent to a "linear density" (Parker and Plummer, 1987) of about 0.02 *N. taxispilota* per meter of shoreline.

Capture locations for *N. taxispilota* were distributed non-randomly on both sides of the river using either a 50-m or 200-m scale (Fig. 2.2; Morisita's I_d = 1.44-1.67, P values < 0.001), and they seem to be associated with specific river segments (Fig. 2.2). Significantly more brown water snakes were captured on outside bends of the river (χ^2 = 46.75, df = 2, $P < 0.001$, n = 184), in areas with steep banks (χ^2 = 32.94, df = 1, $P < 0.001$, n = 335), and in areas with abundant potential perch sites (χ^2 = 25.45, df = 2, $P < 0.001$, n = 193; Fig. 2.3). Neither sex nor maturity of an individual affected its capture location in relation to these habitat variables. The proportion of river sections that exhibited these particular habitat characteristics in the study area were 33% outside bend, 70% steep banks, 40% abundant perch availability (Fig. 2.3). The three habitat variables (bank type, bank slope, and perch site abundance) were intercorrelated ($P < 0.0001$), with bank type and slope showing the strongest correlation ($r = 0.52$).

The river sections with the highest number of captures were near backwater areas (i.e., sloughs, side channels or chutes, oxbow lakes, canals). We captured five or more individuals of *N. taxispilota* (range: 5-8; total = 43) in seven 50-m sections of the study area (Fig. 2.2); six of these sections are within 200 m of backwater areas. When using a 200-m scale and including both banks of the river, the four 200-m sections (8% of study area) with the greatest number of captures (70 individuals of *N. taxispilota*; 17% of total captures) were sections 54-57 (n = 18), 58-61 (n = 15), 126-129 (n = 18), and 130-133 (n =

19; Fig. 2.2). These four 200-m sections include four of the seven 50-m sections previously mentioned and are clustered around the two largest backwater areas within the study site: a human-made canal at left bank section 57 (approximately 50-75 m wide and 400 m long: Pumphouse No. 3 canal), and an oxbow cut-off that is contiguous with the river on its downstream end at right bank section 130 (approximately 75 m wide at the mouth and 750 m long: Cut-off No. 21).

We captured *N. taxispilota* from water level up to 250 cm above water (mean = 55 ± 46 cm, n = 409). Eighty percent of all captured individuals perched at heights <1 m. Males were captured at higher mean perch heights (59 ± 48 cm, n = 212) than females (51 ± 44 cm, n = 197; $U_{197, 212} = 23410$, $P = 0.034$) and adults of both sexes were found at significantly higher perch sites than juveniles ($U_{161, 248} = 26686$, $P < 0.0001$). Individuals <50 cm SVL were never captured at perch heights of >110 cm and mean perch height and variability in perch heights increased with increasing SVL (Fig. 2.4). Perch height did not differ significantly between the sexes within adult and juvenile categories nor did it differ between gravid and non-gravid adult females (Mann-Whitney *U*-tests, *P* values > 0.13). Perch height was not correlated with time of capture.

The thermal environment is an important component of a reptile’s habitat. In this population, brown water snakes usually were perched in shade (71% shade, 22% partial shade, and 7% sun). Snakes sighted but not captured showed similar use of shady perch sites as those captured (73% shade, 17% partial shade, and 10% sun). We found no correlation between perch site exposure and sex ($\chi^2 = 1.90$, df = 2, $P = 0.39$), presence of stomach contents ($\chi^2 = 2.17$, df = 2, $P = 0.34$), presence of embryos ($\chi^2 = 0.056$, df = 2, $P = 0.97$), or time of capture (ANOVA: $F_{2, 372} = 2.25$, $P = 0.11$). Individuals preparing for ecdysis were more likely to be captured in partial or full sun ($\chi^2 = 6.30$, df = 2, $P = 0.043$). Size of individuals varied significantly among the basking conditions of shade (62.3 ± 22.1 cm, n = 266), partial shade (64.0 ± 20.8 cm, n = 79), and sun (73.4 ± 26.9 cm, n = 27; $F_{2, 369} = 3.09$, $P = 0.047$). Basking conditions varied significantly among months ($\chi^2 = 57.06$, df = 16, $P < 0.0001$) with snakes found more often in the sun in the spring.

Because the physical structure of the microhabitat (e.g., log versus vine) probably is more important for identifying and comparing patterns of habitat use than the specific biological components (e.g., maple versus birch log; Reinert, 1993), we grouped all perch substrate observations into seven categories or types: bank, log, roots, tree, vines, water, and other. We usually captured individuals of *N. taxispilota* as they perched in trees (175 of 353 captures) or vines (53 of 353 captures) overhanging the water (Fig. 2.5). Individuals captured on the bank (n = 11) were significantly larger than those captured on other substrates (Kruskal-Wallis test: $H = 19.44$, df = 6, $P = 0.0035$; Fig. 2.5). Those captured on the bank (seven females, four males) were all > 51 cm SVL (mean = 86.6 ± 19.9 cm) whereas all other substrate types were used by snakes < 30 cm SVL. Of the individuals ≥ 100 cm SVL (n = 21), most were perched on logs (24 %), the bank (19 %), or roots (14 %). Sex, maturity, exposure, ecdysis, stomach contents, or presence of embryos did not affect observed substrate use (Contingency Chi Square, P values > 0.12). In addition, time of capture did not differ among substrate types ($F_{6,346} = 0.29$, $P = 0.94$).

MOVEMENT

Recaptured individuals of *N. taxispilota* (n = 50) moved a mean of 270 ± 351 m (13 ± 33 m/day), with days between captures ranging from 1-649 (mean = 115 ± 143 days). We found no significant relationship between movement rate and SVL (r_s = -

0.086, $P = 0.55$), sexual maturity ($U_{16, 34} = 282.0$, $P = 0.84$) or sex ($U_{32, 18} = 299.5$, $P = 0.82$). Most recaptured individuals appeared relatively sedentary, 70% moving <250 m between captures and 78% moving <10 m/day. However, three individuals moved >1 km. This group consisted of one male (69 cm SVL) that traveled 1300 m in 14 days and two females (42 and 81 cm SVL), one that traveled 1050 m in 362 days and one 1650 m in 41 days. No relationship was apparent between the number of days between captures and distance moved ($r = 0.16$, $P = 0.26$).

Most of the long distance movements made by recaptured individuals, including the two longest movements mentioned previously, occurred in late summer and autumn. Ten of the 11 individuals that moved >10 m/day between captures (mean = 53 ± 57 m/day, range = 10.2-200 m/day) did so from 12 August through 15 October. We captured two of these snakes the following spring (10 March) and summer (25 June) and both had moved back towards their original capture locations (100 m and 50 m, respectively).

There was no apparent directionality in movement. Of six individuals captured three times, only one moved in the same direction twice, for a total of 100 m. While more individuals were recaptured upstream (n = 23) than downstream (n = 18) from their previous site of release, this difference was not significant ($\chi^2 = 0.39$, df = 1, $P > 0.5$), nor did the sex or maturity of an individual affect upstream versus downstream movement patterns. Also, mean distance traveled did not differ between those who moved upstream (213 ± 238 m) versus downstream (433 ± 458 m; $U_{18, 23} = 272.0$, $P = 0.08$). However, individuals traveled faster downstream (21 ± 28 m/day) than upstream (12 ± 41 m/day; $U_{18, 23} = 294.0$, $P = 0.02$). Eight individuals that moved across the river were significantly larger than other recaptured individuals ($U_{42, 8} = 278.0$, $P = 0.004$). Only individuals >80 cm SVL crossed the river, and 40% (eight of 20) of the recaptured individuals in this size class did so.

To address our third objective, we analyzed which habitat variables changed when individuals were recaptured (n = 50; Table 2.2). The underlying assumption was that if there were a preference for specific habitat types (e.g., those areas where we captured the most snakes), we would observe recaptured individuals remaining in or moving among these habitat types. All individuals (n = 8) that were recaptured in the same 50-m section were on an outside bend or straight section of river with steep banks and a moderate to abundant number of potential perch sites (Table 2.2). Sixty percent (n = 30) of recaptured individuals had not changed habitat type, of which 87% (n = 26) remained in the above described areas regardless of whether they moved or not (Table 2.2). Of the individuals that did change habitat type, bank slope was the habitat feature that was changed least often, with 70% remaining in areas with steep banks. Eighty percent (n =16) of the changes in habitat type involved changes in the bank type, and 60% of the changes in this variable occurred between straight and outside banks. No recaptured individual moved from an outside to inside bank of the river. Few recaptured snakes remained in or moved to areas with gradually sloping banks (n = 6), on inside bends of the river (n = 5), or with relatively few potential perch sites (n = 7; Table 2.2).

DISCUSSION

SPATIAL ECOLOGY AND HABITAT USE

The low number of recaptured *N. taxispilota* initially marked in 1991 (Table 2.1) may have been a reflection of our inability to recognize scale-clip marks (because of scale injuries and regeneration) in as little as three months after the initial capture. Therefore, only individuals marked with PIT tags (1992 and 1993) were used to estimate population size. Our density estimate of 0.02 brown water snakes/m falls within the range of linear densities (0.02-0.38 individuals/m of shoreline) previously reported for other populations of streamside and semiaquatic snakes (Parker and Plummer, 1987). Our estimate equates to approximately one individual per 50-m section. However, individuals were clustered in areas of high and low densities as would be expected for a large population in a heterogeneous environment (Gregory et al., 1987; Fig. 2.2).

Other studies have shown snake distributions to be closely associated with particular habitats (Hebrard and Mushinsky, 1978; Madsen, 1984; Shine, 1977; Slip and Shine, 1988; Weatherhead and Charland, 1985). In this study we used two methods to test if snake-capture distribution was related to various habitat variables. First, we associated capture locations with habitat types (Fig. 2.3). Next, we examined movement patterns to determine if recaptured individuals were moving differentially to specific habitat types.

Differential use of river segments by snakes is not a definitive indicator of habitat preference but does explain non-random spatial patterns. Few individuals of *N. taxispilota* were found in areas with gradually sloping banks, poor perch availability, or within the inside bend of the river (Figs. 2.2 and 2.3). For example, the right bank near section 90 (Fig. 2.2) is an inside bend with low banks and few potential perch sites. In three years of sampling, no captures were made in this area. Alternatively, 13 captures have been made across the river in a section characterized as an outside bend of the river with steep banks and abundant perch sites.

The highest concentrations of captures for *N. taxispilota* were clustered in areas near backwaters of the river, specifically a human-made canal and a large oxbow. The biological importance of these non-riverine areas to *N. taxispilota* is unknown. There may be higher concentrations of fish adjacent to these areas, as many riverine fish require lentic waters to spawn and brood their young (e.g., *Ictalurus, Lepomis,* and *Esox*; Moyle and Cech, 1982). Prey locations and densities are known to affect distribution patterns of and habitat use by snakes (Gregory, et al., 1987; Mushinsky, 1987; Reinert, 1993).

We tested our initial interpretation of habitat use based on capture frequency by determining if recaptured individuals of *N. taxispilota* (n = 50) moved differentially from one habitat type to another, hypothesizing that the majority of individuals would remain in or move to outside bends or straight sections of river (typically, areas with steep banks and abundant perch sites). Recaptured individuals remained in or moved to straight sections and outside bends of the river (90% of recaptures) with steep banks (88%) and a moderate to abundant concentration of perch sites (86%; Table 2.2). No recaptured individual that changed in at least one habitat variable stayed in an area with gradual banks, inside bend of the river, or areas with few perch sites.

The recaptured individuals that did not change habitat may be subdivided into those that did and those that did not move out of their 50-m sections between captures (Table 2.2). All of those that did not move (n = 8) were in areas of outside or straight sections of river characterized by steep banks and moderate or abundant perch sites. Only two individuals that changed habitat types (n = 20) moved to areas characterized by a combination of gradual bank, inside bend, and few potential perches. Of those that changed sections but moved into the same habitat type (n = 22), only three individuals remained on an inside bend of the river with gradually sloping banks (Table 2.2). These three individuals may have been long-term residents of the areas in which they were found, based on 38, 48, and 191 elapsed days between captures. Although non-preferred habitats are traversed by individual snakes and intermittent sampling can give only a static measure of distribution patterns, a small proportion of *N. taxispilota* may be resident in areas of gradually sloping bank, inside bend, and poor perch availability.

The observed spatial distribution of *N. taxispilota* and its use of particular habitats can be explained in several ways. First, *N. taxispilota* may be selecting the outside bank of the river in response to current velocity. The faster, deeper water may offer some level of protection from aquatic predators such as gar (*Lepisosteus* spp.), largemouth bass (*Micropterus salmoides*), or alligators (*Alligator mississippiensis*), as well as quick escape from terrestrial and avian predators. Second, preferred locations may correspond to areas of high prey density (Robertson and Weatherhead, 1992; Schwaner, 1991). Finally, deep water habitats remain suitable for both foraging and predator avoidance independently of fluctuations in water level (Shine and Lambeck, 1985; Tinkle, 1959) compared to the inside bends of the river that can be shallow or dry. Individuals captured on the inside bends of the river may be transient or may use these areas as water level permits.

Reinert (1993) reviewed multiple factors that may influence habitat use in snakes, including body size, sex, reproductive condition, digestive state, and ecdysis. We examined these factors in regard to several microhabitat features for this population of *N. taxispilota*. Of the variables recorded, we found significant relationships between body size and perch height, perch exposure, and perch substrate.

Larger snakes showed a greater range in their choice of perch heights (Fig. 2.4) and were more likely to be captured on exposed or partially exposed perches. This relationship may be the result of several factors. The preferred perch height of a water snake may be a trade-off between thermal preferences and a tendency to remain near the water for predator avoidance (Tiebout and Cary, 1987). Therefore, if terrestrial or avian predation were size-limited (Mushinsky and Miller, 1993), perhaps only larger snakes could attain a perch height associated with a thermal preference.

Perch height has been found to vary seasonally and between sexes among snakes (Durner and Gates, 1993; Tiebout and Cary, 1987). We found no significant differences in perch height among months, but males were captured on higher perches than females. Durner and Gates (1993) suggested that higher perches used by females of *Elaphe obsoleta* were related to refuge use (tree cavities) and exploitation of avian prey. We suggest that differences between the sexes in perch height observed in *N. taxispilota* may be related to large, heavy-bodied females (especially gravid individuals) choosing relatively lower perch sites (e.g., on the bank or a log: Fig. 2.5) than males of similar length. Similarly, Fitch and Shirer (1971) found that females of *Coluber constrictor* were less arboreal than males and suggested this difference was caused by larger female body size.

Because the majority of both captured and sighted but not captured individuals of *N. taxispilota* were located in shade, our capture data do not appear biased toward potentially cooler individuals located in the shade. Month of capture, ecdysis cycle, and size were related to differences in the relative amount of shading in which individuals were captured. Not surprisingly, those captured in cooler seasons were more likely to be on exposed perches. The thermal requirements of snakes preparing for ecdysis may be species specific (Peterson, et al., 1993). Alternatively, a trade-off may exist between a heat-seeking tendency and the need to seek shelter during ecdysis (Kitchell, 1969; Plummer and Congdon, 1994). Thus, species such as *Crotalus horridus* (Peterson, et al., 1993; Reinert, 1993) and *N. taxispilota* may seek more open habitat prior to ecdysis whereas *Coluber constrictor* seeks refuge underground (Plummer and Congdon, 1994). The significantly larger average size of individuals in sun compared to those in shade or partial sun might be explained by 1) reproductive condition (Peterson, et al., 1993), 2) as suggested previously, smaller snakes using lower, more concealed (shaded) perch sites, thus avoiding predation, or 3) because of their size and lower thermal inertia, smaller snakes reaching a preferred body temperature more quickly than larger snakes in more shaded locations.

MOVEMENT

No association was evident between distance moved and time between captures for *N. taxispilota*. Individuals with the highest rate of movement were recaptured after a short time span, whereas several individuals had moved only short distances over long periods of time. A small proportion of the population may be highly vagile, regularly moving long distances in short periods of time (Kiester, et al., 1982). Alternatively, these observations could also be consistent with shifting activity centers (Tiebout and Cary, 1987). That is, brown water snakes may move long distances in response to seasonally varying prey abundance or environmental stimuli such as changes in water level.

The seasonality of movement patterns of all recaptured snakes and movement data of individuals caught more than twice may be used to determine if shifting activity centers are an explanation. First, almost all long-distance movements (>10 m/day) occurred in late summer and autumn. Second, two individuals that made long movements in late summer and autumn (200 m in 13 days and 300 m in 22 days) had returned toward (150 m and 200 m) their original capture locations when captured the following year.

Movement rates and distances were generally consistent with mark-recapture studies of other species of *Nerodia* (Macartney, et al., 1988). We found no relationship between either sex or size of an individual and distance or rate traveled, although we did see a strong difference in the type of movement. No individual of *N. taxispilota* <80 cm SVL crossed the river, whereas 40% of the recaptured individuals >80 cm SVL were made on the opposite side of the river. Because this larger size class of *N. taxispilota* did not display a greater propensity in movement in terms of distance or rate, it appears that river-crossing was not simply a result of increased vagility of larger individuals. We suggest that the size threshold in crossing the river results from size-limited predation by both avian and aquatic open-water predators (Mushinsky and Miller, 1993). While no regional species of snakes becomes large enough to avoid predation by adult alligators, some probably become large enough to escape predation by most fish and birds. Alternatively, this larger size class may use the deeper river channel in searching for prey. Preferred prey size or type for larger individuals of *N. taxispilota* may be located mid-channel, leading to more frequent movements across the river. *Nerodia taxispilota* is primarily piscivorus (Camp, et al., 1980), and large individuals (>60 cm) in this population feed exclusively on catfishes (Ictaluridae; personal observation). We have observed several large individuals returning to shore from mid-channel with fish in their mouths. Therefore, large individuals foraging in the river for catfish may return to the nearer bank after capturing their prey. Regardless of the reason, this is one of the few reported size-related differences in movement activity in snakes (Gibbons and Semlitsch, 1987; Gregory, et al., 1987; but see Clark, 1974). Plummer (1981) reported channel crossing movements in *Opheodrys aestivus* (3.5% of recaptures crossed a 50-m channel), but did not relate this behavior to size.

Thorough knowledge of where, how, and why aquatic organisms move is essential to address certain environmental concerns, such as impacts of dam and bridge construction or the movement of toxic compounds through aquatic ecosystems. As a common and potentially important biological component throughout much of its southeastern range, *N. taxispilota* could serve as an ideal species to investigate anthropogenic impacts on aquatic systems. In addition, its ictalurid dietary habits, fondness for basking, and occasional overland excursions provide evidence of the species' links with the littoral and benthic aquatic zones as well as the peripheral terrestrial habitat. Insight into movement patterns is critical to a thorough understanding of the biology and ecology of this species as well as an understanding of this ecosystem.

Our study has shown that individuals of *N. taxispilota* are clustered in specific habitat types along the river and are capable of moving long distances. Mark-recapture data may underestimate movement and home range or activity-center size (Weatherhead and Hoysak, 1989), with movements between captures indicating only the minimum distance moved (Secor, 1992). Additionally, we do not know how far into the floodplain this species travels or if riverine snakes move into adjacent streams or other aquatic systems and vice versa. Current and future work using radiotelemetry should elucidate patterns of habitat use and movements for this species.

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Table 2.1 - Number of captures and recaptures of *Nerodia taxispilota*.

Year	Sampling days	New captures	Recaptures (first captured in:) 1991	1992	1993	Total
1991	5	59	1	--	--	60
1992	22	198	0	28	--	226
1993	25	104	1	13	7	125
Total	52	361	2	41	7	411

Table 2.2 - Habitat “choices” made by recaptured individuals of *Nerodia taxispilota* (n = 50) on the Savannah River. Numbers beneath each heading represent the number of individuals in each habitat category (see text for descriptions of habitat variables).

	Recaptures n=50				
	Did not move n=8	Moved n=42			
		Did not change habitat type between captures n=22	Changed habitat type between captures n=20		
Habitat variables			Initial	Final	Final location summary
Bank slope:					
steep	8	18	16	18	44
gradual	0	4	4	2	6
Bank type:					
outside bend	4	9	7	8	21
straight	4	10	11	10	24
inside bend	0	3	2	2	5
Perch sites:					
abundant	6	9	6	9	24
moderate	2	10	10	7	19
few	0	3	4	4	7

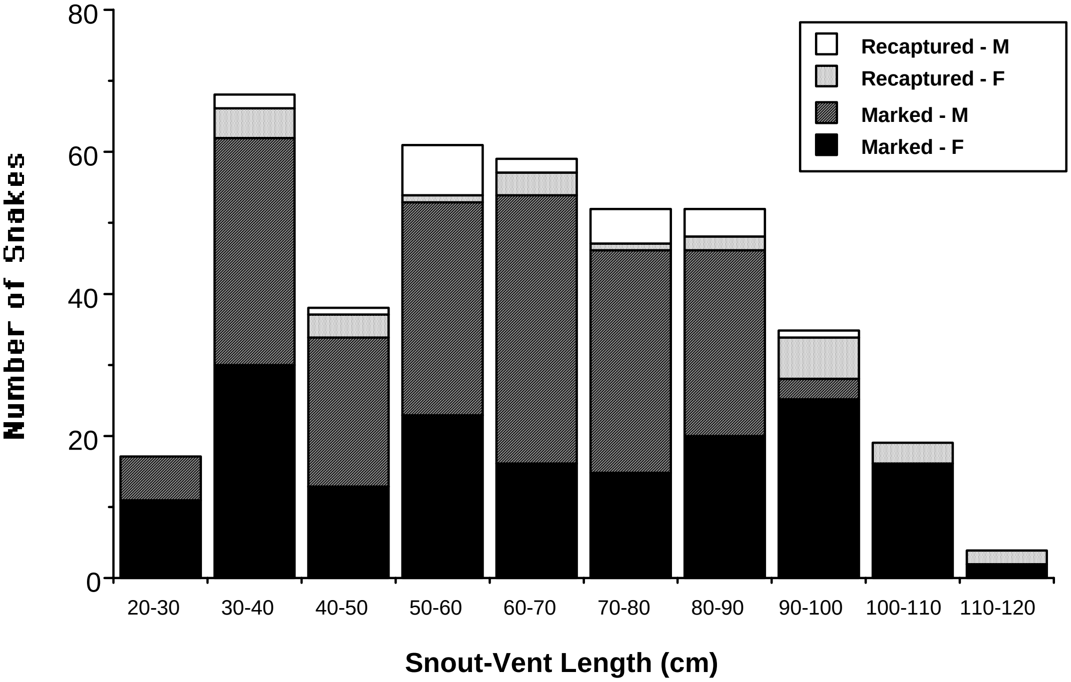

Figure 2.1 - Length-frequency histogram for *Nerodia taxispilota* based on 361 individuals and 411 captures over 3 yrs.

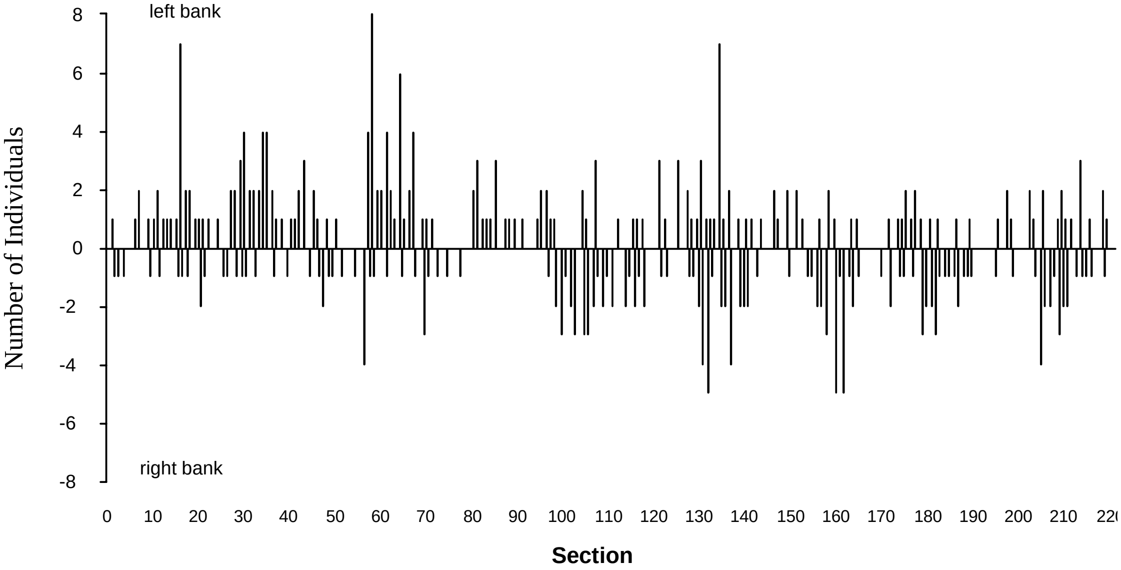

Figure 2.2 - Number of *Nerodia taxispilota* captured over a 3-yr period in each 50-m section of the study area.

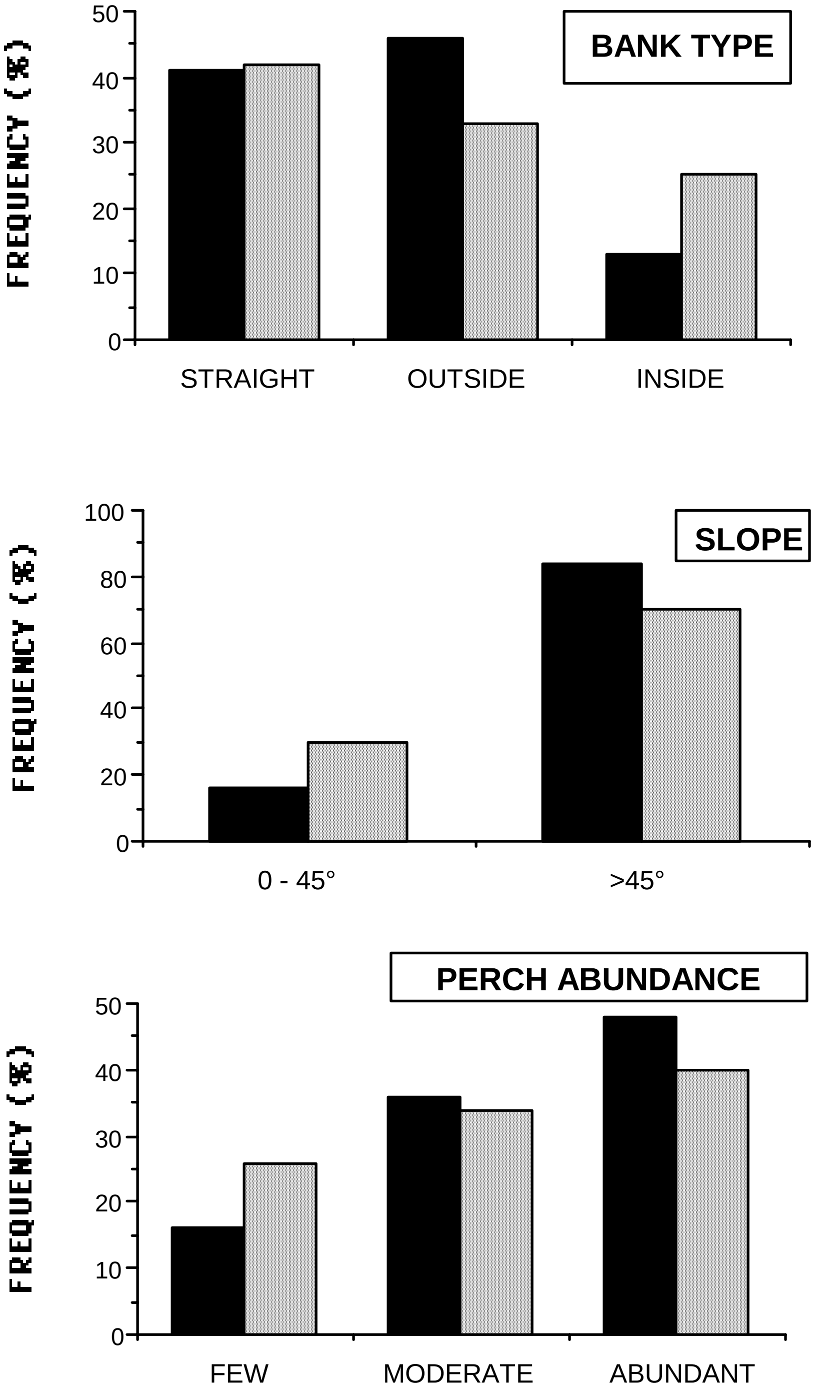

Figure 2.3 - Actual and expected frequency of captures associated with habitat variables. The solid bars represent actual observations and the stippled bars represent the corresponding expected values based on their occurrence on the study site. The categories are explained in the text.

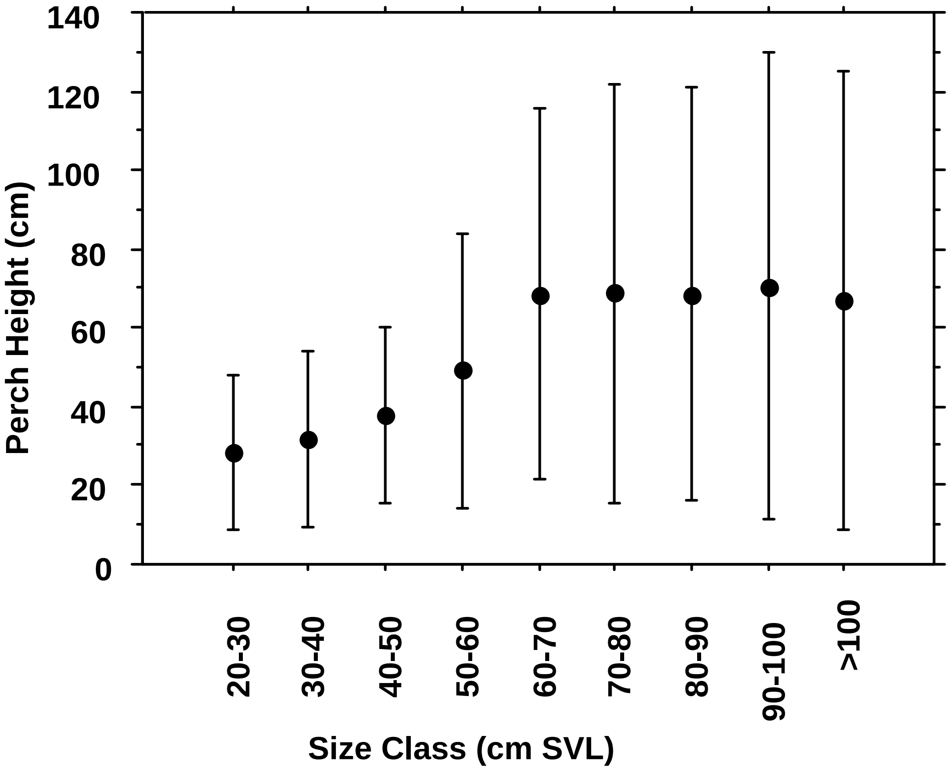

Figure 2.4 - Mean perch heights of basking individuals of *Nerodia taxispilota* (n = 409) as a function of size-class. Bars indicate ±1 SD.

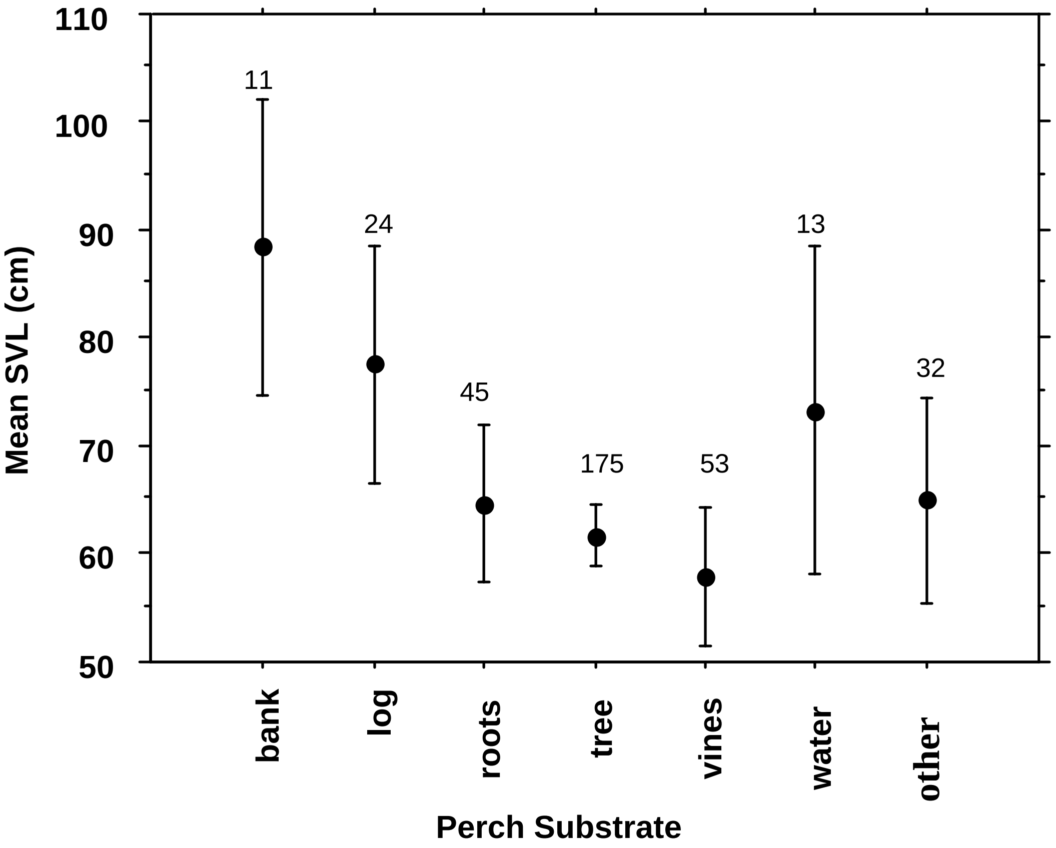

Figure 2.5 - Mean SVL of *Nerodia taxispilota* for each of seven perch substrate categories. Bars are 95% confidence intervals for the mean and numbers are sample sizes.

CHAPTER 3

FORAGING ECOLOGY OF THE BROWN WATER SNAKE, *NERODIA TAXISPILOTA*, WITH A COMPARISON OF COLLECTING TECHNIQUES

ABSTRACT

As part of a long-term study of the brown water snake, *Nerodia taxispilota*, I collected foraging and dietary information from 1565 individual captures. Sixteen percent (n = 257) of all captures had food in their gut and 65% of these prey items were identifiable. *Nerodia taxispilota* were captured with significantly more catfishes than other identifiable food items. Of the identifiable food items (n=168), all were fish and 63% were catfishes (Ictaluridae). A significant shift to an almost exclusively catfish diet occurred at about 60 cm SVL. The mean SVL of those individuals with food was significantly less than those without food, reflecting the disproportionally large number of individuals between 30-40 cm SVL which were captured with food items. Eighteen percent of all females captured (n = 814) had eaten whereas 15% of the males (n = 748) had food, although this difference was not significant. Feeding frequency (percent captured with food) ranged from 15.8%-20.3% between four general study sites and varied monthly, with peek frequencies in May, July, and October. Individuals with food basked lower but the presence/absence of food did not affect basking behavior in terms of relative exposure to the sun. Fewer opaque or shedding individuals had food items and there was no relationship between diet and reproductive condition, although gravid females near parturition were not captured with food. Fitch's nonlethal technique proved more labor intensive, yet satisfactory in dietary studies of this snake when compared with lethal studies. These results are discussed with reference to other dietary studies, habitat selection, community ecology, and toxicological implications.

INDEX WORDS: Diet; *Nerodia taxispilota*; Ictaluridae; Catfish; Ontogenetic diet shift; food chain/web; Water snake

INTRODUCTION

"The range of an animal is the range of its food." --Wright and Wright (1957). Diet is an important part of the natural history and ecology of any animal, including snakes (Fitch, 1949; 1987), and foraging (i.e., prey capture, handling, etc.) has presumably shaped the evolution of snake morphology and activity (Greene, 1983; Mushinsky, 1987; Camilleri and Shine, 1990). Gibbons and Semlitsch (1987) view "Feeding" as one of the three major categories of snake activity acted upon by natural selection. Resource availability, foraging efficiency, diet, and the level of risk associated with foraging directly and indirectly affect components of fitness (and thus evolution) such as optimal reproductive tactics (Pianka, 1976) and reproductive effort (Congdon et al., 1982; Dunham et al., 1989).

Recent theoretical and field studies suggest that most observed spatial patterns of biodiversity can arise from how organisms find and acquire resources (e.g., food) in space (Ritchie and Olff, 1999). Prey abundance and distribution have been implicated in determining the spatial distribution of snakes (Wharton, 1969; Plummer, 1981; Mushinsky, 1987; Schwaner, 1991; Robertson and Weatherhead, 1992) and partitioning of prey type or size may reduce inter- and intraspecific competition (Shine, 1980; Mushinsky et al., 1982; Plummer and Goy, 1984; Toft, 1985; Camilleri and Shine, 1990). Snake communities and niche relationships are interrelated with prey communities (Vitt, 1987) and snake species density and diversity are related to prey types and density (Arnold, 1972). Finally, an understanding of trophic relationships (i.e., who eats whom) is important for conservation of endangered species (Pimm et al., 1991).

Diets of animals are also an important variable to consider when one is looking at ecosystem level questions such as the movement of energy or pollutants through the system. A classic example is that of the biomagnification of pollutants such as mercury and DDT. The movement of contaminants through the ecosystem is of primary importance at the Savannah River Site (SRS) in South Carolina and has been the focus of almost 50 years of research. Therefore, diet and foraging are important in the understanding of the basic ecology and evolution of snakes, yet relatively little is known about snake foraging ecology (Mushinsky, 1987).

The brown water snake, *Nerodia taxispilota*, is a common inhabitant of aquatic systems throughout the Southeast (Ernst and Barbour, 1989) and is common on the SRS (Gibbons and Semlitsch, 1991; Mills et al., 1995); and yet, other than anecdotal records scattered throughout the scientific literature, there is only one published study on the diet of *N. taxispilota* (Camp et al., 1980). On the SRS, *N. taxispilota* may have toxicological importance in that it may serve as a link between the radioactively contaminated sediments and the terrestrial environment. In previous studies it was found that *N. taxispilota* from contaminated sites on the SRS had a significantly higher level of radiocesium than from uncontaminated sites and it was proposed that prey selection may play a role in the amounts and persistence of radiocesium in these and other snakes (Brisbin et al., 1974; Bagshaw and Brisbin, 1984). Therefore, if we are to understand how the snake community is assembled or how nutrients, energy, or contaminants move through this ecosystem, we must first have an idea of what and how often the members of this ecosystem (i.e., brown water snakes) eat.

In this paper I report on the diet of *N. taxispilota* and discuss the diet in relation to other aspects of this species' ecology. The purpose of this study was threefold: 1) to document the foraging ecology and diet of *N. taxispilota* at the SRS and to compare this diet with other published and unpublished records for this species, 2) to compare my nonlethal technique (forced regurgitation) with lethal techniques in terms of dietary studies, and 3) to determine how diet may affect the distribution and abundance of *N. taxispilota* in terms of habitat use and this species' niche in the snake community. Because the present study was part of an ongoing mark-recapture population study, sacrificing the number of animals required to obtain accurate dietary information was not an option. I gauged my success in documenting the diet of *N. taxispilota* by comparing my data with data collected in the same area by sacrificing the animals (Appendix 3.1).

METHODS

FORAGING BEHAVIOR

Descriptions of foraging behavior were collected from both field and laboratory observations (see explanations below). While descriptions on foraging in the wild in most water snakes have been anecdotal because of the rarity of observing snakes foraging, I feel they add to the overall "story" of brown water snake foraging ecology, and thus are included in this chapter.

DIET

I used dietary data collected from 411 *N. taxispilota* from a previous study (1991-1993; Mills et al., 1995) and an additional 1154 individuals captured at various sites on the SRS from 1994-1998; primarily from the Savannah River (SAV), Upper Three Runs Creek (UTR), and Steel Creek (SC; for a map, see Gibbons and Semlitsch, 1991).

Snakes were located visually and captured by hand from a slow moving boat maneuvered 2 to 15 meters from the bank. I recorded snout-vent length (SVL, cm), mass (g), and characteristics of the individual and habitat (e.g., reproductive condition, perch height, and relative exposure to the sun). I palpated each snake for evidence of recent feeding. If I detected food, the stomach contents were forcibly regurgitated, identified, and when possible returned to the snake (Fitch, 1987; hereafter called Fitch's method). I identified prey items to the lowest taxonomic level possible in the field, generally to family or genus and often to species.

PREY DIVERSITY AND COMPARISON OF TECHNIQUES

In order to compare my results with those obtained through other dietary studies (e.g., Gibbons and Semlitsch, Appendix 3.1; Camp et al., 1980), I calculated Shannon's diversity index (H') and a relative diversity index (J') for my data as well as for those studies where sufficient data were presented. Diversity of diet was compared using these diversity indices and a t test (Zar, 1984; p. 146; Brower et al., 1998). The equations are as follow (Zar, 1984):

$$H' = - \Sigma p_i \log p_i \qquad J' = H' / H'_{max}$$

where p_i is the proportion of observations in each category and $H'_{max} = \log k$ (k= number of categories). The number of categories (k) was standardized between studies by using the family level of prey identification. When H' is high, diversity is high and feeding is most generalized (i.e., they are not specializing on any one food category), and when H' is low (nearer to 0), then diversity is low and feeding is specialized. Another way to evaluate feeding specialization is in terms of dominance; 1- J' may be used to express dominance (Brower et al., 1998). This formula has the advantage of being a relative value and having values between 0 (dominance is low) and 1 (dominance is high) and thus may be better for comparisons between species. Magurran (1988) and Bulla (1994) point out the shortcomings of these and other diversity and evenness indexes; therefore, for the three *N. taxispilota* populations I also present the log series (α) diversity index (Magurran, 1988) and Bulla's two new indices, E and D, for comparative purposes:

$\alpha = \frac{N(1-x)}{x}$ where x is estimated by the iterative solution of $S/N = [(1-x)/x][-\ln(1-x)]$

and,

$E \text{ (evenness)} = \frac{O-1/S-(S-1)/N}{1-1/S-(S-1)/N}$ $\qquad D \text{ (diversity)} = E*S$

where S = number of species, N = total number of individuals in the sample, and $O = \Sigma \min(p_i, \mathit{p}_i)$ where p_i and p_i are the observed relative frequency and the expected relative frequency, respectively. The log series (α) species richness index was chosen because 1) it is widely used (and thus is useful for future comparisons), 2) it is relatively easy to calculate, 3) the rank abundance plot for my data most closely fit a log series curve, 4) it is less affected by sample size, and 5) the discriminatory properties of this index are good (Magurran, 1988). Also, Magurran states that this index has been found to be "statistically and ecologically sound" (p.80) and that, "Ideally α should replace the Shannon index as the preferred measure" (p. 106). However, the advantage of Shannon's index is that it has been more widely used than α and indices from two samples may be statistically compared with a t test (Zar, 1984, p. 146; Magurran, 1988, p. 35). I also calculated Simpson's diversity index (D_s) for three *N. taxispilota* populations because it too can be compared using the t statistic (Brower et al., 1998). Simpson's index also includes, or is derived from, a measure of dominance (l).

$D_s = 1 - l$, where $l = \dfrac{\Sigma n_i(n_i - 1)}{N(N-1)}$ and n_i = the abundance or frequency of each category.

In addition to using diversity indices, I compared my data with another data set collected from the SRS (Gibbons and Semlitsch, unpublished data; Appendix 3.1) to determine the effectiveness of Fitch's nonlethal technique. This was accomplished by first square root transforming the data and then comparing the slopes of the two simple linear regression equations using a t test (Zar, 1984). The square root transformation was chosen over others (e.g., log transformation) because it was most appropriate for count or frequency data and because it provided the best-fit regression model for the two data sets.

Most statistical tests were computed using StatView® (Abacus Concepts 1992) for the MacIntosh® with a priori significance level set at alpha = 0.05 unless otherwise stated. When the assumptions of normality and equality of variances were grossly violated, nonparametric tests were used: Mann-Whitney tests (U) in place of a t-test, and Kruskal-Wallis test (H) in place of the ANOVA. In no case did the use of a parametric test vs. a nonparametric test alter the conclusions at the alpha = 0.05 level of significance. My statistical interpretation follows that of Zar (1984). Unless otherwise stated, all means are followed by two standard errors of the mean and all snake lengths are snout-vent lengths (SVL). Probabilities of tests are presented to the nearest 5%; that is, P>0.05 is equivalent to 0.10>P>0.05.

RESULTS

DESCRIPTION OF FORAGING MODES

I captured six snakes in the act of feeding (i.e., fish in mouth) between 1350-1710, and others exhibiting what appeared to be foraging behavior. Brown water snakes apparently use two modes of prey capture: sit-and-wait and active foraging. Using the sit-and-wait method, the snake anchors its body to a solid object (e.g., a branch, root, or rock) with its tail, leaving the head and the rest of the body to orient down or out into the water. The snake then captures prey as they move past. Sit-and-wait foraging has been observed by others and myself at the SRS and elsewhere (e.g., at River Banks Zoo, Columbia, SC, Scott Paff, pers. comm.; Reams and Stevens, 1999).

Nerodia taxispilota also actively hunts for food, a mode of foraging that has been observed less frequently and takes the form of the snake tongue-flicking and probing holes and crevices while moving through the water. This second mode may actually be much more common than observations indicate, based on the large number of catfish found in their diet (Table 3.1), as ictalurids are primarily bottom-dwellers and often frequent cavities and crevices. In addition, I have observed another type of active foraging in a captive animal (male, 39.6 cm). When I placed minnows in a large water dish, this snake would either partially or completely enter the water and pursue the fish with mouth opened and its head sweeping from side to side.

The following description of *N. taxispilota* feeding was taken from observations in a large, semi-natural enclosure designed to study snake ecology (Lee and Mills, 2000). Once the fish had been captured, it was taken to shore where it was manipulated and swallowed headfirst. The snake's jaws moved over the catfish's body until it reached the pectoral and dorsal spines. It then turned the fish 90 degrees so that the dorsal spine was in a lateral orientation and waited for the spines to relax. Once the spines relaxed, the snake proceeded to swallow the fish in this orientation.

I observed a female *N. taxispilota* (75 cm SVL) with a radiotransmitter exhibiting foraging behavior on 21 April 1995. This female may have been gravid as I observed her mating on 12 April 1995. I located her at 1146 on an overhanging maple branch about 30 cm above the water, shortly after she had emerged from the water (she was wet and warming). At 1207 she placed her head in the water briefly, then raised it. At 1208 she wrapped her tail around the branch with half her body extended into the fast deep water; three minutes later she slowly slid into the river after which I departed to locate other radiotelemetered snakes. I returned and relocated her downstream at 1251. She was now in a slow-water backwater area adjacent and upstream of the mouth of UTR, and I again departed (1304). I returned at 1417 and found her 15-20 m out from the bank in the river at the mouth of UTR, in a zone between relatively shallow and deeper water (i.e., a drop-off). I again departed and returned at 1602. She was now approximately 450 m (straight line distance) down river from her original site, perched on a sycamore branch about 30 cm above the water and with a noticeable food item in her gut. Air and water temperatures ranged from 25.5-27.3 and 19.1-19.4 respectively. It was partly cloudy and had been raining earlier in the day and was sunny when she emerged with the food item.

Once captured, it may take several days or more for the prey item to be digested, depending on its size. For example, a large female (113.0 cm) was captured in UTR creek with a recently captured, large fish (ID uncertain; probably a sucker - Catostomidae) in its gut. This snake was captured at 1346 on 2 May and taken to the laboratory at SREL where it was housed at room temperature (ca. 22-23ºC) awaiting transmitter implantation. This large fish was reduced to "mush" by 900, 4 May, although there was still a noticeable bulge. A slight "mushy" bulge was still apparent at 905 on 8 May, but was not apparent the next day (815, 9 May) prior to surgery. This digestive rate is rather conservative because the snake was not given the opportunity to thermoregulate in the cage. Her cloacal temperature at the time of capture (25.6ºC) was higher than room temperature.

FORAGING INJURIES

Many fishes preyed upon by *N. taxispilota* have spines (e.g., catfishes and sunfishes), with some producing mild venom (e.g., the madtoms). At least seven *N. taxispilota* were captured with fish spines protruding through the body wall. These individuals had both recent spines (i.e., fish still intact) and old spines (i.e., spine only), and consisted of six females ranging in size from 54-95.5 cm and a 72.4 cm male. One female was captured on 27 August 1992 with spines protruding through the body wall. She was subsequently recaptured twice, 15 October 1992 and 2 April 1997, growing from her original 59.4 cm to 101 cm.

DIET

Sixteen percent (257 of 1565) of all captures had detectable food in the gut, of which, 65% (n=168) of the prey items were identifiable and 57% (n=146) were identifiable to at least the family level (Table 3.1, Fig. 3.1). Other items were too digested for field identification. Feeding frequency did not significantly differ between males (15.2% with food) and females (17.5%; $\chi^2 = 1.509$, df = 1, P>0.20), nor between adults (15.0%) and juveniles (18.6%; $\chi^2 = 3.189$, df = 1, P>0.05), even when comparing the sexes within adults (13.8% for males vs. 16.8% for females; $\chi^2 = 1.511$, $P>0.20$) and juveniles (18.7% males vs. 18.5% females; $\chi^2 = 0.004$, $P>0.99$). The proportion of individuals captured at all sites with food varied from 11.9% in 1997 to 20.4% in 1995, but did not differ significantly among years (contingency table, $\chi^2 = 6.880$, df = 6, $P>0.30$; 1998 was omitted due to small sample size, but when included did not alter the conclusions, i.e., $P>0.25$). These results were consistent for my primary study area (Sav-a) only (Table 3.2; $\chi^2 = 3.257$, df = 6, $P>0.75$). In addition, feeding frequency did not differ among the Savannah River and other study sites (Table 3.2; $\chi^2 = 1.291$, df = 3, $P > 0.50$).

Nerodia taxispilota began feeding by March and continued through October. The earliest record was of a female (60.7 cm) captured with a catfish on March 12, 1997, and the latest record was a young-of-year male (25.2 cm) captured on October 30, 1996, with an unidentified item. The latest capture with an identifiable prey item was a male (43.0 cm) captured on October 20, 1994, with a pirate perch (*Aphredoderus sayanus*) in its gut. As one would expect for an ectotherm in a temperate region, feeding frequency differed by month (Fig. 3.2; $\chi^2 = 32.744$, df = 10, $P<0.001$), and this held when I removed the months without observed feeding - January, February, and November – from the dataset ($\chi^2 = 18.989$, df = 7, $P<0.01$). Peak feeding occurred in May (20.8%), July (20.9%), and October (22.4%). However, when I analyzed sexes separately, feeding differed by month for males ($\chi^2 = 17.692$, df = 7, $P<0.05$) but not females ($\chi^2 = 11.430$, df = 7, $P>0.10$). I then split the sexes into adults and juveniles and found that juveniles were much closer to the expected feeding frequencies per month (male: $\chi^2 = 8.418$, df = 7, $P>0.25$; female: χ^2

= 6.833, df = 7, $P>0.40$) than adults (male: $\chi^2 = 18.239$, df = 7, $P<0.05$; female: $\chi^2 = 13.647$, df = 7, $P>0.05$).

I hypothesized that observed differences in feeding frequency between sexes and maturity may be related to mating behavior (i.e., males searching for mates rather than eating) or reproductive condition (i.e., gravid females discontinuing to feed as they approach parturition). To test this I compared feeding frequency among adult males before and after the mating season in the spring (May 1 was selected as an arbitrary date for the end of the mating season) and adult females as they neared parturition (August 1 was selected based on records of parturition in the field and laboratory; See Chapter 4). In both cases the observed feeding frequencies were not different from those expected (males: $\chi^2 = 3.202$, df = 1, $P>0.05$; females: $\chi^2 = 2.196$, df = 1, $P>0.10$), however it is worth noting that the observed difference among the adult males was significant at the 0.10 level (90% confidence level) and that this apparent difference was primarily due to the contribution of one contingency table cell (contributed 71% of the chi-square value): adult males were 46% less likely than expected to feed during the mating season.

I did not test intersite variation in monthly feeding because only one site (SAV-a) was sampled consistently throughout the year (Fig. 3.2). Sex, presence of food, and month were not mutually independent (3 dimensional contingency table: $\chi^2 = 42.719$, df = 22, $P<0.01$), however this finding was primarily due to the effect of months in the analysis, although a test for partial independence (Zar, 1984; p. 74) revealed that the sex of the individuals may have also contributed to this significant finding ($\chi^2 = 22.696$, df = 15, $P<0.10$). The test for partial independence was greatly influenced by the contributions of two cells (i.e., together these cells contributed 30% of the Chi-square value): more males and fewer females were captured without food in August than expected.

Of the identifiable food items (n=168) recorded from *N. taxispilota*, all were fishes and 63% (n=106) were catfishes (Ictaluridae: *Ameiurus*, *Ictalurus*, and *Noturus*; Fig. 3.1, Table 3.1). Only three individuals were known to have more than one food item: a female (73.8 cm) with a catfish and sunfish, a male (56.3 cm) with two catfish, and a male (48.0 cm) with a speckled madtom, *Noturus leptacanthus*, and an unidentified fish (it was not an ictalurid). Both sexes were captured with similar food items (χ^2= 13.129, df = 11, P>0.35), however, differences existed between adults and juveniles (χ^2= 34.892, df = 11, P<0.001), and both these findings held when unidentified items were removed from the analyses (P>0.50 and P<0.001). This second result was consistent with the ontogenetic diet shift reported below (see Fig. 3.3A). Observed frequencies of the various families of prey items in the diet differed by month and year, with catfishes (Ictaluridae) being the only family found in the diet in all months and years (Table 3.3).

Samples of fish populations from UTR Creek (electroshocking/seining 10 sites, each 15-20m long) were collected from between my two UTR study sites (about 1mile above Box Landing) in May 1994 and 1995, and documented the presence of 37 species (12 families) making up 630 specimens, with only 15 species being represented by a total of 10 or more specimens and only 8 species representing more than 5% of the total sample (Dean Fletcher, unpublished data). Based on these samples of the prey, *N. taxispilota* were not eating the fish families in proportion to their availability (χ^2= 37.500, df=6, P<0.001; expected frequencies <1 were combined for this analysis, resulting in 7 categories of food; Table 3.4, Fig. 3.4). Two families of fishes (Ictaluridae and

Catostomidae) were eaten in greater proportion than was expected, pirate perch (Aphredoderidae) were consumed in the levels expected, and all other prey items were consumed less than expected (Table 3.4, Fig. 3.4). Approximately 90% of the chi-square statistic was contributed by the over-representation of catfishes and the complete lack of minnows in the diet of snakes captured in UTR Creek. That is, *N. taxispilota* ate about 3.5 times the number of catfishes and 4.5 times fewer minnows than what was expected in UTR. Minnows (Cyprinidae) are conspicuously missing from my UTR samples, although *N. taxispilota* in my Savannah River samples and a Georgia population included them in their diet (Table 3.5). In addition, a small male from the Savannah River readily accepted minnows in captivity (see above: *Description of Foraging Modes*). The large proportion of unidentified food items could include members of these and other missing families, particularly the Cyprinidae because of their small size and lack of spines in the fins, but data from other studies suggest this is not the case (see Discussion, Table 3.5, Appendix 3.1). An adequate, quantitative estimate of resource availability is not available for the Savannah River and may be impossible to obtain due to the constraints of sampling a large river, especially for small, bottom-dwelling fishes.

The smallest *N. taxispilota* captured with food was a 24.1-cm (15g) male with a madtom, and the largest was a 133-cm (2012g) female with a catfish. Individuals captured without food (66.7 ± 1.2 cm, n = 1281) averaged slightly larger than those with food (63.5 ± 3.1 cm, n = 253; U = 176546, df = 1281, 253, P<0.05). This difference was more pronounced in males (60.6 ± 1.3 cm vs. 56.3 ± 3.3 cm, without and with food, respectively; t = 2.582, df = 730, P=0.01) than in females (72.5 ± 1.9 cm vs. 69.2 ± 4.6 cm; t = 1.428, df = 798, P>0.15) and may be related to sexual maturity. Feeding frequency was greater among juveniles (18.6% with food) than adults (15.0%), although not significantly ($\chi^2 = 3.443$, df = 1, $P>0.05$). That is, relatively fewer adults (males > 50 cm; females > 79 cm SVL) compared to juveniles were captured with food. Feeding frequency also did not differ between males and females in either the adults (13.8% vs. 16.8%; $\chi^2 = 1.511$, df = 1, $P>0.20$) or juveniles (18.7% vs. 18.5%; $\chi^2 = 0.004$, df = 1, $P>0.90$), nor did it differ between adults and juveniles within each sex (males: $\chi^2 = 2.760$, df = 1, $P>0.05$; females: $\chi^2 = 0.393$, df = 1, $P>0.50$). Whereas the differences between sexes and between adults and juveniles may not be statistically significant at $\alpha = 0.05$, it is worth noting the possible ecological and biological significance of juveniles eating more frequently than adults, particularly when viewed for each sex. That is, adult males eat less frequently than juvenile males, which may be used in hypotheses of sexual size dimorphism in this species.

Among juveniles, a significant difference in size was discovered within each sex between those captured with and without food. Juvenile females captured with food averaged smaller (48.5 ± 3.3 cm, n = 82) than those without food (53.4 ± 1.6 cm, n = 361; t = 2.668, df = 441, $P<0.01$) and juvenile males with food (35.3 ± 2.1 cm, n = 38) were smaller than those without (39.8 ± 1.2 cm, n = 165; t = 3.386, df = 201, $P<0.001$). Once again, the difference seems to be more pronounced in males. The differences in size among the adult females that were captured with and without food (97.4 ± 2.8 cm, n = 60, vs. 95.7 ± 1.1 cm, n = 297) and adult males with and without food (67.2 ± 2.2 cm, n = 73, vs. 68.1 ± 1.0 cm, n = 456) were not significant ($P>0.20$ and $P>0.45$).

The presence of particular groups of identifiable prey in the diet of *N. taxispilota* was also significantly related to size (H = 54.896, df = 9, $P<0.0001$; Table 3.1, Fig. 3.3).

For example, the mean size of snakes eating catfish (65.9 ± 4.4 cm) was greater than those consuming darters, madtoms, minnows, pirate perch, and temperate bass, although not sunfish and suckers (Table 3.1, Fig. 3.3). Thus, there seemed to be an ontogenetic dietary shift; that is, although all size classes of *N. taxispilota* consumed catfishes, there was a significant shift to an almost exclusively catfish diet at about 60cm SVL (Table 3.1, Fig. 3.3; Catfishes vs. all others, < 60 cm vs. > 60cm, χ^2= 16.039, df=1, P<0.001). The few exceptions to this shift in diet, comprising only 12.5% of those individuals > 60 cm (n = 72), were seven sunfish and two suckers (one was a large spotted sucker, *Minytrema melanops*). This shift in diet with size corresponds to the already mentioned differences between adults and juveniles.

The presence of food affected the height at which *N. taxispilota* basks but not basking behavior (i.e., whether they were in sun, shade, partial shade, exposed, and overcast). Individuals with food in their gut basked lower (62.7 ± 6.5 cm, n = 229) than those without food (70.9 ± 3.4 cm, n=1054; U = 130945, P<0.05). While one might expect basking to be related to digestion in snakes, I found no relationship between the presence of food and whether individuals were basking in the sun, shade, or partial shade (χ^2= 1.491, df=2, P>0.45). However, these results must be interpreted with caution because these two variables may be confounded (i.e., height above the water is related to air temperature and exposure and thus basking behavior; see Discussion).

Ecdysis but not reproductive condition of the snakes affected feeding. Only 6 of 242 individuals shedding or approaching ecdysis (i.e., clouded eyes or scales) had food items (χ^2=40.941, df=1, P<0.0001). While only 13 of 95 (14%) gravid females had eaten, this was very close to the population estimate for feeding frequency (Table 3.2) and was therefore not significantly different than expected (analysis of adult females only; χ^2=0.464, df=1, P>0.25). This second finding is slightly misleading because ten of the thirteen gravid females with food items were captured before August, substantially before parturition (mean parturition date is September 22, n = 122; Chapter 4), and the remaining three individuals had not recently fed (i.e., the food items were mostly digested). In addition, only 2 of these 13 gravid females had identifiable items: both were catfish and both were captured the last week in June.

PREY DIVERSITY AND COMPARISON OF TECHNIQUES

The diversity of food items (expressed as families) was higher in my study (k = 9) than in other populations of *N. taxispilota* that have studied, but was within the range of *Nerodia* spp. (k = 4 to 15; Tables 3.5 and 3.6). Diversity indices indicated that when compared to other water snakes, *N. taxispilota* in the present study (H’ = 0.483) were fifth behind *N. rhombifer* (H’ = 0.900), *N. cyclopion* (H’ = 0.655), *N. fasciata* (H’ = 0.557), and a Georgia population of *N. taxispilota* (H’ = 0.537; Camp et al., 1980) in terms of diversity of diet (when H’ is high, diversity is high; Table 6). If we compare dominance indices (when 1-J’ is high, dominance or selectivity is high), then my population of *N. taxispilota* (1-J’ = 0.494) is third behind *N. cyclopion* (1-J’ = 0.671) and *N. rhombifer* (1-J’ = 0.508), which both specialized on fish of the family Poeciliidae (particularly *Gambusia*) in southern Louisiana (Mushinsky and Hebrard, 1977).

All other cited dietary studies of *Nerodia* spp. (Tables 3.5 and 3.6) used data obtained through dissection (i.e., lethal methods). To compare the effectiveness of Fitch’s nonlethal technique (forced regurgitation) to dietary data obtained through dissection, I compared my data with an unpublished data set collected from the SRS

(Semlitsch and Gibbons, Appendix 3.1; Fig. 3.5). The data were first square root transformed to compare slopes of simple linear regressions. The slopes of the lines (i.e., the rate at which new families are added to the diet per number of captures) were significantly different ($t = 2.500$, $df = 9$, $P<0.05$), indicating that Fitch's nonlethal method of dietary analysis was not as effective, in terms of capture effort, in determining the diet of this species (Fig. 3.5). Using the regression equation, Semlitsch and Gibbons needed to collect approximately 204 snakes to obtain a fifth family, whereas I collected five families of prey with 342 captures, or approximately 1.7 times the capture effort (Table 3.7). Continuing with this line of reasoning, I collected 1439 snakes to obtain nine prey families, or about 2.9 times the effort predicted (captures = 501) for lethal collecting methods. In addition, the effects of sampling effort and diversity of habitats can be seen by comparing my primary study site (Sav–a), which received the greatest sampling effort, with all study sites combined (Table 3.7). Even though over half of the snakes were captured at my primary site, several species were not included in the diet at this site (e.g., madtoms, suckers, and redfin pickerel) that were included in the diet when all sites were combined.

Although my collecting effort was substantially greater than the Semlitsch/Gibbons sample, my dietary diversity indices (H' and D_s) were not different from their sample (H': $t = 0.202$, $df = 31$, $P>0.50$; D_s: $t = 1.314$, df = infinity, $0.20>P>0.10$; Table 3.5). Therefore, it appears that Fitch's method is more labor intensive; however, it seems adequate in dietary studies of this type. Interestingly, although my sample was not different from the other SRS sample, it was significantly different from Camp et al's Georgia sample for D_s but not for H' (D_s: $t = 3.330$, df =

infinity, P<0.001; H’: t = 0.918, df = 158, 0.50>P>0.20), illustrating potential differences in the choice of diversity indices.

PREY SIZE

I did not usually measure prey size because of my (Fitch’s) technique, however several noteworthy observations exist concerning maximum prey size. First, a female (112.5 cm, 1568g) from UTR consumed a large spotted sucker (*Minytrema melanops*; 31.6 cm Standard Length, 548g) that was at least 35% of the snake’s mass. The sucker had been digesting for a minimum of one day and its head was partially digested, therefore it was probably initially heavier. Using an estimated total length of 37 cm and the length-weight equation for spotted suckers in Bennett and McFarlane (1983), this fish could have been ca. 580g, making it 37% of the snake’s mass. Second, two small females (26.5 cm, 15g, and 33.7 cm, 30g) were captured with prey items (5g *Notropis* sp. and 10g *Ictalurus punctatus*) that weighed 33% of their body mass. Finally, a large male (80.9 cm, 465g) was captured holding a 125 g flat bullhead, *Ictalurus* (or *Ameiurus*) *platycephalus*, in its mouth. Had this individual been allowed to consume this fish, the bullhead would have constituted almost 27% of the snake’s mass.

DISCUSSION

FORAGING MODES

I have documented at least three types of foraging behavior exhibited by *N. taxispilota*: sit-and-wait (ambush) and two types of active foraging. Other authors have described similar foraging modes and prey handling methods for *N. taxispilota* and other *Nerodia* species. Richmond’s (1944) description of a *N. taxispilota* swallowing a large catfish is almost identical to mine, although he did not mention the 90 degree turning of the fish's body that I observed. The observed sit-and-wait foraging behavior of anchoring the posterior body with the anterior part of the body extended either down or out (i.e., horizontally) into the water has been observed by myself and others at the SRS and elsewhere (e.g., River Banks Zoo, Columbia, SC, Scott Paff, pers. comm., Reams and Stevens, 1999). Kofron (1978) often observed *N. rhombifer* anchored to debris in water at night and Gillingham and Rush (1974) described a similar sit-and-wait foraging mode for other *Nerodia* sp. They observed three *N. erythrogaster* and one *N. rhombifer* foraging for fish by anchoring their tails to the rocks near a culvert with the snakes' heads facing into the current, all holding their mouths open while remaining motionless. Gillingham and Rush (1974) observed this behavior both in the day and at night. Greene et al. (1994) observed an ambush style of foraging, particularly among juveniles, in *N. harteri*. The sit-and-wait mode of foraging on fish has also been documented for other semiaquatic natricines (e.g. *Natrix maura*, Hailey and Davies, 1986; *Thamnophis* sp., Rossman et al., 1996).

I also observed *N. taxispilota* moving underwater, tongue-flicking while probing crevices and holes. A similar foraging behavior has been reported for *N. harteri* (Greene et al., 1994), juvenile *N. sipedon* (Balent and Andreadis, 1998), sea snakes (e.g., *Aipysurus laevis*, Burns and Heatwole, 1998), *Natrix maura* (Hailey and Davies, 1986), as well as other species of aquatic and semiaquatic snakes (Mushinsky, 1987; Rossman et al., 1996). I propose that this type of foraging behavior helps to explain observed habitat use in this species. In a previous study, *N. taxispilota* used the outside bends and straight sections more than the inside bends of the Savannah River (Mills et al., 1995). Similar to the sea snake mentioned above which moves quickly over open sandy substrate to then forage in the rocky crevices (Burns and Heatwole, 1998), *N. taxispilota* may use the outside bends and straight sections of the river because these habitats offer a clay substrate with numerous cavities, holes, and structures such as debris piles and logs (i.e., catfish habitat), whereas the inside bends of the river are characterized by a lack of these structures and the presence of a rather uniform sandy substrate (although catfish forage in these shallow areas at night).

The final foraging method, moving through the water, sweeping their heads from side-to-side with mouth opened in a “haphazard” pursuit of fish, has been described for other *Nerodia* spp. (Mushinsky et al., 1982) as well as captive *N. taxispilota* (Ditmars, 1907; pers. obs.). Evans (1942, as cited in Mushinsky, 1987) described this behavior and called it “fishing,” and Drummond (1983) described this behavior in garter snakes (*Thamnophis*), calling it the “open-mouth search.” Whereas I have not observed this behavior in the field, I have observed this behavior in a captive individual and it could be useful in shallow-water habitats with high concentrations of fish, such as one might find in a drying swamp or near the shore in shallow water at night.

Nerodia sipedon has been described as a “mixed” forager, using a mixed strategy of tactics including those listed above (Balent and Andreadis, 1998). In their stream population of *N. sipedon*, Balent and Andreadis (1998) observed a variety of foraging techniques and suggested that this species may take inactive prey (e.g., bottom-dwelling species such as suckers and darters) using an active foraging mode, while more active prey (e.g., species swimming in the water column such as minnows) are captured using an ambush or sit-and-wait foraging mode. My observations indicate that *N. taxispilota* may also fit into this “mixed strategy” category of foraging.

Individual *N. taxispilota* foraged both diurnally and nocturnally. I captured six snakes in the act of feeding diurnally and many others that had recently fed. I have also observed a radiotelemetered snake foraging and capturing prey in the day as well as others active (and presumably foraging) at night. Charles Blem and his colleagues have provided field and laboratory data that supports nocturnal activity in Virginia populations of *N. taxispilota* (Blem and Blem, 1990; Blem and Killeen, 1993; Luckeydoo and Blem, 1993), and the captive male mentioned above foraged at night. Camp et al. (1980) commented on this species' diurnal habits (they referenced Mount, 1975), although they did not report observing feeding during the day. Others have also observed *N. taxispilota* foraging during the day (Richmond, 1944; Ream and Stevens, 1999), but this does not preclude nocturnal foraging in this or other populations of *N. taxispilota*. Rather, the large number of observations of diurnal and nocturnal foraging in the field and in captivity suggests that they feed both day and night. The European natricine, *Natrix maura*, and sea snakes (*Aipysurus laevis*) were also found to forage both day and night (Hailey and Davies, 1986; Burns and Heatwole, 1998). I propose that it would be easier for *N. taxispilota* to locate and capture catfishes during the day when these fishes are inactive and more likely to be found in holes and crevices than at night when catfishes are actively swimming and foraging.

Foraging behavior may have more to do with the observed "preference" for catfishes and other bottom-dwelling fishes than actual innate or behavioral preferences. That is, *N. taxispilota* may be more successful at actively foraging for and capturing these bottom-dwelling prey items rather than other potential prey. Because mid- and top-water prey have been recorded in their diet, and *N. taxispilota* have been observed using a sit-and-wait foraging mode, this may serve as a secondary or accessory mode of prey acquisition for this species. Reams and Stevens (1999) watched as an individual *N. taxispilota* attempted to capture sunfish (*Lepomis* sp.) using this strategy. They did not observe a capture, but the snake did have an apparent food item in its gut. A laboratory study on neonate prey preference (unpub. study, Mills) indicated that while catfish odors elicited the greatest response (i.e., most tongue flicks), this result was not significantly different from several other prey odors, including that of a salamander, *Ambystoma talpoideum*, which has not been reported in the diet of *N. taxispilota*. Therefore, apparent "preferences" observed in this field study must be interpreted with caution, but I believe the evidence at hand strongly suggests that *N. taxispilota* is a piscivore with catfishes making up the majority of its diet (see below).

FORAGING INJURIES

Injuries sustained while foraging range from mild to fatal (e.g., Shine, 1986). Brown water snakes regularly consume fish with spines and mild venoms, and would therefore be expected to sustain occasional injuries. Given that *N. taxispilota* eat spined fish, one would expect that natural selection would mold the anatomy and behavior of this species to reduce the number of spine-related injuries and to lessen the effects of these injuries. I captured seven individuals with spines protruding through the body wall, which were not inconsequential injuries. Yet I know that at least one of these seven not only survived the injury, but lived at least another five years and grew about 42 cm. Three of these individuals had "old" spines, meaning the fish had been digested and the spine remained with no apparent infection or healing problems. In addition, many snakes had injuries that could have come from fish spines. This ability to deal with fish spines is not unique to *N. taxispilota*. Kofron (1978) found two *N. rhombifer* with spines protruding through the skin but otherwise healthy, and Shine (1986) captured five filesnakes (*Acrochordus arafurae*) with catfish spines penetrating the stomach wall, one of which had a spine penetrating through the body wall similar to the *N. taxispilota* described above. Might this ability to deal with catfish spines also allow these species to deal better with other wounds or toxins? A study of the brown water snake's healing and immune system is needed.

DIET

Because the number of different food items found can be a function of the number of stomachs sampled (Duever, 1967), one would expect to add new items as additional snakes are collected until all potential prey have been documented. Using the regression equation in Fig. 3.5, I would need to collect an estimated 1455 snakes before adding another (tenth) family, which I have already done without adding new prey items. Therefore, it appears I have more than adequately sampled the potential prey of *N. taxispilota* in this area, with the chance of adding new prey items to the list decreasing (Fig. 3.5).

I found *N. taxispilota* to be exclusively piscivorous. I recorded nine families of fishes in the diet, of which most were catfishes (Ictaluridae). Three new families of fishes were added to the published accounts for this species: Moronidae (temperate or sea basses), Lepisosteidae (gar; Mills and Hudson, 1995), and Aphredoderidae (the pirate perch). Although these are new families, the species involved might be considered ecological equivalents to species already reported in *N. taxispilota*'s diet. For example, Moronidae and Centrarchidae (sunfishes) can both be mid-water fishes, although temperate bass tend to inhabit more open water than most sunfishes. Lepisosteidae and Esocidae (pickerel) might be found in similar habitats and both often remain suspended in the water column as sit and wait predators. Finally, pirate perch (*Aphredoderus sayanus*: sole member of Aphredoderidae), which are abundant in the streams of the SRS but are rare in the Savannah River (Bennett and McFarlane, 1983), are usually found on the bottom in quiet pools and heavily vegetated backwater areas, a similar habitat of many ictalurids (e.g., yellow bullhead and tadpole madtom). Thus, slight differences in the diet may be explained by habitat (river vs. stream) and habitat-specific prey availability. In his survey of the diets of *T. elegans* and *T. sirtalis* at 22 sites, Kephart (1982) found that site (habitat) was a far better predictor of diet than was species. Greene et al. (1994) arrived at similar conclusions when comparing the diets of lake and riverine populations of *N. harteri*. Therefore, some brown water snakes, when foraging on the bottom, might consume whatever bottom-dwelling fish they encounter, be it a catfish, darter, or pirate perch.

It appeared, however, that *N. taxispilota* was selectively foraging on catfishes based on estimates of prey availability (Dean Fletcher, unpubl. data; Table 3.4). Based on the relative abundance of fish species sampled in UTR, *N. taxispilota* would be expected to eat sunfishes, pirate perch, catfishes, and minnows, in that order of abundance, but instead were found to eat almost four times the number of catfish and no minnows in this stream (Table 3.4).

This apparent specialization on catfishes is probably not a local-habitat phenomenon as reported for the diet in other species (e.g., *Thamnophis* sp, Kephart, 1982), rather it is appears to be a phylogenetically conserved trait because other populations (Camp et al., 1980) as well as the sister taxa, *N. rhombifer* (Mushinsky and Hebrard, 1977; Kofron, 1978), also specialize on ictalurids. Anecdotal evidence indicates that other populations of *N. taxispilota* may vary in their diet (Wright and Bishop, 1915; Collins,1980), but further study would be necessary to document this evidence. Laboratory studies should be conducted to test some of the predictions of optimal foraging (e.g., “optimum” search and handling time for the caloric intake) to determine why *N. taxispilota* consume catfish rather than other potential prey items. Other items included in the diet (e.g., centrarchids) may be “partial preferences” and included in the diet based on fluctuations in relative abundance (Pyke et al., 1977).

Other catfish specialists include the sea snake *Enhydrina schistosa*. Approximately 91% of their diet consisted of catfishes (Plotosidae and Tachysuridae) and like the present study (see below), their diet varied somewhat seasonally (Voris et al., 1978). Although not really a catfish specialist, juveniles and adult male *Nerodia harteri* were found to eat more catfish than expected based on quantitative samples of the prey available, and adult females also consumed large numbers (42% by occurrence) of catfishes (Greene et al., 1994). *Nerodia taxispilota’s* closest relative, *N. rhombifer*, also seems to be a catfish specialist, at least in some populations (e.g., Plummer and Goy, 1984). Preference for catfishes may be a phylogenetically conserved trait maintained by natural selection as some evidence exists that specialists may have shorter decision-making times and lower predation risks than generalists (Bernays, 1998).

Diet and feeding frequency (proportion with food) were statistically the same for males and females, but feeding frequency differed by month for males ($P<0.10$) but not females, with adult males 46% less likely than expected to feed during mating season.

Although female reproductive condition did not significantly affect feeding overall, gravid females near parturition were not captured with food, a finding similar to other viviparous species that eat little or nothing while gravid or in the weeks prior to parturition (e.g., *N. harteri*, Greene et al., 1994; *Agkistrodon contortrix*, Fitch, 1999; *Vipera* spp., Saint-Girons, 1979; *Thamnophis elegans*, Gregory and Skebo, 1998). Slightly over 14% of the *N. taxispilota* known to be gravid in this study had eaten, but only two of these had identifiable food items (both catfish) and both of these were consumed during the last week in June, relatively early in the pregnancies. Males may feed less frequently in the spring because they are devoting their time and energy to finding mates (Blanckenhorn et al., 1995) and females may not feed as they approach parturition because of the physical and energetic constrain associated with viviparity, and also because of the increased risk of predation (Seigel and Ford, 1987). Given that sometimes fish spines can penetrate the digestive and body walls, it seems plausible that there should be strong selective pressure against eating fish with spines (e.g., Ictaluridae and Centrarchidae) while gravid. It would be noteworthy to know if *N. taxispilota* alters its diet during pregnancy from the normal catfish prey to something without spines (e.g., suckers, Catostomidae).

Future research in the foraging ecology of *N. taxispilota* should include investigations on the effects of sexual dimorphism on foraging. Do larger snakes (i.e., females) eat larger prey items (Arnold, 1993), or do they select different types of prey? One measurement that would prove useful in answering this and other questions related to sexual dimorphism would be that of relative head sizes and shapes in conjunction with a more detailed study of prey types and sizes (Shine, 1993). Field studies such as the present that identify prey types are necessary before one can attempt laboratory experiments aimed at answering the more theoretical questions associated with optimal foraging, sexual selection, and habitat selection.

Sixteen percent of the captured *N. taxispilota* had food, and this did not differ between sexes nor between adults and juveniles. In a review of feeding frequency among 66 snake populations representing six families and 51 species, Shine (1986) found that the percentage of snakes with food ranged from 5-100% (mean = 49.8%, my calculation), although he later modified his low estimate of 5% for filesnakes, *Acrochordus arafurae*, to reflect the much higher feeding frequencies recorded during the wet season (24% of females and 38% of males contained prey; Houston and Shine, 1993). Whether these and subsequent findings suggest that some snakes are food limited or perhaps the low feeding frequencies are the result of these ectotherm's low energy requirements (or both) remains to be demonstrated (Mushinsky, 1987).

The relatively low frequency of feeding among SRS *N. taxispilota* may be related to the different energetic requirements of their semi-aquatic lifestyle. In order to test the potential effects of habitat on feeding frequency, I categorized the species presented by Shine (1986) as either aquatic or terrestrial and then used an arcsine transformation of the proportions (eq. 14.5 in Zar, 1984) to compare means. Using Shine's data, aquatic snakes fed less frequently (42.3%) than did terrestrial snakes (53.4%), although this difference only approached significance (Mann-Whitney U = 602.0, P>0.05). If we look at only aquatic and semiaquatic colubrid snakes in Shine's table, they range from 8% (*Homalopsis buccata*) to 98% (*Regina septemvittata*) compared with 22% (*Uromacer catesbyi*) to 98% (*Opheodrys aestivus*) for more terrestrial colubrids. Once again, using an arcsine transformation of the proportions presented in Shine (1986), I found that aquatic colubrids (41.6%, n=10) fed less frequently than terrestrial (54.0%, n=26), but this difference was not statistically significant (t = 1.116, df = 34, P>0.25). In addition to the above analyses, among the feeding frequencies reported for *N. taxispilota* (mean = 31%, range = 16-58%; Table 3.5) and for other *Nerodia* spp. presented in Shine's paper and elsewhere (mean = 39%, range = 18-69%; Table 3.6), the *N. taxispilota* in my study had the lowest feeding frequency (16%).

Although the above analyses were not robust tests and do not take into account many phylogenetic, geographic, ecological, or caloric (i.e., energy content of the food) factors, as stated previously these differences between aquatic and terrestrial snakes could suggest that either food is limited in aquatic environments, or more likely that energetic requirements are lower in aquatic environments. Locomotion in water requires less energy than that on land (Bennett, 1982; Lillywhite, 1987). While the energetics of swimming vs. terrestrial locomotion in snakes has not been studied, a comparison between the two forms of locomotion in the marine iguana (*Amblyrhynchus cristatus*) reveals that walking requires about 25% more energy than swimming (Bennett, 1982; Seymour, 1982). Thus, the relatively low feeding frequency in *N. taxispilota* may be related to its aquatic lifestyle as well as other factors (e.g., digestive efficiency, see Shine, 1986). Future studies might test this and other related hypotheses by measuring metabolic rates in the same species that differ geographically in habitat (e.g., *T. elegans* can be either semiaquatic or terrestrial depending on locality) or in closely related species that differ in habitat. Laboratory metabolic rates for *N. taxispilota* are 0.64 KJ/hr at 22C and 0.62 at 32C, compared to 0.74 and 0.51 for *N. sipedon* (Blem and Blem, 1990).

A weak negative correlation (r = -0.31, P<0.05) was found between the proportion of snakes captured with prey and the sample size in Shine (1986). In general, the larger the sample sizes, the smaller the proportion captured with food. This relationship has interesting implications for further comparative studies and should be investigated before further conclusions are drawn from the literature. When I split my data among years and calculated a cumulative proportion of snakes with prey, a correlation did not exist between sample size and proportion with food (r = 0.48, P>0.20). For example, after two years and 418 captures, the proportion with food was 16.7%, and after eight years and 1565 captures it was still about the same, 16.4%. Therefore, the differences seen in Shine (1986) are probably not a consequence of sample size.

The diet of *N. taxispilota* appeared to change slightly over time (Table 3.3). Environmental changes, community succession, and other changes over time may result in changes in the availability of prey (e.g., see Table 6 in Fitch, 1999). This type of temporal change has been documented in other natricine snakes (Kephart and Arnold, 1982; Seigel, 1996; Fitch, 1999). A Missouri population of *Thamnophis radix* changed from a diet of earthworms to frogs as newly metamorphosed *Rana* sp. became available in the summer (Seigel, 1996). Kephart and Arnold (1982) found that the diet of *T. elegans* changed from year to year depending on climatic conditions and corresponding prey availability. Fitch (1999; see Tables 85 and 86 therein) documented dramatic changes, both seasonally and yearly, in the diet of his Kansas populations of *T. sirtalis*. However these and other studies on *Thamnophis* deal primarily with amphibian-eating species. Amphibian populations, especially those that breed in ephemeral waters, are more likely to change from year to year (e.g., Pechmann et al., 1991) whereas fish populations in permanent waters (e.g., the spring-fed rivers and streams of the SRS) are more likely to remain relatively constant. My observed seasonal and yearly changes were relatively slight compared to those mentioned above, and could be the result of sampling effort in each study site (e.g., pirate perch were more common in the UTR Creek samples).

Behavioral factors of the prey may influence the diet of *N. taxispilota* and other snakes. Prey fishes can often recognize predators and adjust their behavior to avoid them (Helfman, 1986). For example, in a laboratory experiment with the sea snake, *Enhydrina schistosa* (Voris et al., 1978), puffers watched the snakes when the experimental tanks were lighted, actively avoiding the snakes. When the holding tanks were dark, the puffers would lie on the bottom, making them more vulnerable to predation. Feeding frequency on these puffers was reflected in this behavior, as these snakes consumed about 30% more puffers in the dark tanks (Voris et al., 1978). Similar predator-prey interactions may occur with *N. taxispilota*. Individuals may be more successful at capturing particular types of prey during certain times of the day or night (e.g., catfishes during the day).

In examining the diet of any animal one must be aware of the possibility of secondarily ingested food items. For example, Neill and Allen (1956) suggested that reports of frogs in the diet of *N. taxispilota* (e.g., *Hyla cinerea*, Appendix 3.1) might have been items secondarily ingested via catfish. If Fitch’s technique is used, most secondarily ingested items probably would fall into my unidentified category. I did find one leaf in a *N. taxispilota* and I have seen two undigested water beetles in their feces, however I would not suggest that either of these are actual or “normal” food items. Even if some of the food items identified were secondarily ingested, it seems clear from the present study and other published and unpublished studies that *N. taxispilota* primarily consumes catfish, especially once they reach a SVL of 60 cm (Fig. 3.1 & 3.3). Its western counterpart and close relative, *N. rhombifer,* also seems to specialize on fish and catfish (Mushinsky and Hebrard, 1977; Kofron, 1978; Plummer and Goy, 1984), indicating, as stated previously, that this may be a phylogenetically conserved trait or preference. One method of testing such a genetically determined preference is to test naive snakes with chemical cues (i.e., prey odors, Burghardt, 1968; review in Halpern, 1992). This type of study was conducted with neonate *N. taxispilota,* and the results were inconclusive (Mills, unpubl.).

Although strong evidence exists for a thermophilic response to feeding in snakes (Peterson et al., 1993), I found no significant relationship between presence of food and basking conditions. One explanation for this apparent contradiction is that brown water snakes are selecting warmer substrates without selecting more exposed substrates. That is, depending on the time of year, they may be able to reach the required body temperature by simply exiting the water or they may select a perch site that was recently exposed or higher above the water and thus warmer than other potential perch sites. Air temperatures in the shade can vary by as much as 5.6ºC over a distance of 1 cm to 100 cm above the water, and this can vary depending on other factors such as water temperature, wind, and sunlight (Mills, unpubl. data).

DIET SHIFT

Ontogenetic diet shifts have been observed in species of the families Colubridae, Viperidae, and Elapidae (Mushinsky, 1987). I observed a shift in the diet of *N.*

taxispilota from several families of fishes to a diet of catfishes at length of about 60 cm. A similar ontogenetic dietary shift has been reported for *N. taxispilota*'s western counterpart, *N. rhombifer*, and other *Nerodia*. Kofron (1978) found that a variety of fish species were found only in young and subadult *N. rhombifer,* and those greater than 85.0 cm "commonly" contained *Ictalurus* sp. and some *Mugil* sp., but he reported catfishes in both juvenile and adult *N. rhombifer*. Plummer and Goy (1984) observed a shift of importance in their fish hatchery population of *N. rhombifer* from minnows and centrarchids to catfish at 50-70 cm. Feaver (1977) reported that juvenile *N. sipedon* fed exclusively on small fish and larger individuals (>30 cm) fed on minnows in spring, switching to amphibians in summer and fall. Similarly, Mushinsky et al. (1982) found two species (*N. erythrogaster* and *N. fasciata*) which changed from a diet of fish to frogs at around 50 cm, and two species (*N. cyclopion* and *N. rhombifer*) that ate fish throughout their lives but changed the size or species on which they fed as they grow. Mangrove watersnakes (*Nerodia fasciata*) also ate fish throughout their lives, but switched from the smaller *Fundulus* sp. to the much larger *Tilapia* sp. as they grew (Miller and Mushinsky, 1990). Greene et al. (1994) observed that adult *N. harteri* have a more diverse diet than the young, switching from a diet of primarily minnows to one that included minnows, catfishes, sunfishes, and gizzard shad. Although my population of *N. taxispilota* changed to an almost exclusively catfish diet at 60 cm, all size classes were found to feed on catfishes (Fig. 3.3A).

Godley (1980) found that *Regina alleni* had a diet shift from odonates (dragonfly larvae) to crayfish at 200-300 mm SVL. He also found that the young tracked the seasonal availability of prey whereas the adults fed selectively. Greene et al. (1994)

found a similar trend in *N. harteri*. Neonate *N. harteri* consumed prey in proportion to its availability, juveniles and adult males consumed more catfish than expected, and adult females ingested fewer minnows than expected. The observations of Greene et al. (1994) may be applied to the type of diet shift seen in the present study. Because of greater energetic requirements, young *N. taxispilota* may be less selective, eating whatever passes by (i.e., ingesting prey in proportion to its availability). Godley states (p. 429), "Under natural conditions the energetic costs of handling a prey are minor compared with the costs of searching for another, thus all prey encountered should be eaten," and Mushinsky et al. (1982) state, "The responses of young snakes in the field seem to be governed more by prey size and apparent availability rather than a preference per se." Godley supports his idea using Pough's (1977) work on ontogenetic differences in endurance and thus prey handling and search time. The difference in endurance between small and large individuals may be accentuated in a riverine environment due to the strong currents. Large snakes, because of their greater endurance, may be able to forage actively for large food items (catfish) whereas small snakes may be relegated to a sit and wait type of foraging and thus be restricted in the habitat and types of food they encounter.

Although shifts in habitat or other resource use are often attributed to competition (Schoener, 1975), I suggest that in the present study it may be the physical structure of the habitat that is the cause of the diet shift. That is, in rivers and streams, it is not energetically feasible for small snakes to forage actively in the same areas as the larger snakes, as the larger snakes may be foraging in deeper water (Shine, 1993). Deeper, open water areas also harbor large fish which may prey on small snakes. Prey preference experiments might be used to address possible differences in diet between size groups. One could offer different food items to both young and old snakes to see if there is an ontogenetic change in preference or handling time.

Pough (1977, 1978) has demonstrated an ontogenetic increase in endurance *in N. sipedon* and *Thamnophis sirtalis*, and suggested that these differences in endurance may be reflected in ecological differences (e.g., prey selection, habitat use) between young and old snakes. He found that adult *N. sipedon* have 8 times the endurance of young and suggested changes in prey selection may be traced to these endurance differences, but provided no data to support this contention. He also found that adult garter snakes have a greater ability to deliver oxygen to their tissues and have an increased capacity for aerobic and anaerobic energy production (Pough, 1977). Water temperature could accentuate these differences; that is, small snakes would become colder faster when foraging in the river rather than in warmer, shallow, sheltered areas.

As stated above, the shift from multiple species and families to one as brown water snakes grow may be indicative of a concurrent change in habitat (Mushinsky et al., 1982). Like *N. rhombifer* and *N. cyclopion* (Mushinsky et al., 1982), *N. taxispilota* may change from shallow water foraging to deeper water as they grow. Sunfish, minnows, temperate bass and gar all tend to be midwater fish while catfish, darters, pirate perch and suckers are usually bottom dwellers. Thus, larger snakes may be foraging in a different location than the young individuals. Small *N. taxispilota* are usually found near the water's edge in a slightly different habitat than larger snakes (pers. obs.). On multiple occasions I have observed the same feeding behavior as Richmond (1944); that is, *N. taxispilota* swim to shore from mid-river with a fish grasped midbody, indicating that the prey were captured out in the river. These observations were always of large individuals, indicating they forage out in the river, capture the fish, and swim to shore to eat it. There is little mid-river structure to hang onto. Smaller snakes on the other hand may forage near shore, anchoring to an object and thus capturing fish as they pass by. Also, smaller fish are less likely to be available in the deeper portions of the river.

My observations and data, coupled with the references above, support the hypothesis that juvenile and adult *N. taxispilota* partition the resources (i.e., food and habitat), possibly reducing intraspecific competition. I offer several hypotheses for the observed shift in diet and its ecological and evolutionary significance: 1) reduced competition, both inter- (discussed below in *Community Ecology*) and intraspecific, 2) concurrent habitat shift, and 3) optimal foraging and prey availability. Why would *N. taxispilota* specialize on catfishes? Are there other species that live in similar habitats that would be "easier" to capture and consume (e.g., suckers)? A laboratory experiment examining capture and handling times for different prey species seems warranted, although it is often difficult to get *N. taxispilota* to feed consistently in captivity (pers. obs.; Scott Paff, River Banks Zoo, Columbia, SC, pers. comm.).

PREY DIVERSITY AND COMPARISON OF TECHNIQUES

In her review of ecological diversity measurements, Magurran (1988) stated, "There is little consensus on the best diversity measure to use and no index has received the backing of even the majority of workers in the field." Because selection of the most appropriate diversity measures continues to be debated (e.g., Bulla, 1994), I attempted to compare the diet of *N. taxispilota* both intra- and interspecifically using various measures of diversity. I present a variety of measures, including those commonly or historically used (e.g., H’), those recommended by Magnurran (e.g., α), and finally two relatively new indices (E and D, Bulla, 1994; Table 6). When diet diversities were compared, my population fell within the published range for *Nerodia* spp. regardless of which measure I used. However, when populations of *N. taxispilota* were compared statistically, the choice of index determined the significance of the conclusions drawn. When comparing my population to a Georgia population (Camp et al., 1980), I found significant differences using Simpson’s diversity index (D_s) but not Shannon’s diversity index (H’), illustrating the problems encountered with choice of appropriate indices. Outside of any statistical conclusions regarding diversity of prey items in the diet, *N. taxispilota* seems to be a fish specialist throughout its range.

Long-term studies are necessary if we are to understand ecological and evolutionary phenomena (Gibbons, 1990), to discern natural variation from human-caused declines in populations (Tinkle, 1979; Magnuson, 1990; Pechmann et al., 1991), and to document among year differences in diet (Kephart and Arnold 1982; Fitch 1999). In addition, one can draw erroneous conclusions based on short-term studies or data collected at only one site or time period (e.g., Shine, 1986; Houston and Shine, 1993). Because this was part of a mark-recapture population study, and I plan to monitor this population over an extended period, sacrificing the number of animals required to obtain accurate dietary information was not an option. I gauged my success by comparing my data with other data collected through sacrificing *N. taxispilota* (Appendix 3.1). When these two sets of data were compared, the slopes of the regression lines were significantly different (Fig. 3.5), indicating that I had to collect far more individuals to arrive at the same conclusions. Camp et al. (1980) collected and sacrificed 96 *N. taxispilota* and identified 4 families of prey, compared with 132 individuals in the Gibbons/Semlitsch study (Appendix 3.1) and 200 captures in my study; although I recorded my fourth family after only 86 captures at my Sav-a study site (Table 3.7). Thus, I had to almost double my effort to collect the same information collected by Gibbons and Semlitsch. Also, in using Fitch's technique, I have potentially sacrificed valuable information. That is, my "unknown" category was relatively large (Table 3.5). Based on the observed restrictive diet of *N. taxispilota*, and data from sacrificed individuals from the same area, unidentified items in my study were probably fish. I could have returned all regurgitated material to the laboratory for detailed observation (e.g., Greene et al., 1994), however it appears the additional information (and labor) would not have added to the list of prey in the diet of *N. taxispilota*.

PREY SIZE

Maximum prey size has evolutionary (Greene, 1983; Arnold, 1993), ecological, and theoretical (Arnold, 1983, 1993; Schoener, 1971) importance for snakes. My observations concerning maximum prey size for *N. taxispilota* (27-35% of snake mass) are particularly noteworthy because they are larger than is typical for colubrids, except for brown tree snakes, *Boiga irregularis*, which are capable of consuming prey up to 70% of their body mass (Rodda et al., 1997). It is generally accepted that viperids consume much larger prey than other snakes (Mushinsky, 1987), and Pough and Groves (1983) experimentally determined maximum prey sizes for groups of non-vipers (18.4%) and vipers (36.4%). I know that my 35% figure is actually low because the individual that consumed this fish had been digesting it for at least one day, therefore *N. taxispilota* may be capable of consuming prey items of the magnitude previously thought possible only for viperids. Is the consumption of large prey possible because of morphological adaptations similar to viperids (e.g., quadrate and mandible length), or is it related to the ecology of this species (e.g., aquatic habitat) or both? Aquatic species, presumably because of the lessened effects of gravity, are often morphologically similar to viperids (e.g., heavy bodied) and thus might be expected to consume prey of a size similar to that taken by viperids. There may also be a phylogenetic component to this scenario within the water snakes. Mushinsky et al. (1982) found that *N. rhombifer*, *N. taxispilota*'s sister species, also consumed large prey. They found that the average prey item consumed by *N. rhombifer* was significantly larger than that ingested by *N. erythrogaster* and *N. fasciata* in the same habitat. Following these lines of reasoning, one might expect other similarities between aquatic snakes and viperids. For example, do they feed with similar frequency? If we examine Shine's (1986, Table 3.5) summary of feeding frequency in snakes, we find that on average aquatic colubrids feed less frequently (proportion of snakes with food, 41.6%, n = 10) than snakes of the family Viperidae (56.9%, n = 18). The suggested similarities between *Nerodia sp.* and other aquatic snakes and viperids are an intriguing premise that deserves further investigation.

Arnold (1993) reviewed studies where prey size was related to snake size and found that in all cases larger snakes tended to eat larger prey, although this is not universal. For example, in a field study there was no significant tendency for larger blacksnakes, *Pseudechis porphyriacus*, to eat <u>heavier</u> prey (Shine, 1991), but they did consume <u>longer</u> prey (Shine, 1977). In an apparent contradiction to the field study, a laboratory study found that maximum mass of prey items increased significantly with blacksnake size (head length), but this difference may be due to the foraging habits of blacksnakes (i.e., prey items are usually take from crevices, Shine 1991). Similar to Shine (1991), my results also suggest a contradiction to Arnold's stated trend. I found small *N. taxispilota* consuming prey items that were nearly as large (proportionally) as the largest snake (33% vs. 37% of snake mass). In addition to the proposed relationship between prey size and the snake's aquatic habits, this apparent contradiction may be partially the result of how prey size is measured; that is, my measurements are of prey mass vs. snake mass whereas most of the studies reviewed by Arnold are for prey length or volume. As Shine (1991) demonstrated (mass vs. length of blacksnake prey items), how you measure prey size can influence the conclusions.

HABITAT USE

As the quote at the beginning of this paper indicates, diet is an important component in determining where and when a particular species is found. On the SRS, *Nerodia taxispilota* are found where there are fish (Gibbons and Semlitsch, 1991). I have discussed their use of habitat and its relation to diet earlier in this paper (see Diet Shift). Other studies with snakes have shown a relationship between habitat use and foraging, specifically the selection of foraging sites through the use of chemical stimuli. An extensive literature has developed concerning the importance of chemical cues in many aspects of the ecology of squamate reptiles, including habitat selection and use (see reviews in Mason, 1992, and Halpern, 1992).

Do *N. taxispilota* choose foraging sites based on chemical cues? In a series of field and laboratory experiments, Duvall and coworkers (1990a, 1990b) demonstrated the importance of prey-based olfactory cues for habitat use in *Crotalus viridis*, and a similar relationship between chemical/olfactory cues and habitat selection was recently reported for another rattlesnake, *Sistrurus miliarius* (Roth et al., 1999). This relationship between diet and habitat selection has also been demonstrated in laboratory experiments with natricine snakes (e.g., *Thamnophis*, Lyman-Henley and Burghardt, 1994), including *Nerodia* (Allen et al., 1984). I conducted a laboratory experiment to determine if naive (i.e., newborn) *N. taxispilota* have an intrinsic preference for fishes and specifically catfishes (Mills, unpubl.). The results, while not conclusive, indicate that they can discriminate between the chemical odors of different prey species, and seem to prefer fish over amphibian odors. Future research in this area of relating food preferences to habitat choice should focus on field experiments similar to those conducted by Roth et al.(1999) on the terrestrial *S. miliarius*, but this may prove difficult for species such as *N. taxispilota* that forage in the water.

Community Ecology

As stated in the introduction, snake communities and niche relationships are interrelated with prey communities (Vitt, 1987) and snake species density and diversity are related to prey types and density (Arnold, 1972). *Nerodia taxispilota* is the most piscivorous snake in the study area and the data indicate it is a catfish specialist (this study; Camp et al., 1980; Ernst and Barbour, 1989). These findings may be viewed as important from two non-exclusive perspectives. First, from a community ecology perspective, *Nerodia taxispilota*'s restrictive diet may reduce intra- and interspecific competition within the snake community (Brown and Parker, 1982; Fitch, 1982; Toft, 1985; Mushinsky 1987) or *N. taxispilota* may be utilizing a relatively unused resource (i.e., an “open” niche). In terms of intraspecific competition, because of the diet shift, they may change trophic levels as they mature (Mushinsky, 1987; Godley, 1980). In terms of interspecific competition, the proposed preference for fish, especially catfishes, sets the brown water snake apart from other aquatic or semi-aquatic snakes (and for that matter, most other vertebrates) in this area. At least three other semi-aquatic snakes occur commonly in the Savannah River at the SRS (listed in order of relative abundance based on captures): *N. erythrogaster*, *N. fasciata*, and *Agkistrodon piscivorus*.

The diet of *N. erythrogaster* varies greatly. They have been reported to ingest fish (Wright and Wright, 1957), but eat primarily amphibians (Mushinsky and Hebrard, 1977; Ernst and Barbour, 1989). Minton (1972, cited in Ernst and Barbour, 1989) suggested the abundance of amphibians in their diet was related to their choice of ephemeral wetlands, but even in areas of permanent water where fish are abundant (i.e., the Savannah River) it is rare to find a fish in a *N. erythrogaster* (usually toads and frogs, pers. obs., although David Scott, pers. comm., removed 4 bluegills from an individual in the Savannah River swamp).

Fish are also reported in the diet of *N. fasciata* (Ernst and Barbour, 1989), however, similar to *N. erythrogaster*, they seem to select amphibians in this area (pers. obs.). Also, evidence exists for an ontogenetic switch from fish to frogs in this species (Mushinsky and Lotz, 1980; Mushinsky et al., 1982).

Nerodia floridana will eat frogs, fish, and salamanders (in that order; Ernst and Barbour, 1989), but is rarely found on the SRS in sympatry with *N. taxispilota*. They prefer lentic rather than lotic waters (Gibbons and Semlitsch, 1991), and I have never observed a green water snake in any of my collection areas on the SRS (Savannah River, Upper Three Runs Creek, and Steel Creek).

Of the other semi-aquatic snakes on the SRS (*Agkistrodon piscivorus*, *Farancia abacura*, *F. erytrogramma*, *Regina rigida*, *R. septemvittata*, and *Seminatrix pygaea*), only *A. piscivorus, F. erytrogramma* and *S. pygaea* are known to regularly ingest fish. *Farancia erytrogramma* eats primarily freshwater eels (Ernst and Barbour, 1989), *S. pygaea* will consume mosquito fish if available (*Gambusia affinis*; Seigel et al., 1995), and *A. piscivorus* will eat almost anything, including ictalurids (Ernst and Barbour, 1989), although is rarely found in my Savannah River study sites in sympatry with *N. taxispilota* (about 1% of snakes sampled; Mills, unpubl. data).

Based on published accounts and personal observation, little dietary overlap exists between *N. taxispilota* and other semi-aquatic snakes of the Savannah River. Therefore, it seems that this predator-prey system could be genetically fixed (Mushinsky and Lotz, 1980) . The results of my studies lend support to this idea. Also, this proposed genetically fixed preference for fish, especially catfish, may be a phylogenetically conserved trait as *N. taxispilota*'s nearest relative, *N. rhombifer*, is also piscivorous and consumes catfish (Ernst and Barbour, 1989).

Toft's (1985) review of the literature revealed that rather than habitat, food was the most important partitioned resource for snakes and in Vitt's (1987) review of snake communities he stated, "The underlying cause of the apparent latitudinal, elevational, and/or habitat patterns in snake species density appears best explained on the basis of the number and abundance of prey types available." Therefore, if we are to understand the assemblage of snake communities as well as the larger communities and ecosystems in which they live, we must understand not only what they eat, but also what prey is available. A neglected component of foraging ecology studies, and resource partitioning studies in general, is a quantitative description of the available prey (Scott and Campbell, 1982). Most studies of diet and foraging ecology in snakes have failed to document prey availability, although there are notable exceptions (Reynolds and Scott, 1982; Platt, 1984; Greene et al., 1994). The fish samples taken from UTR Creek (Table 3.5) show what prey are available to *N. taxispilota* in this habitat, but as I stated earlier, it is not feasible to collect a comparative sample of the prey-base from the much larger and deeper Savannah River. This is not a unique problem to this study as Vitt (1987) was unable to locate a snake study that adequately addresses the question of limiting prey abundance; he attributed this dearth of information to quantitative sampling problems. Nevertheless, I believe the UTR data support the hypothesis that *N. taxispilota* is not eating fish in proportion to their availability and therefore is somehow selecting certain prey items over others.

The second reason my findings are important in an area such as the SRS is because their primary prey, catfish, tend to live and forage in and near the sediments, and at and near the SRS (and for that matter in many areas) these sediments are depositories of radioactive isotopes (Whicker et al., 1990) and other contaminants (e.g., mercury; Anonymous, 1996; Williams, 1998). These isotopes, primarily cesium, are relatively inert if left in these benthic sediments (Whicker et al., 1990). Brown water snakes could serve as a link between these benthic contaminants and the terrestrial environment via their consumption of ictalurids and could aid in the movement of contaminants from one site to another either via their own movements or through the movements of their predators. For example, *N. taxispilota* might eat contaminated catfish and then be consumed by a bird (e.g., red-shouldered hawk, *Buteo lineatus*, barred owl, *Strix varia*, or great blue herons, *Ardea herodias*, all common in the SRS area and potential snake predators), raccoon (*Procyon lotor*), or feral pig (*Sus scrofa*) which in turn can transport the contaminants to other systems (see Bildstein et al., 1992). In addition to describing which toxins *N. taxispilota* carry, future studies must concentrate on the predators as well as the prey of *N. taxispilota* to document if this hypothesized link is significant.

Finally, I will comment on the importance of the diet and foraging ecology of *N. taxispilota* in relation to man. Of the snakes on the SRS, only *N. taxispilota* is exclusively piscivorus and eats primarily catfishes. While no quantitative studies have been carried out, it appears that there is little dietary overlap between *N. taxispilota* and other members of the snake community. Furthermore, catfish as a food source may be a relatively untapped resource in this community as a whole. What other non-ophidian organisms consume catfish, especially in the proportions documented in my study? There is one organism that consumes catfish, man. It is well documented that the fish of the Savannah river contain various contaminants (e.g., mercury) that are known to be harmful to man. Fish consumption advisories are routinely posted by the public health agencies of both Georgia and South Carolina (Anonymous, 1996; Williams, 1998). On a practical level, it is important to know how these toxins are moved within and between ecosystems, and *N. taxispilota* is one species that may play a role in these movements. Current research by Chuck Jagoe's laboratory at SREL is looking into the role of *N. taxispilota* as a carrier of mercury in the system.

In summary, *N. taxispilota* was found to be piscivorous, with catfishes (Ictaluridae) comprising 63% of the identifiable food items in its diet. Individuals were observed using both sit-and-wait and active foraging to locate and capture prey.

Although all size classes consumed catfishes, smaller individuals were captured with a broader range of food items than adults. Males and females were captured with food in approximately the same frequencies, however females near parturition ceased feeding and adult males fed less during mating season. Fitch's nonlethal technique (forced regurgitation) proved to be more labor intensive, yet satisfactory for long-term mark-recapture studies such as the present. *Nerodia taxispilota* is the only completely piscivorous snake on the Savannah River that consumes catfishes, making it a potentially useful candidate for tracking the uptake and transport of toxins (e.g., mercury) within the aquatic environment and between the aquatic and terrestrial ecosystems.

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Table 3.1 - Prey found in the stomachs of 253 *Nerodia taxispilota*[1] captured at all sites on the SRS, ordered from high to low frequency of occurrence (N) for identified prey, and related to the size of the snakes containing these prey items.

Sex	Prey (Family)	N	Mean SVL ± SD (cm)	SVL Range (cm)
Combined	Catfish[2] (Ictaluridae)	99	65.9 ± 21.8	27.5 – 133.0
	Sunfish[3] (Centrarchidae)	8	68.8 ± 10.2	50.0 – 82.0
	Minnow (Cyprinidae)	8	37.2 ± 8.2	26.5 – 51.6
	Temperate Bass (Moronidae)	7	41.8 ± 8.3	34.5 – 54.1
	Darter (Percidae)	7	36.4 ± 5.3	31.2 – 46.3
	Pirate Perch (Aphredoderidae)	6	32.6 ± 5.9	26.2 – 43.0
	Madtom (*Noturus*; Ictaluridae)	5	37.4 ± 9.9	24.1 – 48.0
	Sucker (Catostomidae)	2	101.3 ± 15.9	90.0 – 112.5
	Bass (*Micropterus*; Centrarchidae)	1	58.0	
	Gar (Lepisosteidae)	1	53.0	
	Pickerel (Esocidae)	1	48.5	
	Fish (unidentified spp.)	23	66.0 ± 21.5	24.7 – 100.5
	No ID	87	69.1 ± 27.0	25.2 – 113.0
Female	Catfish[2] (Ictaluridae)	54	69.0 ± 25.7	27.5 - 133.0
	Sunfish (Centrarchidae)	5	73.4 ± 8.1	61.7 – 82.0
	Darter (Percidae)	4	38.0 ± 6.2	31.2 - 46.3
	Temperate Bass (Moronidae)	3	38.8 ± 2.5	36.0 - 40.8
	Minnow (Cyprinidae)	3	30.6 ± 4.9	26.5 - 36.0
	Madtom (*Noturus*; Ictaluridae)	2	34.3 ± 0.4	34.0 - 34.6
	Sucker (Catostomidae)	2	101.3 ± 15.9	90.0 - 112.5
	Pickerel (Esocidae)	1	48.5	
	Pirate Perch (Aphredoderidae)	1	35.3	
	Fish (unidentified spp.)	12	68.8 ± 24.7	24.7 - 100.5
	No ID	56	76.2 ± 28.7	25.3 – 113.0
Male	Catfish[2] (Ictaluridae)	45	62.3 ± 15.4	29.5 - 82.4
	Minnow (Cyprinidae)	5	41.1 ± 7.3	35.0 - 51.6
	Pirate Perch (Aphredoderidae)	5	32.1 ± 6.4	26.2 – 43.0
	Temperate Bass (Moronidae)	4	44.1 ± 10.8	34.5 - 54.1
	Darter (Percidae)	3	34.4 ± 3.7	32.0 - 38.7
	Madtom (*Noturus*; Ictaluridae)	3	39.5 ± 13.4	24.1 – 48.0
	Sunfish[3] (Centrarchidae)	3	61.1 ± 9.7	50.0 - 67.5
	Bass (*Micropterus*; Centrarchidae)	1	58.0	
	Gar (Lepisosteidae)	1	53.0	
	Fish (unidentified spp.)	11	63.0 ± 18.1	31.8 – 91.0
	No ID	31	56.3 ± 17.8	25.2 - 86.3

1 – Four individuals, 2 with catfish and 2 No ID, were omitted from the table because of lack of appropriate measurements. Two individuals are represented twice in this table: the 73.8 cm female with a catfish and sunfish, and the 48.0 cm male with a madtom and unidentified fish, thus giving a total of 255 rather than 253.

2 – "Catfish" includes all catfishes (*Ictalurus*, *Ameiurus*, and *Pylodictis*) other than madtoms.

3 – "Sunfish" does not include the black basses (*Micropterus* sp.).

Table 3.2 - A) Percent of captured *Nerodia taxispilota* with food for each of the four major study sites (for a map, see Gibbons and Semlitsch, 1991), and B) percent with food each year for the primary study site: Savannah River downstream from UTR creek to Four-Mile Creek (Year 1998 was omitted because of low sample sizes).

A

Capture Site	Abbreviation Used in the Text	Number Captured	Number With Food	Percent With Food*
Savannah River near Upper Three Runs Creek (UTR)	SAV-a	978	171	17.5%
Savannah River near Steel Creek	SAV-b	183	29	15.8%
UTR Creek near AEL[1]	UTR-a	188	38	20.2%
UTR Creek near mouth (Sav. R.)	UTR-b	69	14	20.3%

1 – Aquatic Ecology Lab., located where SRS Rd C crosses UTR creek

*Not significantly different between sites: $\chi^2 = 1.291$, df = 3, $P > 0.50$.

B

Site	Year	Number Captured	Number with Food	Percent with Food*
Savannah River "a"	1991	60	8	13.3%
	1992	227	42	18.5%
	1993	128	25	19.5%
	1994	51	10	19.6%
	1995	147	30	20.4%
	1996	112	19	17.0%
	1997	58	7	12.1%
Total		783	141	18.0%

* Not significantly different between years: $\chi^2 = 3.257$, df = 6, $P>0.75$

Table 3.3 - Monthly (A) and yearly (B) variation in the relative frequencies (%) of different prey families consumed by *Nerodia taxispilota*. The categories “No ID” and “fish” were combined.

A.

	Month*							
	March	April	May	June	July	August	Sept.	Oct.
Prey Types	N=4	N=25	N=21	N=65	N=50	N=60	N=23	N=11
Ictaluridae	50.0	28.0	47.6	32.3	52.0	45.0	52.2	9.0
Centrarchidae	25.0	8.0			2.0	3.3	8.7	9.0
Cyprinidae				4.6	2.0	6.7		
Moronidae					2.0	10.0		
Percidae		4.0		1.5	4.0	3.3	4.3	
Aphredoderidae		4.0		4.6				18.2
Catostomidae		4.0					4.3	
Lepisosteidae				1.5				
Esocidae				1.5				
No ID./Fish	25.0	52.0	52.4	53.8	38.0	31.7	30.4	63.6

*Observed prey types differ significantly by month (χ^2 = 109.902, df = 77, P<0.01), but because of the large number of expected values < 5, this chi-square value is biased and therefore statistically meaningless (Zar, 1984).

B.

	Year*							
	1991	1992	1993	1994	1995	1996	1997	1998
Prey Types	N=21	N=50	N=29	N=32	N=67	N=43	N=12	N=5
Ictaluridae	52.4	42.0	31.0	43.8	43.3	30.2	50.0	60.0
Centrarchidae		2.0		6.3	3.0	9.3		
Cyprinidae		4.0	10.3	3.1	1.5	2.3		
Moronidae	14.3	6.0	3.4					
Percidae		4.0	3.4	3.1	1.5	4.7		
Aphredoderidae				3.1	1.5	9.3		
Catostomidae					1.5	2.3		
Lepisosteidae			3.4					
Esocidae							8.3	
No ID./Fish	33.3	42.0	48.3	40.6	47.8	41.9	41.7	40.0

*Similar to Table 3.3A, observed prey types differ significantly by year (χ^2 = 97.239, df = 66, P<0.01), but because of the large number of expected values < 5, this chi-square value is biased and therefore statistically meaningless (Zar, 1984).

Table 3.4 - Fish families collected[1] (May 1994 and 1995) by electroshocking at 10 sites, each 15-20m long, in UTR Creek about 1.6 km upstream of Box Landing, SRS, Aiken, Co., SC, compared with proportions of each family consumed at UTR study sites.

Family	No. of Species	Total Specimens	Percent Available (Expected)	Percent Eaten[2] (Observed)	Observed/ Expected[3]
Centrarchidae	8	139	22.1%	11.1%	0.5
Aphredoderidae	1	127	20.2%	18.5%	0.9
Ictaluridae[4]	5	104	16.5%	59.3%	3.6
Cyprinidae	7	104	16.5%	0	
Percidae	6	61	9.7%	3.7%	0.4
Esocidae	2	44	7.0%	3.7%	0.5
Anguillidae	1	36	5.7%	0	
Poeciliidae	1	8	1.3%	0	
Catostomidae	3	4	0.6%	3.7%	5
Lepisosteidae	1	1	0.2%	0	
Amblyopsidae	1	1	0.2%	0	
Umbridae	1	1	0.2%	0	
Totals	37	630			

1 –Dean Fletcher, Savannah River Ecology Lab, unpublished data.

2 –Data from UTR Creek only; includes only identified fish (n = 27).

3 –Calculation based on observed and expected frequencies, not percentages.

4 –Includes madtoms (*Noturus*)

Table 3.5 - Percent* occurrence of food items in the diet of Savannah River Site (SRS) populations of *N. taxispilota* compared with other populations[1].

	This Study SRS (n=1566)	Gibbons [2] SRS (n=135)	Camp et al. (1980) (n=96)	Collins (1980) (n=16)	Wright and Bishop (1915) (n=11)
Prey Items	% Occurrence				
Ictaluridae	41.2	29.4	32.1	25.0	
Centrarchidae	3.5	5.9	19.6	75.0	33.3
Cyprinidae	3.1		10.7		
Moronidae	2.7				
Percidae	2.7		7.1		
Aphredoderidae	2.3				
Catostomidae	0.8				
Lepisosteidae	0.4				
Esocidae	0.4	11.8			
Unident. Fish	8.9	44.1	5.4		33.3
Frog (*Rana* sp.)					33.3
Frog (*Hyla* sp.)		2.9			
Unidentifiable	34.8	5.9	26.8		
No. with food	257	34	56	4	3

*Total Percent may be over 100 because some snakes had more than one food item.

[1] All studies except the present dissected the snakes.

[2] Unpublished data from snakes collected from various localities throughout the SRS (see Appendix 3.1).

Table 3.6 - Diversity of food items in diet of *Nerodia taxispilota* compared with other *Nerodia* sp. See text for the computation and interpretation of H', J', 1- J', α, D_s, E and D. Simpson's measure of dominance (l) can be back-calculated using 1 - D_s. The category "Groups (k)" is equivalent to species richness (S), and in the following table is the number of families of food items.

Species	Location	Groups (k)	H'	J'	1- J'	α	D_s	E	D
N. taxispilota[1]	SC/GA	9	0.483	0.506	0.494	2.114	0.470	0.269	2.420
N. taxispilota[2]	SC	4	0.465	0.773	0.227	1.650	0.618	0.410	1.641
N. taxispilota[3]	GA	4	0.537	0.891	0.109	1.117	0.691	0.638	2.552
N. cyclopion[4]	LA	4	0.198	0.329	0.671				
N. cyclopion[5]	LA	10	0.655	0.655	0.345				
N. rhombifer[4]	LA	7	0.416	0.492	0.508				
N. rhombifer[5]	LA	15	0.900	0.765	0.235				
N. erythrogaster[4]	LA	4	0.409	0.679	0.321				
N. fasciata[4]	LA	5	0.458	0.656	0.344				
N. fasciata[6]	FL	5	0.557	0.797	0.203				

1 - This study; 2 - Unpublished data, Appendix 3.1; 3 - Camp et al. (1980); 4 - Mushinsky and Hebrard (1977); 5- Kofron (1978); 6 - Miller and Mushinsky (1990).

Table 3.7 - The addition of new food items with number of captures for the entire dataset and for the primary study site (site “a”). See also Fig. 3.5.

Food Item	Primary Study Site (Sav-a)		All Study Sites Combined	
	# of captures	% of total captures	# of captures	% of total captures
Catfish (*Ictalurus*)	18	2%	2	0.1%
Bass (*Morone*)	16	2%	28	2%
Sunfish (*Lepomis*)*	68	9%	177	11%
Minnow (Cyprinidae)	86	11%	200	13%
Darter (Percidae)	221	28%	342	22%
Gar (*Lepisosteus*)	334	42%	477	30%
Sunfish (*Lepomis*)*	610	77%	591	38%
Bass (*Micropterus*)			763	49%
Pirate Perch (*Aphredoderus*)	607	76%	780	50%
Madtom (*Noturus*)			924	59%
Sucker (Catostomidae)			1082	69%
Pickerel (*Esox*)			1439	92%
Total Captures	797	100%	1566	100%

* The first occurrence of a sunfish was in combination with a catfish. The first time a sunfish alone was recorded was at captures 610 and 591 for site “a” and the complete dataset, respectively.

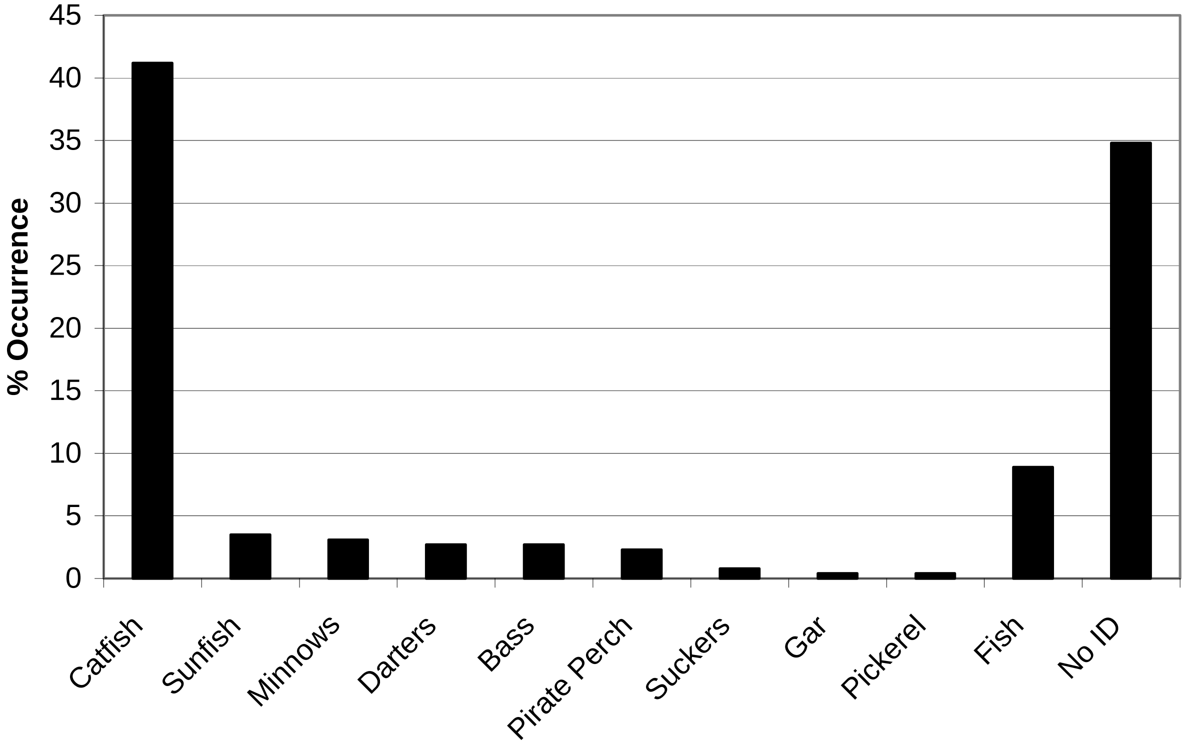

Figure 3.1 - Percent occurrence of identified and unidentified prey (n = 257) in the diet of *Nerodia taxispilota* on the Savannah River Site.

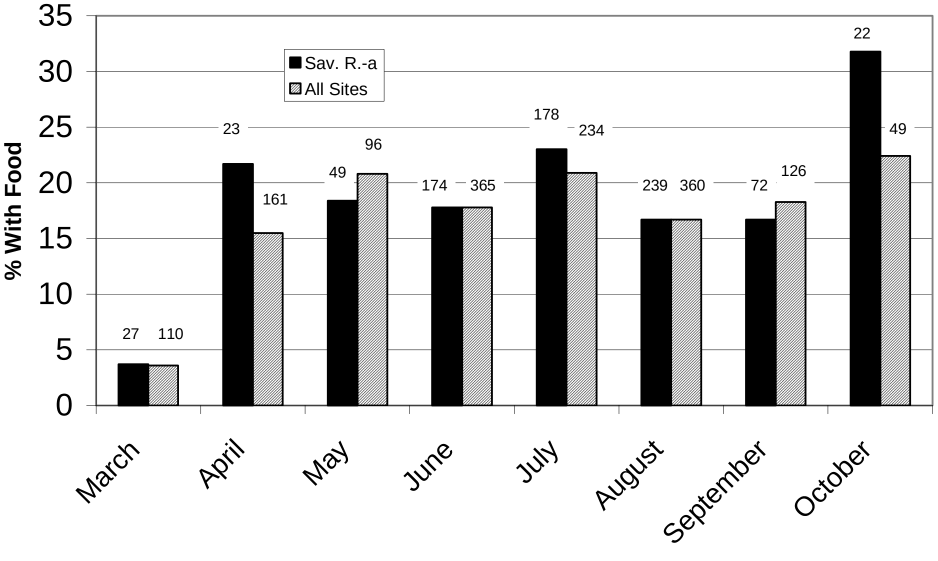

Figure 3.2 – Frequency of *Nerodia taxispilota* captured with food each month. Numbers on bars are sample sizes.

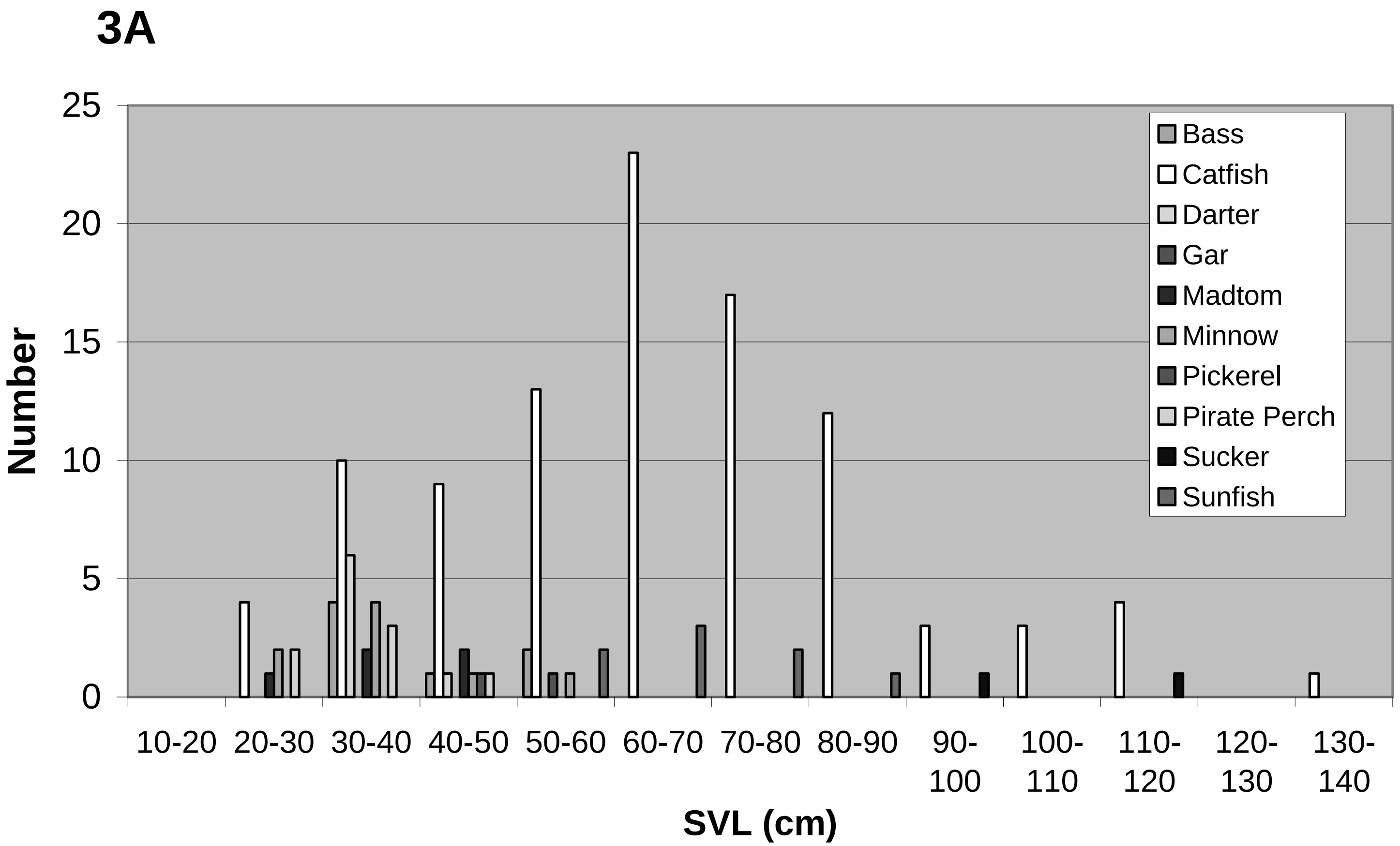

Figure 3.3 - A) Prey items partitioned by *Nerodia taxispilota* size class (SVL, cm).

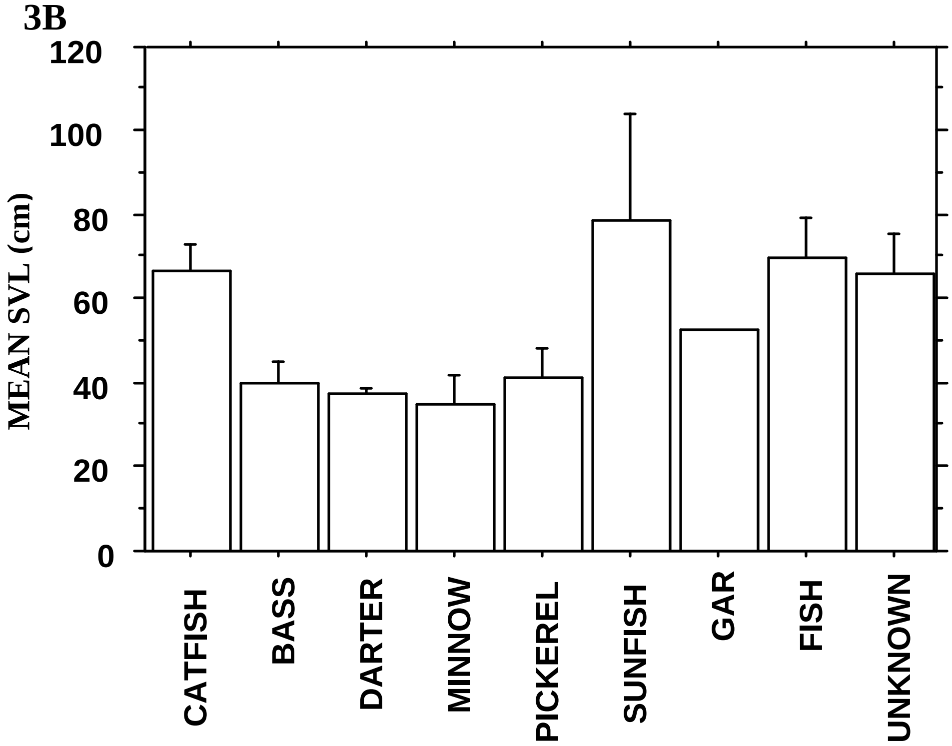

Figure 3.3 - B) Mean SVL (cm) of *Nerodia taxispilota* captured with each prey type. Bars represent two standard errors of the mean and numbers are sample sizes.

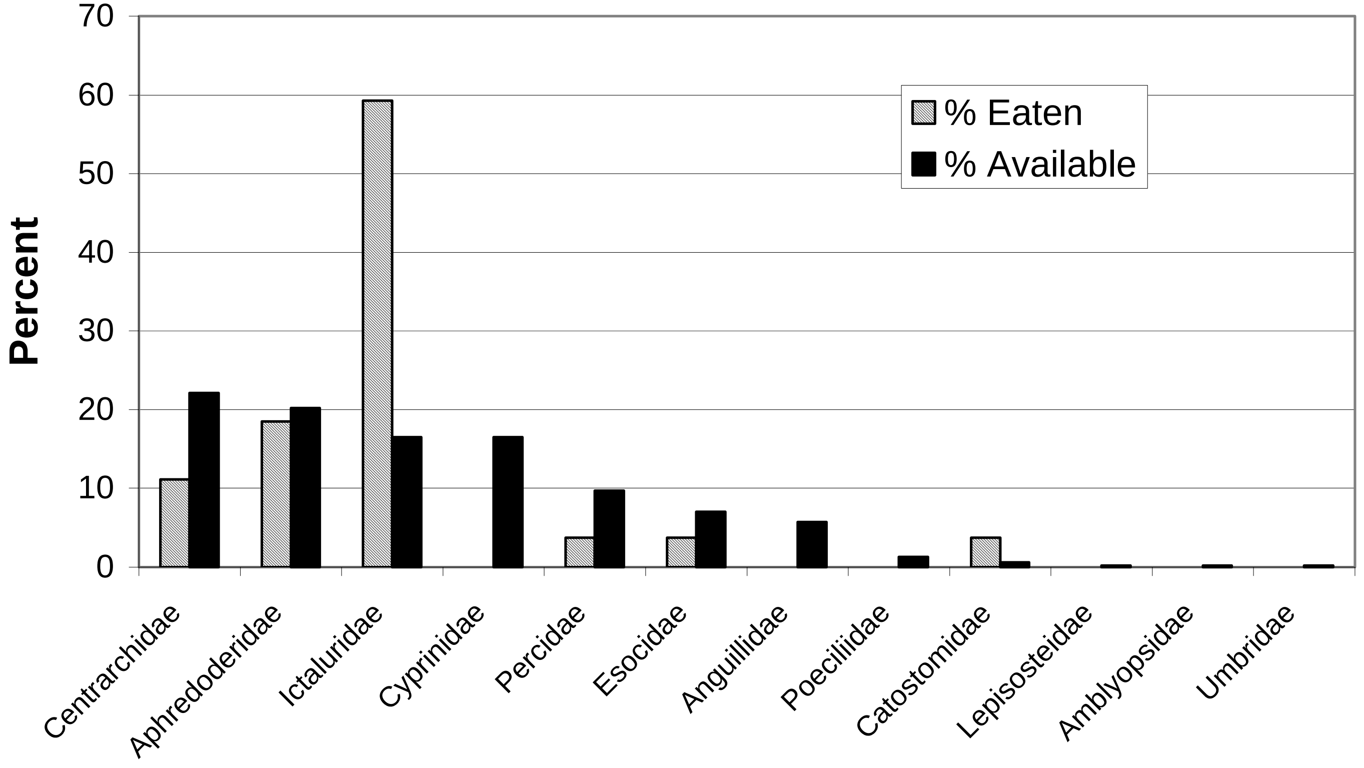

Figure 3.4 - Percent occurrence of fish families in the diet of *Nerodia taxispilota* (open bars) and their percent occurrence based on electro-shocking samples from UTR Creek (black bars). See Table 3.4.

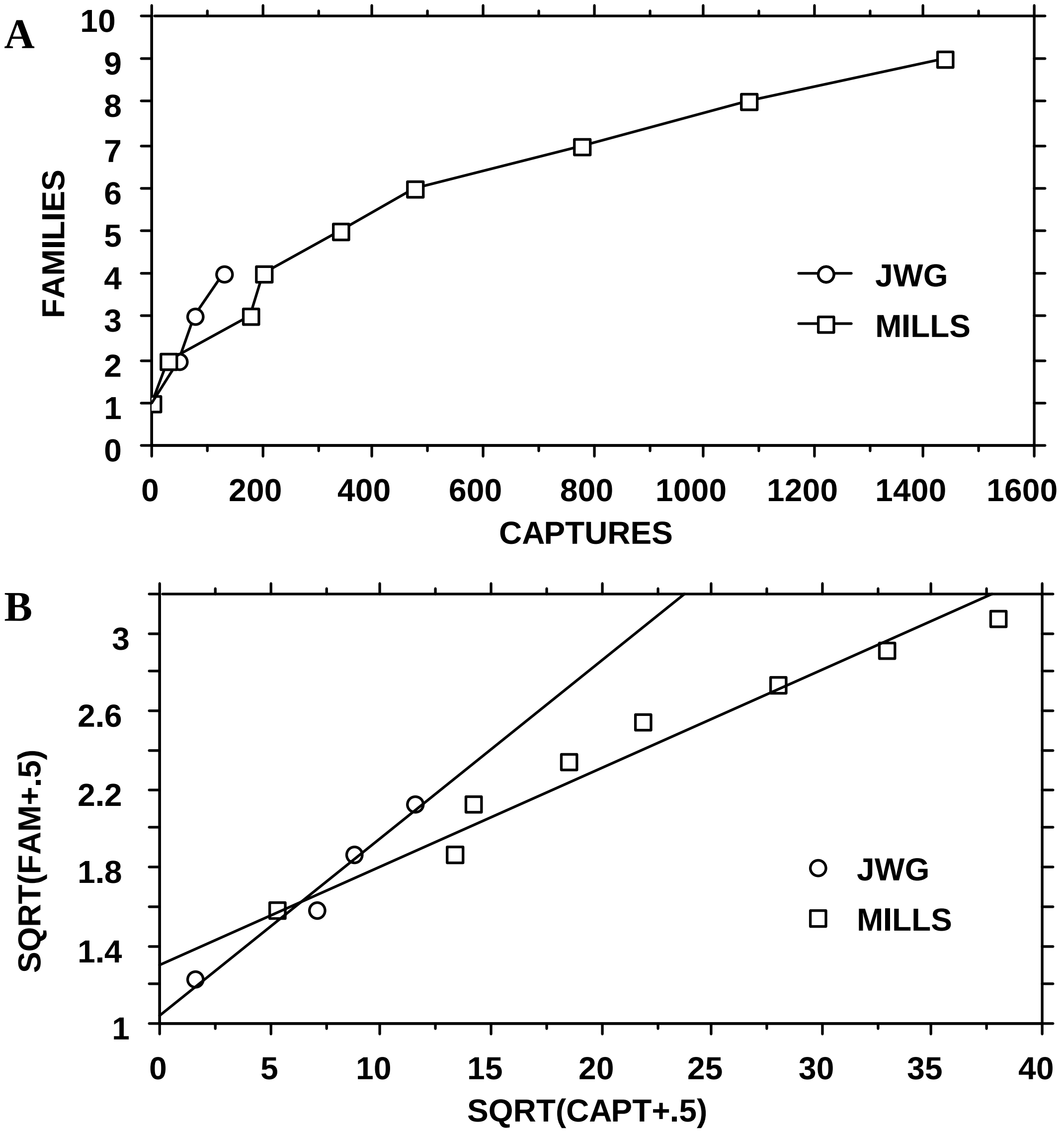

Figure 3.5 - A) The number of prey Families in the diet of *Nerodia taxispilota* as a function of the number of snakes captured. The boxes represent the present study and the circles are based on unpublished data from Semlitsch and Gibbons; both data-sets are from the SRS. B) Regression plots for square root transformations (√X+0.5, √Y+0.5) of prey families as a function of captures. Symbols are as described in 5A. Regression equations are as follows: Data Set JWG: SQRT (FAM + .5) = 1.044 + 0.091 * SQRT(CAPT + .5), R^2 = 0.966; Data Set MILLS: SQRT(FAM + .5) = 1.295 + 0.051 * SQRT(CAPT + .5), R^2 = 0.968

APPENDIX 3.1 - Gibbons/Semlitsch Data Set

Food items taken from 34 of 137 dissected *Nerodia taxispilota* by Ray Semlitsch, Whit Gibbons, and others at the Savannah River Site near Aiken, South Carolina.

Location	Date	Sex	SVL (cm)	Food Item	Family
UTR	10/18/67	F	90.0	Catfish (*Ictalurus* sp.)	Ictaluridae
UTR	7/12/73	F	51.0	Fish	
UTR	7/18/73		65.0	No ID	
UTR	4/10/74	F	87.0	Fish	
SC	6/11/74	F	134.0	Catfish (*Ictalurus* sp.)	Ictaluridae
SC	5/22/75	F	109.5	Catfish (*Ictalurus* sp.)	Ictaluridae
UTR	5/30/75	F	89.5	Fish	
UTR	5/30/75	F	91.5	Sunfish (*Lepomis* sp.)	Centrarchidae
UTR	6/6/75	M	44.5	Fish	
UTR	6/6/75	M	58.5	Fish	
UTR	6/6/75	M	69.0	Fish	
UTR	6/6/75	M	67.5	Fish	
UTR	6/6/75	M	67.0	Fish	
SC	6/11/75	F	126.0	Fish	
SC	6/11/75	M	66.5	Fish	
UTR	6/14/75	M	37.0	Redfin pickerel (*Esox americanus*)	Esocidae
UTR	6/16/75	F	45.0	No ID	
UTR	6/16/75	M	39.0	Redfin pickerel (*Esox americanus*)	Esocidae
UTR	6/22/75	F	54.0	Tadpole madtom (*Noturus gyrinus*)	Ictaluridae
UTR	6/22/75	M	71.0	Tadpole madtom (*Noturus gyrinus*)	Ictaluridae
SC	6/26/75	M	35.5	Fish	
SC	6/26/75	M	66.0	Fish	
SC	6/26/75	M	87.0	Fish	
SC	6/26/75	M	78.5	Fish	
SC	6/26/75	M	76.5	Catfish (*Ictalurus* sp.)	Ictaluridae
SC	6/26/75	F	113.5	Catfish (*Ictalurus* sp.)	Ictaluridae
UTR	7/1/75	F	66.5	Sunfish (*Lepomis* sp.)	Centrarchidae
UTR	7/17/75	F	51.5	Redfin pickerel (*Esox americanus*)	Esocidae
UTR	7/19/75	F	47.5	Catfish (*Ictalurus* sp.)	Ictaluridae
Par Pond	7/20/75	M	46.5	Fish	
SC	8/1/75	M	58.0	Catfish (*Ictalurus* sp.)	Ictaluridae
SC	8/1/75	M	76.0	Catfish (*Ictalurus* sp.)	Ictaluridae
SC	8/1/75	M	62.0	Tree frog (*Hyla cinerea*)	Hylidae
UTR	8/6/75	F	37.5	Redfin pickerel (*Esox americanus*)	Esocidae

ERRATUM

After all data were analyzed and this chapter was written, I discovered that one snake was classified as having consumed a “No ID” food item, when it should have been an “Unidentified Fish”. This was a 113 cm female from site b (UTR Creek) captured on 2 May 1999. This does not significantly change the overall findings or statistical conclusions reported in this chapter.

CHAPTER 4

POPULATION ECOLOGY AND REPRODUCTION OF *NERODIA TAXISPILOTA*

ABSTRACT

Population size, population and individual growth rates, reproductive traits and life history characteristics were determined or estimated using mark-recapture data of *Nerodia taxispilota* collected over an 8-yr period (1991-1998) from the Savannah River adjacent to the Savannah River Site, South Carolina, USA. Population size for a 10-km section of the Savannah River was estimated at 2782 (approximately 0.14 snakes/m of shoreline) using Bailey's triple catch and 3956 (or 0.20 snakes/m) using the Jolly-Seber method. Present population size estimates were higher than a previous estimate for this population (0.02 snakes/m; Mills et al., 1995). Growth was similar in juvenile males and females, but adult males grew significantly more slowly than adult females, and this was reflected in their sexual size dimorphism. Although a life table could not be constructed because of uncertainty of age, life history traits for this population apparently include: 1) relatively high adult survivorship, 2) estimated age at maturity of approximately 5-6 years for females and 3 years for males, 3) reproductive contribution to the next generation is spread over several size and presumably age classes, 4) individuals are relatively long-lived (6+ yr), 5) relatively high fecundity (mean litter size =18.2), and 6) annual reproduction for females larger than 115 cm SVL. Significant positive correlations existed between litter size and female length and mass. No apparent trade-off exists between litter size and offspring size; however, substantial variation existed in neonate mass and length both between and within litters. The life history traits of this population were compared with other populations of *N. taxispilota* and other members of the genus *Nerodia*.

INDEX WORDS: *Nerodia taxispilota*, Brown water snake, Mark-recapture, Population size, Growth, Reproduction, Life history

Life history, which revolves around how the individual adaptively allocates energy among reproduction, growth, maintenance, and repair, is an integral and vital part of understanding a species' overall ecology. Life history traits include number, size, and sex ratio of offspring, age-specific survivorship and reproduction, growth pattern (as it relates to reproduction), age and size at maturity, and longevity (Stearns, 1992). Some life history traits can be difficult to determine, and their tractability depends on particular ecological characteristics of the species. For example, because most snakes are secretive and may remain inactive for long periods of time, most species are difficult to locate and capture, resulting in operative population densities or sizes that are too low for effective field studies. Also, known ages of older individuals cannot be accurately determined among snakes except by mark-recapture of previously aged neonates. My goal was to conduct long-term mark-recapture studies of a large population of brown water snakes, *Nerodia taxispilota*, to acquire information on selected life history traits that are difficult to measure with most species of long-lived organisms, especially snakes. Much of the emphasis in life history theory has been placed on trade-offs between how energy is allocated to and among offspring compared to other aspects of the organism's biology. Thus, in addition to a basic description of the reproductive characteristics of *Nerodia taxispilota*, I address the proposed trade-offs and interactions among factors affecting the number and size of the offspring.

Reviews of snake demography and life history characteristics can be found in Seigel and Ford (1987), Parker and Plummer (1987), and Dunham et al. (1988), but these and other authors have emphasized the relative shortcomings or complete lack of appropriate data for snakes when compared to other reptilian and vertebrate groups. In particular, a dearth of information exists on age-specific patterns of fecundity and mortality of snakes (Parker and Plummer, 1987), and life tables for snakes are extremely limited (e.g., Feaver, 1977; Parker and Brown, 1980; Brown and Parker, 1984; Plummer, 1985). The lack of data on life history characteristics for snakes, particularly variation in these characteristics, limits our ability to compare and test more broad-based evolutionary hypotheses concerning life history patterns (Dunham et al., 1988).

Concern has been expressed that most of the limited life history data available for snakes are based on short-term (<5 yr) studies, and thus often fail to account for among-year variation (Madsen and Shine, 2001). The importance of among-year variation in reproductive traits in snakes lead Seigel and Ford (1987) to state, “Perhaps the most serious deficiency in our understanding of snake reproduction relates to temporal variation in reproductive traits… Long-term field studies designed to assess such variation are crucial.” Madsen and Shine (2001) demonstrated that long-term studies are necessary to characterize mean values and variation for many life history traits. Few long-term studies have been done on snakes, with a few notable exceptions, including Henry Fitch’s work in Kansas (Fitch, 1999), Blanchard et al. (1979) in Michigan, Fukada (1969; 1989) in Japan, Madsen and Shine (2000; 2001) in Australia, Brown and Weatherhead (1999) in Ontario, Plummer (1997) in Arkansas, Bronikowski and Arnold (1999) in California, and Andren and Nilson (1983) in Sweden. The present study surpasses the arbitrary definition of “short-term” (<5 yr) and addresses some of the statistical and interpretational problems associated with short-term studies on long-lived animals.

Lack (1947) formalized a hypothesis for the evolution of offspring number and attempted to explain the average clutch size in birds, and more specifically the factors that might influence the upper limit of clutch size. He hypothesized that the optimal clutch size is the one that produces, on average, the most fledglings (the “Lack” clutch). Williams (1966) expanded on Lack’s optimal clutch size hypothesis and proposed a trade-off by stating that there should be, “…some optimum compromise between the advantages of high fecundity and of adequately providing for each of the young.” Smith and Fretwell (1974) constructed a model that proposed that if a limited amount of energy were available for reproduction, then an increase in egg size (or size of the young in viviparous species) would require a decrease in clutch or litter size. The basic concept of Smith and Fretwell’s (1974) model is that given the limited amount of energy, a parent should produce offspring of an optimal size (in most cases measured by offspring survival) while producing the most offspring that this size will allow. If offspring in larger clutches have a reduced probability of survival due to smaller body size, then natural selection may favor placing energy into fewer, larger offspring or parent growth. Thus relationships exists between survivorship of offspring, litter size, and offspring size.

Brockelman (1975) modified and expanded the Smith and Fretwell (1974) model to address the possible effects of factors such as competition, mortality, and environmental predictability on offspring size and number. Brockelman (1975) predicted, as did Williams (1966), that as juvenile mortality increases, so does birth rate (i.e., clutch size). Brockelman (1975) also predicted that in a variable environment, there should be a relatively constant, optimal allocation of energy per offspring and that as the environment fluctuates, the number of young rather than the size of the offspring will fluctuate. That is, natural selection would favor some optimal offspring size based on survivorship and competitive ability, and during a good year (abundant resources) the female would produce more, not larger, offspring.

In support of Smith and Fretwell's (1974) model, apparent trade-offs between offspring size and number exist in some species of squamate reptiles (e.g., Ford and Seigel, 1989; King, 1993; Madsen and Shine, 1996; Olsson and Shine, 1997). Whereas selection for optimal offspring size does not necessarily favor larger body size, larger body size may impart some advantages to lizards, particularly territorial species (e.g., *Uta stansburiana*, Ferguson and Fox, 1984), and larger snakes may be able to better escape predation (Jayne and Bennett, 1990). Alternatively, smaller individuals may have greater difficulty capturing and subduing prey items such as fish (Halloy and Burghardt, 1990), particularly in moving water. Although I did not experimentally test optimal offspring size models, I analyzed my reproductive data for *N. taxispilota* to determine if a trade-off between offspring number and size could be detected.

The three goals in the present study were 1) to describe the basic population ecology of *Nerodia taxispilota*, which builds on previous work (Mills et al., 1995), 2) to document reproductive traits and selected life history traits of the brown water snake, and 3) to evaluate the proposed trade-off between offspring number and size using reproductive traits of this population.

METHODS AND MATERIALS

As part of a long-term mark-recapture study of *N. taxispilota* at the Savannah River Site (SRS) in South Carolina (Mills et al., 1995), I collected data on reproduction, growth, and survivorship from 1991-1998. My data set was augmented with unpublished data on reproduction of *N. taxispilota* collected by Stevan Arnold in 1990 – 1993. Snakes were captured by hand as described previously (Mills et al., 1995), measured, weighed, and palpated to determine reproductive status. Sex was determined using one or a combination of three techniques (Fitch, 1987): 1) comparing tail length and the thickness of the tail immediately posterior to the vent (adult males have relatively longer and thicker tails than similar-sized females), 2) using a blunt probe to determine the presence of hemipenes, and 3) applying gentle pressure on one side of the tail base and causing a hemipenis to evert. Female reproductive condition was assessed by palpation to detect enlarged follicles or embryos. Minimum size at maturity was determined based on previous studies (Semlitsch and Gibbons, 1978; Aldridge, 1982; White et al., 1982; Mitchell and Zug, 1984) and the smallest gravid female captured in the present study. Litter size and other litter characteristics were measured from litters born in captivity to wild-caught females. Neonates were sexed using the latter two methods described above. Snakes were usually individually marked (ventrally scale-clipped in 1991, PIT-tagged thereafter; Camper and Dixon, 1988) when captured. I concentrated my sampling in three primary sites and several adjacent tributaries of the Savannah River Site, Aiken County, South Carolina (Fig. 4.1). The notation for the study sites is as follows. Sites a1, a, and a2 are contiguous sections of the Savannah River corresponding respectively to upstream from the mouth of Upper Three Runs Creek (UTRC), from UTRC downriver 10 km (roughly to Four Mile Creek), and then downstream several kilometers. Sites b and c are both in UTRC, with b near the mouth (downstream of SRS Rd A or Hwy 125) and c primarily upstream of SRS Rd C. Sites d and f are contiguous sections of the Savannah River, with d beginning near the mouth of Steel Creek (SC) and continuing downriver to Little Hell Landing, and f continuing downriver to the Hwy 301 bridge. Site e consists of the lower portion of SC, from an area known as Steel Creek Delta to the mouth. Additional areas where snakes were sampled were the coal-ash basins at the headwaters of Beaver Dam Creek (n = 3), Beaver Dam Creek (n = 22), and near Ellenton Bay (n = 1).

POPULATION SIZE

Population size was estimated using two similar open population models: Bailey's triple-catch and Jolly-Seber (Caughley, 1977; Tanner, 1978). Bailey's triple-catch was used because of its relative ease of calculation and for comparison to previous estimates for this population (Mills et al., 1995), and the Jolly-Seber model was chosen because the study is easily broken into multiple capture periods (i.e., years) and it is the preferred estimator in open populations. I tested the assumption of equal catchability using a zero-truncated Poisson distribution to calculate the expected values for the chi-square statistic (Caughley, 1977; Zar, 1984). That is, if each individual has an equal probability of being captured, it should follow a random (Poisson) distribution.

I calculated Bailey's triple catch population estimates using the following equations (Tanner, 1978):

$$M_2 = F_2R_{13}/R_{23} + R_{12}$$

$$N_2 = M_2C_2/R_{12}$$

Where the subscripted numbers represent the specific capture periods (one, two, or three), N_2 is the estimated population size at the second capture period, and M_2 is the estimated number of marked individuals in the population at capture period two. F is the number marked and released, C is the total number captured (both marked and unmarked individuals), and R is the number of recaptures.

The Jolly-Seber estimate is the preferred estimator of population size in open populations and accounts for both recruitment and removal of animals from the population (Tanner, 1978). The equations used are similar to the triple-catch estimate and are as follows:

$a_i = R_i/ C_i \quad i = 2, \ldots z$

$M_i = F_i U_i/V_i + R_i \quad i = 2, \ldots z-1$

$N_i = M_i/a_i$

Where a is the proportion of marked animals in the population, U is the number of marked animals not captured but known to be alive, and V is the number marked that are caught subsequently. All other variables are as above for Bailey's triple catch and details of these and other accessory equations and calculations can be found in Tanner (1978).

SURVIVORSHIP

Survivorship in the present study was estimated using two methods. First, a log-polynomial transformation of the estimated age frequencies (see Growth Rates and Estimating Age) was used to obtain a "smoothed" age frequency (Caughley, 1977), which was then used to calculate survivorship (l_x) by dividing the frequency of each age class (f_x) by the frequency of age class 0 (f_0). The disadvantage of this method is that when age frequencies are smoothed, the resulting constant survivorship is not biologically accurate because it probably overestimates juvenile survivorship and underestimates adult survivorship. Therefore, to make the survivorship estimate better reflect observed patterns, age class 0 was removed before smoothing the age frequencies in an attempt to reduce the error introduced by the neonate age class.

The second method used to estimate survivorship was to apply the estimates of mortality/emigration obtained from mark-recapture data. Both the Jolly-Seber and Bailey's triple catch population estimates allow the calculation of recruitment (birth plus immigration) and removal (mortality plus emigration). Assuming immigration and emigration rates cancel each other, the mark-recapture estimates can be used to calculate survivorship.

GROWTH RATES AND ESTIMATING AGE

Growth rates, age and longevity were estimated based on recaptured individuals. A growth rate was calculated for each recaptured individual as follows: (length at capture – length at previous capture) / growth days between captures. I deducted 120 days from the number of growth days between recaptures for individuals captured in successive years (i.e., 120 days for each winter, November through February) because *N. taxispilota* do not feed and presumably do not grow during these months (Chapter 3). Growth was modeled using the von Bertalanffy model (see below) because the instantaneous change in length decreased linearly with length (Fabens, 1965; Andrews, 1982). As snakes cannot be aged using external characteristics (e.g., annuli on turtle shells), age at first capture was estimated using the individual's size and the von Bertalanffy growth equations. Age of the individual at subsequent recapture was based on the estimated age at first capture plus the number of years between captures (Brown and Parker, 1984; Brown and Weatherhead, 1999).

I applied the von Bertalanffy growth model to tentatively estimate age as a function of body size. I conservatively estimated age for all individuals that were of a size intermediate between two estimated age classes; that is, if a snake could be either three or four based on size, I classified it as a three year old. To calculate growth rates and age, I first regressed growth rates by mean SVL of recaptured individuals using the finite difference approximation (Andrews, 1982):

$\text{Growth Rate (mm/d)} = rA_L - rL$

or

$\text{Growth Rate (mm/d)} = a - b(SVL)(1)$

Where a is the y-intercept (initial growth rate), b is the slope (growth constant), and SVL is the mean SVL of the first and second captures. Because the measurement of SVL is highly variable with live snakes (pers. obs.), and larger snakes are more prone to this type of error, I followed Plummer (1997) in excluding from equation 2 all small snakes (<60 cm) captured within 30 d of their original capture and all larger snakes (> 60 cm) in which captures occurred within 60 d. Age at a particular size was then modeled using the von Bertalanffy model, which is the integrated form of Equation 1:

$\text{Age (d)} = (1/b)\ln(a + b(SVL)) + c(2)$

To calculate c (integration constant), I used the mean SVL at birth (age = 0) for males and females.

SIZE AND AGE AT MATURITY

Size and age at maturity were estimated indirectly for this population. I first used published estimates for both sexes. Herrington (1989) estimated that males in central

Georgia mature between their second and third years, or at about 58.0 cm, and females mature during their fourth year at about 85-90 cm. In Virginia, males are mature between 46 and 51 cm and females mature at about 72.5 cm (White et al., 1982; Mitchell and Zug, 1984). Based on the presence of enlarged follicles, sexual maturity in females on the SRS occurs between 72.5 and 80.0 cm (Aldridge, 1982). In the present study, the smallest gravid female captured was 79.5 cm, and the smallest female to give birth in captivity was 80.0cm. These sizes were then used in the von Bertalanffy growth equation to estimate age at maturity.

REPRODUCTION AND FECUNDITY

The following traits related to reproduction were measured using both field and laboratory: litter and neonate size, relative clutch mass (RCM), and female body size and condition. Litter size and body size of offspring were recorded from two data sets of wild-caught females housed in the laboratory: one set recorded by Stevan Arnold (SA, n = 106 females) and one by myself (MM, n = 12 females). Stevan Arnold’s litters were born in captivity from 1990 to 1993 and my litters were born in 1993 (n = 1), 1995 (n = 2), and 1996 (n = 9). Litter size was defined as the total of live young (tertiary clutch size in Dunham et al., 1988); stillborn young and undeveloped eggs were not included (Gregory and Larsen, 1993). Relative clutch mass (RCM) was calculated as the sum of the masses of all young, living and dead, and undeveloped eggs, divided by the postpartum mass of the mother. In addition to recording maternal length and mass, I calculated maternal body condition using the residual values of the regression of maternal mass on length. The residual index of body condition is not affected by body size (residual body condition vs. female length, r = 0, P = 1) as is the ratio index (body mass/body length vs. female length, r = 0.68, P<0.0001) and approximates a normal distribution, making the residual mass measure of body condition more desirable when using parametric tests. Relationships among maternal body size and condition, litter size, neonate size, and RCM were evaluated with correlation (partial correlations and Spearman rank correlations) and linear regression analyses.

In an effort to assess variability in litter size, I calculated litter size variance using standard measures of dispersion (standard deviation and coefficient of variation) and two “new” measures of variance: “uncorrected deviation score” and “standardized deviation score”, which are analogous to SD and CV, respectively (Shine and Seigel, 1996). The uncorrected deviation score was the absolute deviation of each clutch size from the mean clutch size and the standardized deviation score was calculated by dividing the previous score by the mean clutch size. I calculated these deviation scores for comparison purposes, but I also used the absolute value of residuals of the maternal length-litter size regression as an estimate of dispersion. The residual values of the maternal length-litter size regression are a better measure of variance from the mean because litter size increases with body size in *N. taxispilota*. Using Shine and Seigel’s (1996) deviation scores, larger snakes tend to always have litters greater than the sample mean and smaller individuals have litters less than the sample mean.

Size-specific fecundity was estimated by regressing litter size on female SVL to determine a mean number of young per female at particular body lengths. Because of the importance of determining the proportion of females that reproduce each year (Frazer et al., 1990), I adjusted estimates of annual fecundity with a size-specific estimate of the proportion of gravid females in the population.

Most statistical tests were computed using StatView® (Abacus Concepts, 1996) or SuperANOVA™ (Abacus Concepts, 1989) for the MacIntosh® with a priori significance level set at alpha = 0.05 unless otherwise stated. When the assumptions of normality and equality of variances were grossly violated, nonparametric tests were used: Mann-Whitney tests (U) in place of a *t*-test, and Kruskal-Wallis test (H) in place of the ANOVA. My statistical interpretation follows that of Zar (1984). Unless otherwise stated, all means are followed by two standard errors of the mean and all snake lengths are snout-vent lengths (SVL).

RESULTS

POPULATION SIZE, SURVIVAL RATE, AND RECRUITMENT

From 1991 to 1998, I made 1753 captures of 1589 marked individuals (including neonates born and marked in captivity), of which 774 were males and 815 females (1:1 ratio; χ^2= 1.007, $P>0.25$), with a mean of 1.1 captures per snake (Table 4.1). Not including neonates marked in captivity, I captured 661 males and 725 females in approximately a 1:1 ratio (χ^2= 2.864, $P>0.05$). One hundred thirty six individuals (9.8% of those marked) were recaptured one to five times for a total of 164 recaptures. Of these 136 snakes, females (n=81) were significantly more likely to be recaptured than males if one assumes a 1:1 sex ratio (n=55; χ^2= 4.596, $P<0.05$). When adjusted for the greater number of marked females in the population, this difference became nonsignificant (χ^2= 3.370, $0.10>P>0.05$).

I captured and recaptured individuals of all size classes, although the smallest individuals were under-represented in both the original captures and the recaptured *N. taxispilota* (Fig. 4.2). *Nerodia taxispilota* exhibits sexual size dimorphism (Fig. 4.2), with a mean (± SD) female SVL of 72.03 ± 25.12 cm (range: 22.9-133.0 cm, n = 748), and mean male SVL of 59.13 ± 16.10 cm (22.3-97.0 cm, n = 675).

Most snakes (92%) were captured only once, and a few were captured as many as five times (Table 4.2, Fig. 4.3), but the number of captures per individual was not significantly correlated with the number of days between first and last capture ($r = 0.21$, $P>0.05$). In estimating population size and related parameters using mark-recapture methodology, one must test for equal catchability and the frequency of immigration and emigration (Wilbur and Landwehr, 1974; Parker and Plummer, 1987). Problems associated with estimating population size when there is immigration and emigration were addressed by using “open” rather than “closed” population models (Tanner, 1978). I tested for equal catchability for Site-a (the main study site and the site with the most captures and recaptures of individuals) using a zero-truncated Poisson distribution and the Chi-Square statistic (Caughley, 1977; Zar, 1984) and rejected the hypothesis of random or equal likelihood of capture for all individuals (Table 4.2; $\chi^2 = 514.287$, df=3, $P<0.001$). The differences between the observed and expected number of captures per individual were substantial, with single captures over-represented (Observed/Expected = 1.66; Table 4.2) and multiple captures under-represented in this sample (Fig. 4.3). In an attempt to reduce the number of single-capture individuals, compensate for the known under-representation of small snakes (particularly those < 1 year old), and thus improve the estimates of catchability, I recalculated the Poisson distribution and the Chi-Square statistic after removing from the data set neonates born and marked in the lab (n = 177), under the hypothesis that their low survivorship and cryptic habits preclude them from being sampled adequately. Although it slightly improved the fit of the observed data to the expected, the null hypothesis was again rejected (χ^2= 392.248, P<0.001). I used the relationship between the mean number of captures per individual and the variance of this estimate to determine if my sample was uniform (if variance/mean < 1.0) or contagious (i.e., clustered, if variance/mean > 1.0). The variance to mean ratio for Site a was 0.14, indicating that the number of captures per individual was more uniform than random or clustered. Therefore, the assumption of equal catchability does not hold for my study (and probably very few other studies); therefore, care should be taken in the interpretation of the population estimates and related parameters (but see Discussion).

Significant differences existed between recaptures in size classes (χ^2= 17.263, P<0.001), with far fewer in the <50 cm class and far more than expected in the ≥50 cm class. The frequencies of male and female recaptured individuals did not differ from the expected values, although the difference was very close to being significant (χ^2= 3.432, 0.10>P>0.05). To explore the specific sources of the violation of the equal catchability assumption, I examined the differences in recapture rates related to size, sex, or a combination of these factors. I first split the original captures into sex and size (<50 cm or ≥50cm) classes and performed a goodness-of-fit test using a 2x2 contingency table. The observed frequencies in these categories did not meet the expected values (χ^2= 5.873, P<0.05); therefore, the relative proportions of original captures (i.e., new marks) in each size-sex category were used to calculate the expected values for the following tests. Using Site-a recaptured animals only (n=164), I then tested observed versus expected frequencies between size (<50 cm or ≥50cm) and sex classes. An interaction between size class and sex was apparent (Fig. 4.4). When treating the 4 size-sex groups (i.e., males <50 cm, females <50 cm, males ≥ 50 cm, females ≥ 50 cm) as separate categories, the frequencies differed significantly from the expected values (χ^2= 20.837, df = 3, P<0.001). The two categories that contributed the most to this large Chi-square value were males < 50 cm and females $\geq$ 50cm (Fig. 4.4): males < 50 cm were recaptured far less than expected based on original captures, and females $\geq$ 50 cm were recaptured far more than expected based on their original captures. Therefore, I removed these categories (i.e., subdivided the Chi-square analysis) and found that the remaining categories did not differ from their expected values (χ^2= 3.045, P>0.05).

I estimated a population size of 2782 using Bailey's triple catch and 3956 using the Jolly-Seber method (Table 4.3), both substantially higher than a previous estimate (426 individuals; Mills et al., 1995) for this population calculated using Bailey's triple catch method and based on three years of data. A perhaps more meaningful way to express the population size of a riverine snake is as a linear density (Parker and Plummer, 1987): one snake per 7.2 m of river bank or 0.14 snakes/m (Bailey's), or one snake per 5.1 m of river bank or 0.20 snakes/m (Jolly-Seber). My current estimates are six to nine times higher than our previous estimate of population density (46.9/m; Mills et al., 1995).

Estimates of the survival rate from one year to the next averaged 0.85 and the number recruited ranged from 953 to 4022 (mean = 1926; Table 4.3). Survival rate and recruitment were estimated using the Jolly-Seber method (Tanner, 1978). The estimates of recruitment and survival using the Jolly-Seber method also include immigration (recruitment) and emigration (mortality). An estimated survivorship of 0.68 for individuals > 1year old was calculated by smoothing the age-class distribution (i.e., estimated age; see discussion below concerning age estimation for this population) using a log-polynomial transformation of the age frequencies (Caughley, 1977).

The population estimates are highly variable among years and have high variances (e.g., for 1995 the standard deviation of N_i was 1576; Table 4.3). Roff (1973) suggested that an estimate is reliable only if the SD is less than 5% of N_i. My standard deviations of N_i range from 38-86% of N_i. The variability in these estimates is primarily due to the low recapture rate, which could be the result of high population densities, high levels of recruitment and/or low survivorship.

INDIVIDUAL GROWTH PATTERN AND AGE STRUCTURE

Growth rates for individual *N. taxispilota* ranged from 0-1.11 mm/d (mean ± 2 SE = 0.31 ± 0.05, n = 107; Table 4.4A). Using mean SVL as the covariate, growth rates of all recaptured individuals were not significantly different between the sexes (ANCOVA: $F_{1,101}$ = 0.878, P = 0.35), and the results were similar when the slopes of the regression lines were compared directly using a t-test (t = 0.936, df = 101, P>0.20). The above comparisons are based on mean growth rates over the full range of body sizes and thus mask observed size-related differences in growth between males and females (Fig.'s 4.5 & 4.6). Therefore, I subdivided growth rates between adults and juveniles and again compared the growth rates using analysis of covariance with SVL as the covariate. I classified males ≥ 50 cm as mature based on the work of White et al. (1982) and females ≥ 79.5 as mature based on the present study. I pooled juvenile males and females together because of the small sample size for males (Table 4.4A). Growth rates differed significantly among adult males, females, and juveniles (ANCOVA, $F_{2,101}$ = 5.021, P = 0.008). Direct comparisons of the regression coefficients of the ANCOVA model revealed that adult females (mean ± 2SE = 0.282 ± 0.066 mm/d, n = 32) did not grow at a significantly different rate than juveniles (0.456 ± 0.082 mm/d, n = 37; F = 0.108, P =

0.743); however, adult males (0.203 ± 0.062 mm/d, n = 38) grew at significantly slower rates than both juveniles (F = 23.992, P = 0.0001) and adult females (F = 6.734, P = 0.011). Additionally, female growth was more variable than male growth (Fig. 4.5). The regression equations for female and male size-specific growth rates explained only about 4% (R^2 = 0.041, P = 0.105) and 21% (R^2 = 0.206, P = 0.0029) of the variability, respectively (Fig. 4.5).

Young *N. taxispilota* grow from 0.256-0.828 mm/d (mean = 0.419 mm/d). Juvenile growth rates were pooled, although variability in size at birth and variable growth rates could create a large range in body size at one year. Combining the variability in growth rates with the variability in size of neonates at birth and the three-month period between early and late parturition dates creates the potential for extreme variability in size at the end of the first year (Table 4.4B). For example, an individual born early (7/28) at maximum size (284 mm), and growing at the maximum rate (0.828 mm/d) could be as much as much as 557 mm at the end of its first year; whereas an individual born late in the season (10/21) at the minimum size (200 mm), and growing at the minimum rate (0.256 mm/d) would be only 263 mm at the end of its first year (Table 4.4B). The latter scenario produces an individual at the end of its first year that would be within the size range of a newborn individual.

Despite difficulties with aging individuals in the present study, *Nerodia taxispilota* seems to be a relatively long-lived snake based on recapture data of 164 snakes recaptured after 4-6 years (Table 4.5). For example, a female estimated to be two years old (52.1 cm SVL) was recaptured nearly six years later at a less-than-maximum body length of 106.9 cm SVL, and a large (79.5 cm) adult male was recaptured five years after its initial capture (Table 4.5). Size-specific growth rates (Fig. 4.5) determined from all size classes of recaptured individuals were used to construct von Bertalanffy growth models that estimate age at a given length (Fig. 4.6a). Using the von Bertalanffy growth equations I estimated age at first capture based on the individual's length. The age at subsequent captures was determined by using the estimated age and adding the time elapsed between the first and last capture (Table 4.5, Fig. 4.6b). However, the variability in individual growth rates and the low number of juveniles and known-aged individuals included in building the von Bertalanffy growth model results in equivocal age estimates.

SIZE AND AGE AT MATURITY

Based on the presence of enlarged follicles, sexual maturity in females on the SRS occurs between 72.5 and 80.0 cm (Aldridge, 1982), and the smallest gravid female captured in my study was 79.5 cm; therefore I used 79.5 cm SVL for female size at maturity. Size at maturity was determined from previous studies of males. I based my estimate of male size at maturity (50 cm SVL) in the present study on estimates that males in central Georgia mature at about 58.0 cm (Herrington, 1989) and Virginia males mature between 46-51 cm SVL (Mitchell and Zug, 1984).

Hypothetical females born at the minimum (20 cm) and maximum (28 cm) sizes and growing at minimum (0.256 mm/d) and maximum (0.828 mm/d) rates would reach size at maturity as much as 6 years apart from one another (4 – 10 years; Table 4.6). Therefore, estimates of potential age at first reproduction, necessary for the construction of a life table, based on length would be highly variable. Nonetheless, using body lengths of 50 cm for males and 79.5 cm for females, I estimated the ages at maturity using the von Bertalanffy growth equation at approximately 3 years for males and 5-6 years for females. Because growth rates were highly variable, I explored the potential variability in age at maturity based on variability in size at birth and variability in growth rates.

LITTER CHARACTERISTICS

From 4 to 50 living young were born per litter (mean = 18.2 ± 1.4, n = 118), with the majority of litters (n = 104) belonging to females captured on the Savannah River (Table 4.8). Characteristics of the litters and neonates were determined from young born to wild-caught females housed in the laboratory. As previously stated, litters can be divided into two data sets: those litters recorded by Stevan Arnold (SA) at the University of Chicago and those recorded by me (MM) at SREL; however, all females were captured at or near the SRS. I will first discuss the differences or similarities between these two data sets, then I will discuss the data as a whole.

Between 1990 and 1996, 2275 living and stillborn young were born to 121 females; however, only 2148 living young were included in the following analyses (Table 4.7) because of highly significant differences in SVL and mass between living and stillborn young (Mann-Whitney U, $P<0.0001$; Fig. 4.7). Males (n = 1065) outnumbered females (n = 1046), a ratio not significantly different from 1:1 ($\chi^2 = 0.153$, $P>0.50$). Neonates measured by SA were longer (grand mean of litters ± 2SE = 24.51 ± 0.23 cm, n = 106) than those measured by MM (22.74 ± 0.67 cm, n = 12; U = 181.5, $P<0.0001$), a difference attributed to SA measuring euthanized neonates (Stevan Arnold, pers. comm.) and MM measuring live neonates (i.e., I was more cautious when stretching a living neonate for fear of harming it). Mean mass of neonates in litters weighed by SA (10.78 ± 0.31 g, n = 106) and MM (10.95 ± 0.92 g, n = 12) did not differ (U = 610.0, P = 0.82). Combining both data sets, males (24.42 ± 0.09 cm, n = 1065) and females (24.38 ± 0.09, n = 1046) were not significantly different in length (U = 575110, P>0.15) but did differ significantly in mean mass (U = 588841, P<0.05), with females averaging about 0.2 g more at birth (males: 10.72 ± 0.11 g, n = 1067; females: 10.91 ± 0.10 g, n = 1045; Table 4.7).

In addition to comparing neonates size between the SA and MM data sets, I compared the following maternal and reproductive variables between the data sets: maternal length, litter size, and RCM. Captive gravid females did not differ in mean length between SA (96.76 ± 1.35 cm, n = 106) and MM (95.58 ± 4.18 cm, n = 12; U = 677, P>0.80). Mean litter size was not significantly different (ANCOVA, female SVL as covariate: $F_{1,114}$ = 1.738, P = 0.19) between SA (18.52 ± 1.53, n = 106) and MM (15.42 ± 2.34, n = 12). Finally, relative clutch mass (RCM) was not significantly different (ANCOVA, female SVL as covariate: $F_{1,116}$ = 1.707, P = 0.19) between SA (0.310 ± 0.018, n = 108) and MM (0.267 ± 0.039, n = 12). Therefore, I combined the two data sets for all subsequent analyses (Tables 4.7 & 4.8). However, because of small sample sizes and the confounding factor of site differences in female body size, I removed the Edisto River, UTR, and Steel Creek litters from subsequent analyses (Table 4.8).

Females from the Savannah River were not significantly different in mean SVL among years (H = 3.508, df = 4, P>0.45). I tested for differences in maternal, litter, and neonate size among years, including in the analyses only those females and their litters from the Savannah River (n = 107). Using ANCOVA with female SVL as the covariate, I found no significant differences among years in mean litter sizes ($F_{4,94}$ = 1.083, P = 0.37), mean neonate SVL ($F_{4,94}$ = 0.139, P>0.95), or mean neonate mass ($F_{4,94}$ = 0.427, P>0.75), nor were there significant interaction effects in these analyses. Thus, when examining only the Savannah River data, litter characteristics were similar among years, allowing me to combine all years into one data set for subsequent analyses.

PARTURITION DATE AND RELATIONSHIPS BETWEEN FEMALES AND THEIR LITTERS

Parturition dates for captive females ranged from 30 August to 21 October (Table 4.9A). Most (76%) captive females gave birth in September (Table 4.9A). Mean parturition date was 22 September and did not differ appreciably between the two data sets (17 Sept. for MM and 23 Sept. for SA). Precise parturition dates in the field populations were unknown, but could be inferred from captures of postpartum females (Fig. 4.9) and young-of-year (YOY) or neonate snakes (Table 4.9B).

Most captures of postpartum females occurred in October (67%, Table 4.9A; Fig. 4.9), but a 97.2 cm female captured on 29 July 1992 was determined to be postpartum based on her emaciated condition, and postpartum females were also captured on 15 and 28 August. In addition, two individuals measuring 23.5 cm and 25.5 cm were captured on 28 July 1995 and 1997, respectively (Table 4.9B). The larger of the two individuals could have been born the previous year, but the smaller individual had an umbilical scar indicating that it was a neonate (Table 4.9B). The records of neonates in late July, combined with the observations of postpartum females, indicate that at least a small proportion of the females gave birth by late July and early August.

Females determined to be gravid or postpartum in the field ranged in size from 79.5-130.5 cm (n = 135, mean = 98.19 ± 8.35); captive gravid females were between 80.0 and 115.8 cm (mean = 96.64 ± 1.28). Based on data collected after July 1, when gravid females were more easily distinguished from non-gravid females, I determined that the proportion of gravid females increased with size, ranging from 7% of the 75-85 cm females to 100% of the larger females, with an average of 49.5% over all mature size classes (Fig. 4.10).

Based on several measures of the maternal size (SVL, mass, and body condition) and characteristics of the litters (litter size, mean neonate SVL, mean neonate mass; Table 4.10), significant correlations (Spearman Rank Correlations) existed between maternal SVL and litter size ($r = 0.58$), maternal mass and litter size ($r = 0.53$), and maternal mass and mean mass of the neonates in the litter ($r = 0.21$; Table 4.11). Maternal length was also significantly correlated with RCM ($r = 0.22$) and maternal body condition was correlated with mean mass of the neonates in the litter ($r = 0.333$; Table 4.11). Relative clutch mass was significantly correlated with litter size ($r = 0.81$, $P<0.0001$).

Only maternal SVL was significant in the stepwise regression model with litter size as the dependent variable. Whereas female length was determined to be the best predictor of litter size, the regression explains only 35% of the variability in this relationship (Fig. 4.11). Additionally, stepwise regressions indicated that only female body condition was significant in the model with mean neonate mass as the dependent variable and litter size, maternal mass, and mean neonate mass were all found to be significant in the model with RCM as the dependent variable. None of the variables (maternal SVL, maternal body condition, and litter size) selected for the model with mean neonate SVL as the dependent variable were significant in the stepwise model. Therefore, female length was correlated with litter size, female body condition was correlated with neonate mass, and litter size, female mass, and mean neonate mass were all correlated with RCM. Neonate SVL appears to be independent of litter size and maternal characteristics. Three litters consisted entirely of stillborn individuals and were not included in the regressions and other analyses.

I used multiple regression to assess the relative strength of the relationships among maternal traits, litter size, and offspring traits. Significant variables from the stepwise regression procedures were combined with others that I hypothesized may have an influence on offspring characteristics, and were compared as follows: 1) litter size regressed on maternal SVL and body condition, 2) mean offspring mass regressed on maternal SVL, maternal body condition, and litter size, 3) mean offspring SVL regressed on maternal SVL, maternal body condition, and litter size, and 4) maternal SVL and body condition, litter size, and mean offspring SVL and mass.

The multiple regressions supported the results of the stepwise regression procedure and all models were significant (ANOVA, $P<0.01$) except for the mean offspring SVL model ($P = 0.23$). Maternal SVL and mass were significantly correlated with litter size, offspring mass, and RCM, but not the mean SVL of the offspring in those litters. Maternal body condition was not correlated with litter size, but was a significant variable in the regressions for mean offspring mass and RCM. The only variable that was not significant in the RCM model was mean offspring SVL.

I constructed a path diagram based on hypothesized relationships among reproductive characteristics in order to evaluate the direct as well as the indirect relationships among females and their offspring (Fig. 4.12). Arrows on the diagram indicate the probable causal relationships among reproductive traits based on the correlation and regression analyses presented above. Multiple regressions were used to calculate the path coefficients, which are equivalent to the standardized partial regression coefficients (King, 1993; Madsen and Shine, 1996). The variables used in the multiple regression models and the path diagram are presented in Table 4.12. Similar to the stepwise regression procedure discussed above, the multiple regression models found significant relationships among 1) maternal SVL, litter size, and RCM, and 2) maternal body condition, offspring mass, and RCM, and 3) all included independent variables (maternal SVL, body condition, litter size, and mean offspring mass) were significantly correlated with RCM (Table 4.12). An interesting finding of the multiple regression model that supports the stepwise regression model was that none of the independent variables used in the model (maternal length, maternal body condition, and litter size) with mean offspring SVL as the dependent variable were significant and the multiple regression model for SVL was not significant ($F_{3,100} = 1.469$, $P = 0.23$). The standardized partial regression coefficients from the multiple regressions, along with the path diagram (Fig. 4.12), were used to estimate direct, indirect, and overall effects (i.e., effect coefficients = sum of direct and indirect effects) relating female size and condition to litter size, neonate mass, and RCM (Table 4.13). The values for indirect effects were determined by calculating products of path coefficients (standardized partial regression coefficients) along indirect pathways on the path diagram (King, 1993; Madsen and Shine, 1996). For example, the effect of maternal SVL on RCM through litter size (0.634) is the product of the direct effect of SVL on litter size (0.592) and the effect of litter size on RCM (1.071; Fig. 4.12, Table 4.13). The path diagram (Fig. 4.12) and effect coefficients (Table 4.13) indicate that maternal SVL most strongly affects litter size and RCM (through litter size) but has little influence on neonate mass. Alternatively, maternal body condition has little affect on litter size or RCM, but has a positive effect on neonate mass. Larger females produce more young and females in better condition produce heavier young.

VARIABILITY WITHIN LITTERS AND RELATIONSHIPS BETWEEN LITTER SIZE, OFFSPRING SIZE, AND MATERNAL SIZE

A nested ANOVA model (offspring sex nested within the litter effect) showed that offspring mass and length were significantly different among litters (mass: $F_{101, 100} = 26.724$, $P < 0.0001$; SVL: $F_{101, 100} = 24.946$, $P < 0.0001$) and mass differed between sexes within litters ($F_{100, 1675} = 1.441$, $P = 0.0035$); however, male and female offspring did not differ in length (SVL) within litters ($F_{100, 1674} = 1.045$, $P = 0.364$). Female offspring were heavier than males in 70% (81 of 115 litters) of the litters. In 14 of these 81 litters females were significantly (t-tests, $P<0.05$) heavier than males, whereas in only one case in all litters ($n = 115$) were males significantly heavier.

Because neonate size varied among litters, and evaluating only pooled data may mask biologically meaningful characteristics such as variability in neonate size within litters, I analyzed within-litter differences in size of neonates. In order to assess the details of the within-litter differences in neonate mass, I compared neonate mass between the sexes in each litter to determine if these sexual differences in mass were common among litters.

Litter size was not correlated (Spearman rank) with either neonate mass ($r = 0.010$, $P = 0.92$) nor length ($r = 0.026$, $P = 0.79$). However, because litter size is positively correlated with maternal body size (Fig. 4.11), I controlled for possible influences of maternal body size on the litter-offspring size relationship by computing residual scores from the regression of clutch size on maternal SVL. The resulting size-corrected litter sizes (residual scores) were not significantly correlated with neonate body size (Fig. 4.13).

Although I could not detect a trade-off between offspring size and number in the full data set, I hypothesized that a trade-off could exist that may not be detected using the full data set; that is, the large number of litters near the mean could mask a trade-off present in the extremes. I addressed the question of a potential trade-off between offspring size and number in two ways using subsets of the full data set. First, I examined characteristics of those litters that fell outside of one SD for mean offspring mass and length. Second, I compared neonate and maternal characteristics between the largest and smallest litters; that is, those litters that fell outside of one SD of the mean litter size. If a trade-off between offspring size and litter size exists, one would expect to observe this trade-off in the litters with the largest or smallest neonates even if the trade-off was not apparent in litters closer to the mean for offspring size. Therefore, I sorted all litters ($n = 118$) by mean offspring mass (Fig. 4.8), selected those litters that fell outside of the mean offspring mass ± 1 SD, and compared the litters with the mean lightest offspring ($n = 13$) to those with the mean heaviest offspring ($n = 11$). Mean litter size was not significantly different between these two groups (Table 4.14A).

Maternal body condition differed significantly between the lightest and heaviest litters (t-test, $t_{22} = 3.548$, $P = 0.002$) and differences in maternal mass were nearly significant ($P = 0.059$), with heavier females in better condition producing the heaviest litters (Table 4.14A). Heavy litters also consisted of longer neonates, with mean offspring SVL differing between the two groups (Table 4.14A). In a similar comparison using those litters that fell outside of mean ± 1 SD litter SVL, only mean neonate mass (t

= 7.239, P<0.0001) and RCM (Mann-Whitney U, P = 0.039) differed significantly between the litters containing long offspring (n = 15) and shorter offspring (n = 18). Unlike the differences observed in mean litter offspring mass, maternal body size (SVL and mass) and condition were not significantly different between the longer and shorter offspring groups.

Mean litter size was not significantly different between litters that contained combinations of both the heaviest mean neonate mass and longest mean SVL (“heavy-long”, N=7), and the lightest mean neonate mass and shortest SVL (“light-short”, N=8). However, maternal body condition differed significantly between these two groups (t-test, t_{13} = 2.690, P = 0.019; Table 4.14B). Therefore, only maternal body condition and mass were significantly correlated with differences between litters with large versus small mean offspring size – females producing the heaviest litters were of better body condition and averaged 136 g heavier than those females producing the lightest litters. Only one female produced offspring >2 SD above the means for both length and mass. This particular female produced relatively few (N=13), large offspring (mean SVL = 27.54 cm; mean mass = 17.45 g). Based on her body size (99.8 cm SVL) and the regression equation relating litter size to SVL, this female’s litter size was well below the predicted mean litter size (n = 20) for her size class.

Neither mean neonate SVL ($U_{15,17}$ = 119, P = 0.748) nor mean mass ($U_{15,17}$ = 123, P = 0.865) differed between the largest (> 25 offspring, n = 17) and smallest (< 11 offspring, n = 15) litters. Although mean maternal body condition was lower for females that produced the small litters (-28.326) versus the largest litters (12.491), this difference was not significant ($U_{14,17}$ = 89, P = 0.234). The female with the largest litter (n = 50) was also the largest individual for which I had litter data (Table 4.10, Fig. 4.11). Using the linear regression of litter size on SVL, she produced 18.5 more young than would be predicted for her length (115.8 cm SVL). If a trade-off existed between litter size and offspring size, even if the trade-off could not be detected in the full data set, then it seems plausible that the trade-off should be apparent in this large litter. Mean size for the neonates in this litter of 50 was 24.02 cm SVL and 10.22 g, values nearly at the sample means for all litters (24.32 cm, 10.80 g; Table 4.10). At the other end of the extreme in litter size, two females each produced litters of four offspring, 14 to 16 offspring less than predicted by the regression equation for their sizes (90.5 and 93.0 cm SVL). Although one of these two females (90.5 cm SVL) produced offspring of mean length (23.60 cm SVL) near the sample mean for neonate length (24.32 cm), the other female (93.0 cm SVL) produced the litter with the smallest average offspring length out of 104 litters (20.05 cm; Table 4.10). Both of these small litters also consisted of relatively light offspring (mean litter masses of 8.28 and 7.13 g).

VARIABILITY IN LITTER SIZE

Although litter size is highly variable, litter size variation did not differ among years irrespective of the measure of dispersion used to tests the differences, although the tests using the residuals of litter size were nearly significant (P = 0.068; Table 4.15). I analyzed among year variability in litter size variation using two measures of dispersion. First, I calculated a “standardized deviation score” (Shine and Seigel, 1996). Secondly, I computed the residuals of the regression of litter size on maternal SVL and used these values as measures of dispersion (Litter Residuals).

As variation in litter size increased, mean neonate size decreased. Three separate measures of litter size dispersion were significantly correlated with one another and showed similar correlations with neonate body size: variation in litter size was negatively correlated with mean neonate SVL and mean neonate mass (Table 4.16). In examining the relationships between variability in litter size with mean neonate body size (mass and SVL) and dispersion (CV) of neonate body size, I used Shine and Seigel's (1996) "standardized deviation score" (CV in Table 4.16), and the residuals of litter size regressed on female SVL (Litter Residuals). I also calculated CV2 as the absolute value of the Litter Residuals (Table 4.16) because I was interested in the effects of variability in general and not specifically whether or not that variability was negative (below the mean) or positive (above the mean).

Path analysis indicated that RCM was affected most by litter size and maternal length (Fig. 4.12, Table 4.13). Mean RCM (±2SD) for *N. taxispilota* was 0.306 ± 0.182 (range 0.072-0.567) and did not vary significantly among years (ANCOVA, maternal mass as the covariate, $F_{5,108}= 0.840$, $P = 0.524$). Although a significant positive correlation existed between RCM and maternal length ($r = 0.224$, $P<0.05$; Table 4.11B), the linear regression for this relationship was nonsignificant and highly variable ($P = 0.06$, $R^2 = 0.03$).

DISCUSSION

POPULATION SIZE, SURVIVAL RATE, AND RECRUITMENT

My estimates of population size and density (0.14-0.20 snakes per meter; Table 4.3) were substantially higher than a previous estimate (Mills et al., 1995) for this population (0.02 snakes per meter) using Bailey's triple catch method, but within the range of linear densities reported for other snakes (0.02-0.38 snakes per meter, Parker and Plummer, 1987). As stated previously, a more useful way to view these linear densities is as follows: one snake per 7.2 m (Bailey's), 5.1 m (Jolly-Seber), and 46.9 m (Mills et al., 1995). The estimates reported here are six to nine times higher than my previous estimate of population density. Have *N. taxispilota* numbers increased since the previous study, or have the additional recaptures allowed for an improved estimate of population densities? These explanations are not mutually exclusive alternatives. The population was growing as indicated by the population recruitment estimates (Table 4.3). However, with relatively low recapture rates, the population estimates have a great deal of variability and thus potential error. As stated previously, Roff (1973) suggested that a population estimate is reliable only if the SD is less than 5% of N_i (i.e., coefficient of variation < 0.05), and that such values can only be obtained with "very high" sampling intensities (greater than 0.4, or 40% of N). My standard deviations of N_i range from 38-86% of N_i, and my sampling intensity was about 0.23 (given an estimated N of 3956), indicating a low level of reliability.

Because the assumption of equal catchability was not met and recapture rates were low, estimates of some population parameters are highly variable. Few researchers test the assumption of equal catchability in studies of snake populations (Parker and Plummer, 1987; but see Plummer, 1985). The overall high densities of *N. taxispilota*, under representation of juveniles in my samples, and the mobility of the individuals in the study areas hampered my ability to recapture marked snakes. The lack of neonates and young snakes could be due to differences in habitat use between the various size classes (Mushinsky et al., 1982; Savitzky and Burghardt, 2000). Small *N. taxispilota*, similar to

N. rhombifer (Savitzky and Burghardt, 2000), may be more difficult to locate because of their small body size and the habitat they select. In a series of laboratory experiments coupled with previous field observations, Savitzky and Burghardt (2000) found that neonate *N. rhombifer* were highly aquatic and remained in vegetative cover, habits that make small aquatic snakes more difficult to observe and capture. Many of the small snakes captured in the present study (Table 4.9B) were seen and captured "secondarily" while the collector was swimming for a larger snake that was initially observed from the boat. If perch height is considered as one measure of habitat use (Mills et al., 1995), then significant differences existed in this habitat variable between small snakes (<30 cm SVL) and larger snakes, with small individuals perching an average (± 2 SE) of 30.1 ± 7.3 cm (n = 51) above the water and larger snakes perching an average of 70.6 ± 3.1 cm (n = 1211) above the water (unpublished data), making longer snakes more likely to be seen in areas of heavy vegetation or debris.

My study sites do not encompass well-defined populations; therefore, immigration and emigration were expected and could be substantial. Snakes were free to move up or downstream, as well as into and out of adjacent bodies of water. I sampled adjacent areas (e.g., upstream and downstream and tributaries of site a, Fig. 4.1), but not as intensively as the primary study areas, and documented five individuals that moved from one study site to another (e.g., UTR creek to the Savannah River). Sampling outside of the main study sites might be a productive area for future efforts in order to better estimate movement in and out of my Savannah River study site. An alternative approach is to enlarge the size of the prescribed study area in order to encompass a larger portion of this species home range or activity area. However, either approach would be costly in terms of research effort.

The low number of recaptures may result from animals periodically moving from, then returning to the study area. The present mark-recapture study and concurrent radiotelemetry work (Mills, unpubl.) have shown that individuals will often return to the same area (and often to the exact basking site) even after long-distance movements. For example, I captured a 52.1 cm female in the Savannah River (site a) in September of 1993. In June of 1999, almost six years later, she was recaptured for the first time and had grown to 106.9 cm (Table 4.5). Where had she been for six years? Why was she never captured during that period? In terms of population and survivorship estimates (Table 4.3), she was considered to be dead or to have emigrated from the population during her absence. When she was recaptured six years later, she was included in the recruitment estimates. Similar observations were made of a male that was captured five times. I captured this 53.0 cm male in August of 1993, recaptured him 21 days later in September, then again the following March. He was then not recaptured until over four years later, in June of 1997, then again in September of 1997 at 74.0 cm (Table 4.5). Because this male was captured multiple times on either side of his four-year absence, it is possible that during the four years he was unavailable for recapture (i.e., he was not in the study site). Blanchard et al. (1979) documented similar extended absences in a Michigan population of *Diadophis punctatus*, recapturing two male ring-neck snakes that had escaped capture for seven and eight years, respectively, and both males and females with 2-5 years between clusters of recaptures. Feaver (1977) would have counted “missing” individuals as dead in his four-year study of *N. sipedon*, because his survivorship estimates assumed that if an individual was not recaptured then it was dead. Counting the missing individuals as dead could partially explain why Feaver's (1977) survivorship estimate (0.35) for *N. sipedon* is the lowest survivorship estimate for any snake (Parker and Plummer, 1987; Shine and Charnov, 1992). Thus, Feaver's (1977) interpretation of low survivorship may have been, in part, the consequence of a short-term study.

Estimated survivorship for this population of *N. taxispilota* was relatively high but within the range reported for snakes (Parker and Plummer, 1987; Shine and Charnov, 1992). Mean adult survivorship for other species of snakes ranges from 0.35 to 0.85 (mean±SD = 0.65 ± 0.15, n = 17), and is positively correlated with age at maturity (Shine and Charnov, 1992).

GROWTH PATTERNS

Growth patterns and age/size classes were reported for a central Georgia population of *N. taxispilota* (Herrington, 1989) and correspond closely to mine (see Chapter 1). The reported growth curves (Fig. 4.6) and sexual size dimorphism (Fig. 4.2) place *N. taxispilota* in Feaver's (1977) Group 2 category (males smaller than females). Growth was similar for juveniles of both sexes, but adult males grew significantly slower than both adult females and juveniles (Table 4.4A). Reduced male growth rates may be due in part to decreased foraging by adult males. Adult males feed less frequently during mating season and eat less frequently than juveniles throughout the year (Chapter 3). Lipid reserves and body condition of adult male snakes have been shown to decrease during mating season (Blem and Blem, 1990; Bonnet and Naulleau, 1996), possibly as a result of decreased feeding and increased energy used to fuel mate-searching activities

(Brown and Weatherhead, 1999). Decreased growth in males versus juveniles and females is one explanation for the smaller mean body size observed in males as compared to females in this and other species of snakes. Other explanations for sexual size dimorphism observed in *Nerodia* sp. and other reptiles include sexual differences in juvenile growth rates and differences in age at maturity between males and females (Dunham and Gibbons, 1990; Gibbons and Lovich, 1990; Shine, 1993). Similar to turtles (Gibbons and Lovich, 1990), sexual size dimorphism in *Nerodia* sp. seems to be the result of differences in body size (and presumably age) at maturity (this study; Brown and Weatherhead, 1999), although potential sexual differences in juvenile growth rates not detected statistically in the present study cannot be excluded (Shine, 1993; Brown and Weatherhead, 1999).

Whereas adult males are smaller than females, body size is highly variable in both sexes (Fig. 4.2). A benefit exists for females to attain larger body size – fecundity increases with size (Fig. 4.11). Because growth continues after maturity, larger males presumably have some advantage over smaller males, perhaps in terms of acquiring mates, greater survivorship through predator escape, or prey acquisition.

Size of offspring at the end of their first year may be influenced by several factors, including date of parturition, size at birth, and variability in growth rates. I estimated a potential size difference of almost 295 mm between hypothetical individuals born early at a large size and growing at a maximum rate, and those born late at a small size and growing at a minimum rate (Table 4.4B). The projected difference in potential body sizes at the end of the first year of growth for imaginary offspring (Table 4.4B) may not be realistic, but offers some insight into the variability observed in the estimates of age. Early birth at maximum body size is not supported by other studies that show an early parturition date negatively affects offspring body size in viviparous snakes (e.g., *Storeria dekayi*; King, 1993). However, neonates born earlier have a longer period to grow than those born late in the season. For example, *N. harteri* born in early August have been reported to nearly double in size prior to hibernation (Greene et al., 1999). The relationship between parturition date and neonate body size was not tested in my study, but if I assume a minimum size at birth (200 mm), the potential body-size difference at the end of the first year of individuals growing at the maximum and minimum rates would be approximately 210 mm. Therefore, parturition date alone could have a profound influence on the size of individuals at the end of their first year and presumably on the subsequent age at maturity (assuming maturity is based on size and not age).

AGE AT MATURITY

Age at maturity for *N. taxispilota* (approximately 6 years for females, 3 years for males) was estimated based on size at maturity and the von Bertalanffy growth equations. However, the actual size of individuals was variable for a given predicted age (Fig. 4.6B). The variability between predicted and actual ages would become problematic if these age estimates were used in constructing a life table. For example, an imaginary female in the Savannah River may reach maturity (age at first reproduction) in 4-10 years depending on her size at birth and growth rate (Table 4.6). Compared to other snakes, even the minimum estimate for age at maturity for females (4 yr; Table 4.6) places *N. taxispilota* in the “late maturing” category of snake life histories (Parker and Plummer, 1987).

Although most studies of reptile and amphibian life history use estimates of age based on size at initial and subsequent captures, significant differences in individual growth rates within a population can weaken the reliability of age estimates obtained in this manner (Dunham et al., 1988). Unlike growth annuli on the shells of turtles, snakes and other squamates do not possess external structures that allow individuals to be aged, therefore the most reliable method is to mark known-age individuals (i.e., neonates). Halliday and Verrell (1988) reviewed the literature relating body size to age in amphibians and reptiles and concluded that the large variance in body size at any given age precludes accurately assigning ages based on body size. They also suggested that growth prior to age at maturity was largely responsible for the variability in adult body size. Using skeletochronology on tail vertebrae of garter snakes, Waye and Gregory (1998) concluded that predicting age based on an individual's size would be impossible, especially in older snakes (after the fourth hibernation). Some species of turtles, which have growth rings or annuli that can be used to age younger individuals, can be difficult (impossible?) to age after they reach maturity without a prior capture history. For example, in *Emydoidea blandingi* mean plastron length of an older cohort (47+ yrs) was not significantly different from that of a much younger group (mean age of 21 yrs) of females (Congdon and van Loben Sels, 1991).

Life history traits such as growth rates, age at maturity, and frequency of reproduction may be greatly under- or overestimated in short term studies (< 5 yr) on long-lived snakes, especially in a variable environment (Bronikowski and Arnold, 1999; Madsen and Shine, 2001). The error in estimates of the above mentioned traits is increased if traits such as growth rates are estimated with an under-representation of juveniles, for which growth will be the greatest and perhaps most variable. For example, Madsen and Shine (2001) point out an error in properly assessing growth rates in an earlier study of the same population of filesnakes, primarily because of the lack of small snakes used in those estimates, which led to the conclusion that filesnakes mature somewhere between 5-7 yr, whereas a longer-term study which included growth rates of juveniles concluded that age at maturity is closer to 3 yr. Whereas the present study is long-term by Madsen and Shine's (2001) definition, it suffers from the problem of their short-term study, namely a lack of small snakes in the estimates. Of course, the definition of a "long-term" or "short-term' study is relative, and really depends on the lifespan of the study organism (Cody, 1996); that is, if an organism does not reach sexual maturity until it is 18, then a 10-yr study is hardly "long-term."

LONGEVITY

Individuals of both known and estimated age revealed that *N. taxispilota* is a relatively long-lived species of snake, living a minimum of eight years (Table 4.5). Estimated longevity for other species of colubrid snakes range from 5-20 years (Table 9-5 in Parker and Plummer, 1987). The only natricines in their table, *Thamnophis sirtalis* and *N. sipedon*, both have estimated longevities of eight years or less. Ring-neck snakes (*Diadophis punctatus*) may be the longest-lived colubrids reported, with individuals in a Michigan population recaptured after 15-17 years and estimated to be >21 years old (Blanchard et al., 1979). In captivity, the natricines *N. sipedon*, *N. erythrogaster*, and *Regina septemvittata* have been documented to live at least 7.3, 8.8, and 19.3 years, respectively (Bowler, 1977).

LITTER CHARACTERISTICS

Mean litter size reported in the present study (18.2 offspring/litter) falls within the range of reported values for other *Nerodia* sp. (Tables 4.17 & 4.18) and other colubrid snakes (Seigel and Ford, 1987; Dunham et al., 1988; Shine and Seigel, 1996), although reported litter sizes for *N. taxispilota* and other *Nerodia* species are typically higher than for colubrid snakes in general.

I observed an increase in mean number of offspring as the female increased in size (approximately 1 offspring for every additional 1.44 cm of body length), although the variability in litter size at any given maternal body size was substantial and increased with the size of the female (Fig. 4.11). Female SVL explained only 36% of the variance in litter size when data were combined for all years (Fig. 4.11). However, annual differences in female SVL-litter size relationships (Fig. 4.14) were a potential source for variability observed in combined data for all years (Fig. 4.11), and female SVL explained as much as 82% of the variance in litter size in a single year (1993, Fig. 4.14). Possible sources of variation that I did not explore were the date of birth and the number of days in captivity, both of which have been shown to influence litter size in snakes (King, 1993; Madsen and Shine, 1996).

Although mean litter sizes among individuals in the present study was high, litter size did not vary significantly among years. Shine and Seigel (1996) reviewed clutch-size variance in snakes, including *N. taxispilota*, hypothesizing that among-year differences in variance of yearly means may be biologically significant. In addition to using standard measures of dispersion (including standard deviation and coefficient of variation), they devised two “new” measures of variance: “uncorrected deviation score” and “standardized deviation score”, which are analogous to SD and CV, respectively (Shine and Seigel, 1996). I also used the residual values of the maternal length-litter size regression and the absolute value of these residuals scores as estimates of dispersion (Table 4.15). Regardless which measure of dispersion was calculated, among year variability in litter size variation was nonsignificant for all natricine snakes presented in Table 4.15; although the tests for *N. taxispilota* were nearly significant using the litter residuals as estimates of dispersion (P = 0.068; Table 4.15).

Based on the present study, neonate *N. taxispilota* are relatively large (24.4 cm SVL; Table 4.7) compared to other colubrid snakes. For example, Parker and Plummer (1987) reported mean female neonate length ranging from 7.9 cm (small viviparous colubrids) to 28.0 (large oviparous colubrids) with a mean of 17.1 cm for all colubrid categories at (n = 6 categories of colubrid snakes). Greene et al. (1999) reported within-litter sexual size dimorphism in *N. harteri*, with females exceeding males in SVL. Within-litter sexual size dimorphism was also evident in the present study; however, in *N. taxispilota* neonate females exceeded males in mass but not length.

PARTURITION AND RELATIONSHIPS BETWEEN FEMALES AND LITTERS

Not all females in my study reproduced in a given year. Based on postpartum females in the field and captive females, parturition begins in late July and extends into October, a pattern observed in most north temperate zone snakes (Seigel and Ford, 1987). Among adult females captured after July 1, 49.5% were determined to be gravid or postpartum. The proportion of adult females reproducing varied by size class from less than 10% in the smallest size class to 100% of the largest individuals. Sexually mature females “skipping” reproduction in a given year is relatively common in snakes. Among

85 species or populations of snakes reviewed, the proportion of females breeding in a given year can range from 7-100% (Seigel and Ford, 1987).

Several reasons can be given to explain the observed variability in reproductive frequency. Because of the variability in age or size at first reproduction in the present study, a portion of the females included in my smallest size-classes may not have been mature (e.g., 75-85 cm size class, Fig. 4.10). The proportion of females breeding in a population may also be a function of body condition or lipid reserves (Aldridge, 1979; Blem, 1982; Blem and Blem, 1990; Madsen and Shine, 1996; Naulleau and Bonnet, 1996). Many temperate-zone snakes can, but may not, reproduce annually based on lipid reserves which in turn are influenced by such factors as foraging, injuries, and previous reproduction (Blem, 1982). Therefore, body condition (i.e., how robust or fat a snake is), as an indirect measure of lipid stores, should be correlated with reproductive allocation and has been in some squamates (e.g., Naulleau and Bonnet, 1996; Olsson and Shine, 1997). Naulleau and Bonnet (1996) found a body condition threshold below which *Vipera aspis* did not reproduce regardless of size and Madsen and Shine (1996) reported a similar finding for water pythons (*Liasis fuscus*).

Nerodia taxispilota feed during the early stages of pregnancy (Chapter 3) and significant positive correlations exist between body condition and offspring mass but not litter size (Table’s 12 & 14). Partial yolking of ova occurs in the fall before hibernation in *N. taxispilota* (Blem and Blem, 1990); although White et al. (1982) observed vitellogenesis only in the spring (April-June). Betz (1963) found that primary oogenesis begins 2 years prior to ovulation in the closely related *N. rhombifer*. Thus, the female’s body condition (i.e., relative lipid reserves) the prior year may determine not only whether she is able to reproduce, but also the litter size and/or the size of the offspring. Because ova begin yolking the previous fall, feeding (i.e., additional energy) during pregnancy would be expected to alter the size but not the number of young, or the “extra” energy could be placed into the soma for future reproduction (Gregory and Skebo, 1998). Additionally, if females vary in their energy acquisition during pregnancy, then trade-offs may be undetectable through comparisons of different individuals (Gregory and Skebo, 1998). Gregory and Skebo (1998) found no significant differences in either litter size or neonate size between females fed during pregnancy and those that were not fed; however, females that were fed had significantly higher postpartum masses than unfed females. My study supports Gregory and Skebo’s (1998) proposal that increased body condition (via feeding during pregnancy) should affect offspring mass but not number.

In reviews of squamate life histories and reproduction, many of the reproductive and life history traits (e.g., age at maturity, proportion of females breeding, offspring size and number, and RCM) are significantly correlated with female body size (Seigel and Ford, 1987; Dunham et al., 1988). However, the interrelationships among these traits are often complex and not always intuitively obvious (Dunham et al., 1988). One method used to elucidate the complexity of these interrelationships (i.e., evaluate both direct and indirect relationships) is through path analysis.

Indirect effects can be as important and often more important than direct effects when analyzing the relationships between the reproductive traits of females and their offspring (King, 1993; Madsen and Shine, 1996). Additionally, potential trade-offs may be masked by these indirect effects. For example, in water pythons female length and body condition are both positively correlated with egg mass and clutch size; however, egg mass is negatively correlated with clutch size (Madsen and Shine, 1996). These conflicting relationships reduce the direct effect of female length on egg mass from 0.74 to 0.16 (standardized partial regression coefficients; Madsen and Shine, 1996).

Indirect effects are also evident in my study. A negative direct relationship exists between maternal size and RCM; however, once the indirect effects of litter size and neonate mass are accounted for, the overall effect (effect coefficient) becomes positive, largely due to the effects of litter size on RCM (Fig. 4.12, Table 4.13). The effect coefficients calculated from the path diagram indicate that maternal size most strongly affects litter size and RCM, whereas maternal body condition has the strongest effect on offspring mass (Table 4.13). In contrast to my results, several other studies on snakes determined that body condition had a significant positive influence on litter size (King, 1993; Madsen and Shine, 1996; Gregory and Skebo, 1998). Large values (0.35-0.94) for unexplained variance in the path diagram (Fig. 4.12) indicate that variables exist that I did not measure. Indirect effects not included in the path diagram (e.g., parturition date and days in captivity) may help explain the relatively large proportion of “unexplained” variance in most of the regression and correlation coefficients presented in the present study and offer a fruitful avenue for future research and analysis.

RELATIVE CLUTCH MASS

The ratio of clutch mass to body mass (RCM) is adaptive and reflects evolutionary compromises between increased reproductive output (higher RCM) and physical constraints and ecological costs associated with relatively larger clutch masses (Vitt and Congdon, 1978). Vitt and Congdon (1978) and others (e.g., Vitt and Price, 1982; Seigel and Fitch, 1984; Seigel et al., 1986) have concluded that RCM need not be correlated with reproductive effort (the portion of the energy budget allocated to reproduction) and should be viewed as a distinct life history trait under different selective pressures than clutch size or offspring size. Relative clutch mass is related to female survivorship, foraging mode, predator escape behavior, and may also vary due to resource availability and acquisition (Vitt and Price, 1982).

Relative clutch mass was weakly correlated with female size (SVL), and did not vary significantly between years in *N. taxispilota*, consistent with studies on other snake species (Seigel and Fitch, 1984; Seigel et al., 1986). Relative clutch mass for *N. taxispilota* (mean = 0.306) was similar to other viviparous colubrids (mean = 0.295) and fell within the range of other *Nerodia* sp. (mean = 0.257, range 0.112-0.396; Seigel and Fitch, 1984). The among year consistency in RCM in snakes (Seigel and Fitch, 1984) and lizards (Olsson and Shine, 1997) may be an artifact of the calculation of RCM (Olsson and Shine, 1997). In the sand lizard, *Lacerta agilis*, females in better body condition produced heavier offspring, thus increasing both the numerator and denominator of the RCM ratio and producing an RCM value similar to females in poorer body condition that produce lighter offspring.

The RCM favored by natural selection should reflect a compromise between maximum number or size of offspring and the physical burden of the clutch on the gravid female. Assuming additional clutch mass would play a lesser role in the neutrally buoyant aquatic environment, one might expect RCM to be higher in aquatic versus terrestrial snakes. However, using Seigel and Fitch’s (1984) data, Shine (1988) found that RCM was significantly lower in aquatic (mean = 0.23, range: 0.11-0.29) than terrestrial snakes (mean = 0.33, range: 0.11-0.55), with those classified as semiaquatic being similar to terrestrial species (mean = 0.32; range: 0.20-0.61). Although Shine's classification of species as aquatic, semiaquatic, or terrestrial may have influenced his conclusions regarding exact means and ranges of RCM's (e.g., based on his reported ranges, he omitted at least two *Regina* sp. from his "aquatic" category), the trend towards lower relative clutch masses in aquatic snakes was documented in multiple families of snakes (Shine, 1988). Shine related the lower RCM in aquatic species to the physical limitations placed on swimming performance by the presence of the clutch in the posterior portion of the snake's body. By measuring the relative position of the clutch in the snake's body, Shine (1988) was able to show that the clutches of highly aquatic species were truncated posteriorly, presumably reflecting the impact of locomotion (swimming) and habitat (aquatic) on RCM.

Although RCM should not be used as a direct estimate of reproductive effort (Vitt and Congdon, 1978), Blem and Blem (1990) suggested that RCM could be calculated by converting reproductive mass into kilojoules and then regressing this energy (kJ) on body mass to evaluate reproductive allocation, which would allow the central ideas of life history theory to be addressed, i.e., the allocation of energy (not mass) to reproduction, growth, maintenance, or storage. Mass may not be a good predictor for energy expended on the offspring because the female may expend energy that is not included in the offspring's mass. Additionally, in *N. taxispilota* lipid content of fat bodies changes as the fat bodies increase in size and weight, from about 20% lipid in small fat-bodies to about 98% in large fat-bodies (Blem and Blem, 1990).

Body size and shape and RCM are linked; that is, the female's body volume determines, in part, the upper limits of RCM (Vitt and Congdon, 1978; Shine, 1992), or selection for increased RCM has influenced the evolution of body shape (Shine, 1992). In conjunction with the limits set by body shape, RCM may be determined by the maximum burden the female can accommodate in consideration of the resulting effects this additional burden may have on performance and thus survivorship (e.g., swimming or crawling; Shine, 1988; Plummer, 1997).

TRADE-OFF BETWEEN OFFSPRING SIZE AND NUMBER

Selection against additional mass and girth may ultimately set the upper limit of clutch mass and size. However, the upper limit of reproductive investment is also set by energy availability, given a female must allocate assimilated energy among reproduction, growth, maintenance, and storage (Congdon et al., 1982; Dunham et al., 1989). Therefore, reproductive output is potentially governed by energy availability (responsible for among-year variation) and constraints set by body size (Olsson and Shine, 1997). Given that an upper limit exists and is controlled by natural selection or sexual selection, the female may partition the reproductive mass (i.e., energy) between more smaller offspring or fewer larger offspring (Smith and Fretwell, 1974). I examined the hypothesized trade-off between offspring size and number in the present study using the reproductive data collected for *N. taxispilota*.

Mean litter size was not significantly different between the lightest and heaviest litters. Although offspring size was highly variable (Fig. 4.7), no apparent relationship existed between offspring size and size-corrected litter size (Fig. 4.13). However, relationships, and particularly “trade-offs,” between reproductive traits can be difficult to detect (Stearns, 1992). Although I could not detect a trade-off between offspring size and number in the complete data set, when I subdivided the data (see Results) to examine possible differences in the extremes of offspring size and litter size, still no difference was observed. In addition to these observations, variability in litter was negatively correlated with mean neonate size. As litter size varied from the mean in either direction, mean neonate body size decreased. Therefore, based on the comparisons of neonate body size and litter size in both pooled and partitioned data sets, I could not detect a trade-off between litter size and offspring size.

A trade-off between offspring size and number was not evident in the present study, although apparent trade-offs between offspring size and number exist in some species of squamate reptiles (e.g., Ford and Seigel, 1989; King, 1993; Madsen and Shine, 1996; Olsson and Shine, 1997), but have not been demonstrated in others (see Table 4.19). No relationship existed between litter size and length or mass of neonate *N. taxispilota* (Fig. 4.13, Table 4.12). Mean offspring size was similar among litters of all sizes, although the variation in offspring size (both above and below the mean) tended to increase in litters below the predicted mean litter size (Fig. 4.13). Litters that deviated both above and below the mean litter size (based on female SVL-litter size regression) tended to produce smaller young (Fig. 4.13, Table 4.16). Although this finding is not a trade-off in the traditional sense (i.e., larger litters = smaller offspring), it does potentially represent an example of stabilizing selection. If deviations from the mean litter size result in smaller neonates, and neonate size is correlated with some measure of quality, then natural selection should work against deviations in litter size. Additionally, whereas a trade-off was not detected statistically, limited qualitative support exists for a trade-off in selected individual litters. The largest mean offspring sizes (mass and length) were observed in the smallest litters below the mean litter size (i.e., negative residual litter values; Fig. 4.13), and the largest litters tended to have smaller offspring (below mean offspring size for positive residual litter values).

Despite this finding for the extremes in litter size, the overall conclusion remains that no trade-off exists between offspring size and litter size in *N. taxispilota*, a finding similar to that of *N. rhombifer*, where larger litters were not significantly different from smaller litters in either the length or weight of the neonates (Plummer, 1992). This conclusion is also consistent with data from other natricine snakes (Table 4.19). For example, *N. harteri* produces more, rather than larger, offspring with increasing female body size (Greene et al., 1999), and some populations of *Thamnophis elegans* produce both larger litters and larger offspring with increasing female body size (Bronikowski and Arnold, 1999).

The relationship between clutch (litter) size and egg (offspring) size among reptiles remains equivocal (Ford and Seigel, 1989). Contrary to my study, Ford and Seigel (1989) found a negative correlation between clutch size and egg size in three species of oviparous snakes, and King (1993) found that larger *Storeria dekayi* and females in better condition produce larger litters of smaller offspring, providing support to the offspring size-litter size trade-off. Ford and Seigel (1989) suggested that the lack of negative correlations between these variables as reported in the literature (e.g., Table 4.19) may stem from improper analyses, specifically not adjusting for female size before testing for correlations. The lack of an apparent trade-off could also result from not accounting for indirect effects (see discussion above). King (1993) found a relationship between time in captivity during gestation and offspring size, with females that were held longer producing both smaller offspring and offspring in worse condition. Time in captivity could explain, in part, the large variability in offspring size and weight seen in my study. Some females were held for less than one week (MM snakes) whereas others (SA snakes) were held for as long as three months before parturition, although mean SVL of SA neonates was greater than MM neonates.

Reproductive success and ultimately fitness are affected by factors other than clutch size. Theoretical models of reproductive effort (e.g., Niewiarowski and Dunham, 1994) suggest that RCM, clutch size, offspring size, and offspring survival have interacting effects on lifetime reproductive success. Perhaps in *N. taxispilota* the benefits to fitness of producing more young outweigh the potential benefits of producing larger, higher quality young. The fitness benefits of large versus small young need to be demonstrated in the laboratory and the field to answer questions related to optimal offspring size theories (e.g., Sinervo et al., 1992).

At least four primary factors potentially influence offspring size and number: 1) female survival, 2) female body size, 3) offspring survival, and 4) “fecundity fitness” (i.e., selection favoring larger numbers of offspring; Sinervo et al., 1992). As previously discussed, maternal body size, survivorship, and clutch size are interrelated. Increased body size and mass of gravid females could potentially lower survivorship because of reduced locomotor performance or increased exposure to predation. For example, gravid skinks are more vulnerable to predation because they are slower and bask more often than their conspecifics (Shine, 1980), and gravid snakes are slower than non-gravid snakes (Seigel et al., 1987; Brodie, 1989; Plummer, 1997). Pregnancy decreases locomotor performance in green snakes, *Opheodrys aestivus* (Plummer, 1997) and garter snakes, *Thamnophis* sp. (Seigel et al., 1987; Brodie, 1989), but aquatic snakes are not under the same constraints of gravity as terrestrial species, so the additional mass of offspring presumably would have less of an effect on their locomotor performance. For example, experiments with water snakes (*N. sipedon*) found no difference in swimming speed between gravid and nongravid females. However, these tests were conducted early in the pregnancy and perhaps failed to document differences that would be seen during the later parts of gestation (Brown and Weatherhead, 1997). Contrary to Brown and Weatherhead, Shine (1988) suggested that higher RCM's may reduce swimming performance in snakes (see discussion of RCM above).

Gravid *N. taxispilota* may behaviorally overcome or compensate for problems such as reduced speed and greater exposure to predators due to thermoregulatory requirements of pregnancy by choosing different basking sites. I found that gravid females often basked on banks with more cover than that of exposed limbs over the water, and frequently basked with only a loop of the body exposed while the rest of the body was in a hole in the bank or under other cover (pers. obs.; Mills et al., 1995). However, this alteration of behavior could pose a potential trade-off or cost of reproduction. Gregory et al., (1999) reviewed potential trade-offs documented in gravid versus nongravid viviparous snakes, including: 1) gravid snakes bask more frequently and thermoregulate at higher, more precise (i.e., less variable) temperatures, 2) gravid snakes have higher metabolic rates, 3) gravid snakes sometimes have higher mortality rates, and 4) postpartum females are at risk of higher mortality because of their emaciated condition. Gravid *T. elegans* maintained in a laboratory setting with unlimited food eat less and maintain higher body temperatures than nongravid females (Gregory et al., 1999). These two factors, less energy intake and greater energy consumption through higher body temperature and the maintenance of developing embryos, would act together to reduce growth and energy storage and therefore future reproduction. Contrary to Gregory et al. (1999), Brown and Weatherhead (1997) found that gravid *N. sipedon* eat as much as nongravid snakes, and the authors related this ability to continue feeding to their aquatic foraging habits (but see Shine, 1988).

Clutch or litter size may be the indirect outcome of natural selection acting on the female's total investment into reproduction and the size of eggs or young that she produces (Shine, 1991). Larger neonates are often assumed to have a selective advantage over smaller individuals. Differences in size-based predation or neonate speed are often invoked as rationales, yet few studies actually attempt to test this assumption. Jayne and Bennett (1990) field-tested this assumed relationship between size and survivorship in garter snakes (*Thamnophis sirtalis*), and also tested for potential causative mechanisms (i.e., burst speed, endurance, and distance crawled on a track) for increased survivorship. They indicated that greater burst speed significantly favored survival in garter snakes and that larger neonates typically had greater burst speeds as measured in the laboratory (Jayne and Bennett, 1990).

Optimality arguments propose that the observed litter and offspring size are the result of stabilizing selection; that is selection against the extremes. The upper size of offspring in most vertebrates is imposed by constraints of the female's morphology, the most obvious being the size of the pelvis (e.g., Congdon and Gibbons, 1987). However, snakes lack a pelvis and therefore lack this constraint, although other constraints such as reduced maternal mobility may be important. The lower size limit is often selected against through reduced survivorship of the offspring, through congenital problems (e.g., birth defects), reduced performance, greater susceptibility to predation, or a combination of these factors. Selection against small neonate body size may result from small snakes having very little reserve energy, thus increasing their chances of starvation during hibernation (Blem and Blem, 1990) and perhaps reducing their ability to forage and escape predators after hibernation. In the present study, the smallest snakes exhibited more deformities than larger snakes, and stillborn neonates were significantly smaller than living offspring. Apparently smaller individuals are at some disadvantage or, alternatively, congenital defects may have contributed to the smaller size of these individuals.

Larger body size may impart some advantages to lizards, particularly territorial species (e.g., *Uta stansburiana*, Ferguson and Fox, 1984), and larger snakes may be able to better escape predation (Jayne and Bennett, 1990). Whereas larger body size may allow *N. taxispilota* to escape some predators, size differences among neonates would be of little consequence to most predators of small snakes. If a size advantage exists, then it is probably exhibited in escape speed (Jayne and Bennett, 1990) or in prey acquisition (Halloy and Burghardt, 1990) or both. Juveniles may have greater difficulty capturing and subduing small fish, particularly in moving water. Larger *N. taxispilota* have been observed swimming to shore to swallow a captured fish (pers. obs., Chapter 3), and presumably a larger body size would be an advantage to a snake holding a large fish while attempting to swim in a strong current. Future experiments concentrating on predator escape (i.e., locomotive performance) and size-based differences in prey acquisition and handling might prove fruitful in addressing optimal offspring size theories in this species.

A trade-off between offspring size and number as proposed by Smith and Fretwell's (1974) model is not apparent in the present study. Larger litters do not consist of smaller offspring. However, Brockelman's (1975) prediction that natural selection would favor an optimal offspring size, and that females would produce more, not larger offspring during "good" years, seems to apply to *N. taxispilota*. Could the lack of an observed trade-off between litter size and offspring size be a consequence of *N. taxispilota* young already being large in comparison to other *Nerodia* sp.? The selective advantages or disadvantages of being a 27-cm neonate or a 22-cm neonate are unknown. Would potential predators (e.g., birds, fish, and small mammals) discriminate between these size classes? Would a slightly larger body size allow the juvenile to better escape predation? Perhaps a possible neonate body-size advantage could be tested by measuring some component or correlate of fitness (e.g., swimming speed, Brodie and Garland, 1993) in neonates, then releasing them and documenting their survivorship to maturity through mark-recapture efforts.

Barry Sinervo and colleagues (Sinervo and Licht, 1991; Sinervo et al., 1992; Sinervo, 1999) have provided the best evidence yet for the trade-off between offspring size and number with the lizard *Uta stansburiana*. In a series of allometric engineering experiments (i.e., experimentally altering offspring size) coupled with field tests of juvenile survivorship, they found two opposing examples of directional selection at work: fecundity selection (large numbers of smaller offspring) and survival selection that favored larger offspring. Offspring size in this lizard was determined to be a result of the conflict between these two forms of selection.

If we assume that natural selection has acted to produce the "optimal" body size in neonate *N. taxispilota*, it seems from the comparisons made in the present study that survival selection favors offspring length because offspring length appears to be decoupled from maternal influences. Selection for neonate body size (SVL) seems to be stronger than fecundity selection. Similar to *N. harteri* (Greene et al., 1999), female *N. taxispilota* seem to have little influence on neonate length, rather as the females grow they partition energy into more rather than larger offspring. As already stated, neonate body size (particularly SVL) may be at its optimum in *N. taxispilota* because 1) neonate SVL is not correlated with any of the maternal traits nor most of the litter traits tested (except variability in litter size, Table 4.16), and 4.2) neonate brown water snakes are already relatively large compared to other water snakes.

LIFE HISTORY

As Dunham et al. (1988) stated, "Adequate tests of life history theory and theories of population regulation are impossible without life table data." I could not construct an age-structured life table for *N. taxispilota* given the level of variability in my estimates of age based on length. However, using the traits I could measure or estimate, I compared the reproductive and life-history parameters of *N. taxispilota* to other snakes of the genus *Nerodia* (Table 4.17).

First, as expected because of their presumed close phylogenetic relationship, *N. taxispilota* seems to be most similar to *N. rhombifer* with respect to size at maturity, both maturing at a larger size than other members of this genus. Whereas Semlitsch and Gibbons (1982) reported that *N. taxispilota* matures at about 45 cm SVL, based on the presence of mature follicles (their Fig. 1), my observed length of 79.5 cm at first reproduction and Aldridge's (1982) report of 72.5 to 80.0 cm SVL for maturity are probably more realistic. In their graph, Semlitsch and Gibbons (1982) presumably showed follicle sizes of any that could be measured, not necessarily only those that were mature (Gibbons, pers. com.). Although the follicles that Semlitsch and Gibbons measured were probably in an earlier stage of development, another more intriguing possibility is that some *N. taxispilota* matured earlier during the 1970's, possibly due to heated effluent from nuclear reactors (Gibbons, pers. com.). Betz (1963) observed primary oogenesis 2 years prior to ovulation in the closely related N. rhombifer and partial yolking of the ova occurs in the fall before hibernation in *N. taxispilota* (Blem and Blem, 1990), indicating that the presence of vitellogenic follicles does not mean the individual will reproduce in that year.

Secondly, a great deal of variability in reported litter size exists both among and within species (Table 4.18). Among species, mean litter size ranges from 11.1 (*N. harteri*) to 37.1 (*N. rhombifer*, but see Table 4.17 footnote *a*). Geographic variation in clutch and litter size in snakes was reviewed by Fitch (1985). Sixty percent of the snakes for which Fitch had data showed a trend towards larger clutch sizes in the northern part of the species' range, although Fitch suggests that other factors (e.g., food availability) may act to blur or override observed within-species latitudinal variations. But there is a problem with Fitch's review as well as other similar reviews of reproductive and life history data (e.g., Seigel and Ford, 1987; Parker and Plummer, 1987; Dunham et al., 1988). A standardized definition of variables such as clutch (litter) size has not been followed. For example, Fitch (1985) uses two sources for litter size of *N. taxispilota*: a southern population with a mean litter size of 28 (Semlitsch and Gibbons, 1982; the same population as the present study), and a more northern population with a mean litter size of 33.9 (White et al., 1982). Why does the Semlitsch and Gibbons mean litter size (28) differ from my estimate of litter size (18)? The apparent difference in litter sizes has several possible explanations, but the most obvious is the difference in definitions of what constitutes litter size. I argue that only living young should be included in a life table, and other terminology should be used in comparisons when referring to all neonates (living and dead) and follicles or undeveloped ova. Semlitsch and Gibbons (1982) used follicle or embryo number and not litter size. Some follicles do not develop, and of those that do, some of the developed neonates are dead at birth (i.e., stillborn). Betz (1963) found that as they matured, the number of follicles decreased and that not all those that matured became fully-formed embryos in *N. rhombifer*. Atretic follicles were common in a Virginia population of *N. taxispilota*, with 100% of the individuals captured in June showing atresia, and atretic follicles accounting for as much as 41% (4.4-41.2 %) of the total number of follicles (White et al., 1982). I recorded a mean of 1.05 stillborn (range 0-14) or undeveloped young in 121 litters; 39 of these 121 litters (32%) had stillborn young with a mean of 3.26 ± 3.70 (SD) stillborn neonates in these 39 litters (range 1-14).

White et al. (1982) reported a mean litter size of 33.9 based on number of vitellogenic follicles and embryos but state that, “A mean of 28.0 may be more accurate…” based on living young; therefore indicating no latitudinal variation in Fitch’s (1985) original review rather than the weak trend indicated in Fitch’s Table 7. However, in defense of Fitch’s hypothesis, one can see a possible latitudinal trend using my mean clutch size of 18 (South Carolina) and the “adjusted” clutch size of White et al. (1982) of

28 (Virginia), although two data points could still be challenged. It would be useful to gather litter size data from a Florida population of *N. taxispilota* to help substantiate the proposed trend of smaller litters in the southern part of a snake's range.

Individual traits in the life history and reproductive biology of *N. taxispilota* may be phylogenetically conserved (genetic) or may result from proximate, environmental factors. It can become quite difficult to separate genetic factors from environmental factors when examining the life history of an organism, but comparative (both intra- and interspecies) studies may help tease these factors apart.

Nerodia taxispilota is potentially a good candidate for intraspecific comparisons of life history traits because it is a wide-ranging monotypic species. Tables 4.17 and 4.18 summarize the reproductive traits of the genus *Nerodia* and of *N. taxispilota* based on this and other studies from throughout its range. As already discussed, Fitch (1985) notes that a northern increase in clutch size is weakly indicated based on two studies (Semlitsch and Gibbons, 1982; White et al., 1982), with my study supporting the northward trend (18 vs. 28; Table 4.17B), but with a different number than Semlitsch and Gibbons (1982). Although size at maturity is slightly less in the Virginia population (72.5 cm) than in my South Carolina population (79.5 cm), it is unknown if the difference in size translates into different ages at maturity. The presumed cooler winters and shorter growing seasons in the northern part of their range may require earlier maturation, or at least maturation at a smaller body size in order to compensate for differences in juvenile or adult survivorship. Regardless of the age at which Virginia *N. taxispilota* mature, my population's relatively late age at maturity is consistent with other long-lived snakes as reviewed in Parker and Plummer (1987).

Although adequate data may not be available to determine latitudinal variation in clutch size or other traits, I have data from multiple years in my study sites to evaluate possible environmental influences on clutch size. For example, despite a consistent positive relationship between female size and litter size (Fig. 4.11), extensive year-to-year variation existed in the slope of these regressions (although not significant: $F_{4,94} = 1.081$, P>0.50), ranging from 0.15 in 1996 to 0.86 in 1990 (Fig. 4.14). What are some of the possible proximate causes of this variability? Year-to-year variability in temperature and precipitation may influence reproduction (Seigel and Fitch, 1985), but for aquatic piscivorous snakes, water level or flow may be of more importance (e.g., Madsen and Shine, 2000), although all of these factors may be linked. Brockelman (1975) predicted that as the environment fluctuates, the number of young rather than the size of the young would fluctuate. Support for Brockelman's prediction comes from a study on *Uta stansburiana* in which rainfall and subsequent increases in prey increased the size of the first clutch, but not of the eggs or offspring in the first clutch (Ferguson et al., 1990) I tested for correlations among litter size, mean neonate size (mass and SVL), and the following stream-flow variables of the Savannah River: streamflow (cfs), streamflow of the previous year, number of months above flood stage, and variability (SD) in streamflow. Although none of these correlations were significant (P-values > 0.16), and Savannah River flow did not differ statistically among the years of the study ($F_{8,99} = 0.61$, P = 0.77), the relationship between the river's flow and *N. taxispilota* reproduction may have biological significance. The year with the greatest number of months above flood-stage (6 months) and the highest mean streamflow (mean = 12218 cfs) was 1993. This was also the year that mean female body condition and mean litter size (21) were at their highest, and the year female SVL explained the most variance in litter size (over 80%).

How might flooding be related to reproduction in *N. taxispilota*? It could be through resource acquisition. Field and experimental studies have shown a positive relationship between food intake and clutch size in snakes (Andren and Nilson, 1983; Seigel and Ford, 1992; Ford and Seigel, 1994; Barron and Andraso, 2001). Flood years may benefit the fish these snakes prey upon (especially catfishes) by adding nutrients to the system and by providing larger areas in which the fish can forage and breed. Inundated floodplains may also provide the snakes with easier (i.e., less energetically expensive) opportunities for capture and handling of the prey. As the flood waters recede, fish become trapped in the shallow waters on the floodplain making them easy targets for predation. Bronikowski and Arnold (1999) have field data to support that years with high rainfall and thus high anuran densities were followed by years of higher reproduction in a garter snake. A relationship between flooding, fish abundance, and number of young was documented in the Arafura filesnake, *Acrochordus arafurae* (Madsen and Shine, 2000), although in their study rainfall and the resulting increase in prey abundance did not increase litter size, rather it increased offspring survival. Plummer (1997) also found correlations between weather patterns, body condition, and clutch size in his studies of the green snake, *Opheodrys aestivus*. In one of the two populations he studied, he documented reduced clutch size in snakes with lower average body condition, which in turn was correlated with periods of hot, dry weather. (Bronikowski and Arnold, 1999) found higher numbers of pregnant garter snakes, *Thamnophis elegans*, in the years following years of heavy rainfall and high food abundance (frogs). The correlations between climate, body condition, and reproductive output have also been documented for lizards. Regardless of the exact causal mechanism or relationship between rainfall or water level and reproduction, it seems reasonable that changes in the aquatic environment would affect the biology of an aquatic snake. Although the present study does not offer significant answers to the relationship between reproduction and environmental variables, it does offer hypotheses for future tests.

N. taxispilota in the present study was similar to other late-maturing colubrids (Parker and Plummer, 1987) and was characterized by relatively high adult survivorship, long life, high fecundity, and annual reproduction. The population estimates for a 10-km section of the Savannah River indicated densities as high as one snake/5m of shoreline. Growth was similar in juveniles of both sexes, but males matured earlier and grew more slowly than adult females. Female body size (length and mass) was positively correlated with litter size, and female mass and body condition were positively correlated with neonate mass. Finally, I examined the relationships between offspring size and number and found no definitive support for the hypothesized trade-off between these traits.

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Table 4.1 – Capture histories for all marked (PIT tag or scale clipped) *Nerodia taxispilota* across 6 locations on the SRS, South Carolina, 1991-1998. Site a in this table includes contiguous sites a1 (four individuals captured twice, one captured three times, and one five times, although the last four of these five captures were in site a) and a2 (one individual captured twice).

No. of Times Captured	Site a	Site b	Site c	Site d	Site e	Site f	Total	Males	Females
1	894	59	146	120	120	53	1392	693	699
2	83	4	20	2	3	1	113	46	67
3	14	1	4	1			20	7	13
4				1			1		1
5	2						2	2	
Total Captures	1112	70	198	131	126	55	1692	816	876
Total Individuals	993	64	170	124	123	54	1528	748	780
Captures/ Individual	1.12	1.09	1.16	1.06	1.02	1.02	1.11	1.09	1.12

Table 4.2 – Test of equal catchability for Site-a, based on the zero-truncated Poisson distribution (random or equal chance of capture) and a goodness-of-fit statistic (Chi-Square test).

Number of Captures	Observed Number of Individuals	Poisson Probability P(X)	Expected Number of Individuals P(X)n
1	894	0.542475	538.7
2	83	0.303733	301.6
3	14	0.113373	112.6
4	0	0.031739	31.5
5	2	0.007107	7.1
Total Captures	1112		
No. of Individuals (n)	993	Chi-Sq. =	514.287 (P<0.001)
Mean Captures/Individual	1.12		df = k-2=3

Table 4.3 – Jolly-Seber population estimates for *Nerodia taxispilota* at Study Site a (Savannah River). Each snake was counted only once per year regardless of the number of times it may have been captured that year. See Tanner (1978) for the equations used to calculate the following estimates: proportion of marked animals in the population (a_i), total number of marked animals in the population at time *i* (M_i), population size at time *i* (N_i), survival rate (s_i), and the number recruited to the population between times *i* and *i*+1 (B_i).

		Recaptures from						
i	C_i	1991	1992	1993	1994	1995	1996	F_i
1991	59							59
1992	198	0						198
1993	120	1	13					120
1994	50	0	1	5				50
1995	137	0	3	3	4			137
1996	241	0	5	5	0	5		241
1997	97	0	4	3	0	5	2	97

	1991	1992	1993	1994	1995	1996	1997
a_i		0	0.117	0.120	0.073	0.062	0.144
M_i		8	112	294	243	564*	
N_i		0	953	2446	3327	9097	
SD of N_i			366	1552	1576	7810	
s_i	0.129	0.542	1.349	0.720	1.525		
B_i		953	1160	1567	4022		

* M_6 = 1461, but M_i cannot logically exceed the known number of marked animals in the population at time *i* (564); therefore the number of known marked animals was substituted for M_i (see Tanner, 1978).

Table 4.4A – Growth rates of marked individuals of *Nerodia taxispilota* from the Savannah River, Savannah River Site, South Carolina. Mean length (SVL) between the two capture periods was used to classify individuals as juvenile or mature. Means are followed by 2 SE.

Sex and Size Class	N	Mean (mm/d)	Range (mm/d)
Males < 50 cm SVL (juvenile)	3	0.50 ± 0.40	0.29 – 0.90
Males ≥ 50 cm SVL (mature)	38	0.20 ± 0.06	0.0 – 1.01
Females < 79.5 cm SVL (juvenile)	34	0.45 ± 0.08	0.08 – 1.11
Females ≥ 79.5 cm SVL (mature)	32	0.28 ± 0.07	0.0 – 0.71
Total	107	0.31 ± 0.05	0.0 – 1.11

Table 4.4B – Variability in growth of *Nerodia taxispilota* during the first year based on the following minima, maxima, and means: 1) size at birth (SVL; Table 4.7), 2) parturition dates (Table 4.9A), and 3) growth rates. Minimum (0.256 mm/d) and maximum (0.828 mm/d) growth rates are based on juveniles recaptured more than 60 d apart during the growing season and the mean growth rate (0.419 mm/d; Table 4.4A) is based on recaptures of all juveniles both within and between years. Minimum size (200 mm) does not follow minimum observed size at birth, but rather was selected based on observed size distribution of neonates (Fig. 4.7) with the assumption that smaller individuals do not survive.

Size at Birth (mm SVL)	Size (mm SVL) at End of 1st Year (10/21)								
	Early Birth (7/28)			Late Birth (10/21)			Mean Date of Birth (9/22)		
	Growth Rates			Growth Rates			Growth Rates		
	Min. Rate	Max. Rate	Mean Rate	Min. Rate	Max. Rate	Mean Rate	Min. Rate	Max. Rate	Mean Rate
200 (min.)	284.5	473.2	338.3	262.7	402.9	302.7	270.1	426.9	314.8
284 (max.)	368.5	557.2	422.3	346.7	486.9	386.7	354.1	510.9	398.8
244 (mean)	328.5	517.2	382.3	306.7	446.9	346.7	314.1	470.9	358.8

Table 4.5 – Estimated ages (based on size) of first and last captures of *Nerodia taxispilota* captured a minimum of two years apart. Age for each size (SVL) at first capture is estimated from the von Bertalanffy growth curves (Fig. 4.6A) and rounded to the nearest year[1]. The observed age (Obs) at last recapture is based on the previous estimated age (column 4) plus the number of years between recaptures. The expected age (Exp; rounded to the year) in parentheses is based on the SVL at last capture. The (*) indicates the only known-age snake.

First Capture				Last Capture			
Sex	Date	SVL (cm)	Age (yr)	Date	SVL (cm)	Obs (Exp) Age (yr)	Years Between Captures
Male	7/15/92	80.6	10	7/11/94	85.0	12 (12)	2
Male	7/19/93	67.3	6	7/28/95	73.8	8 (8)	2
Male	5/29/95	44.5	2	8/27/97	56.0	4 (4)	2
Male	2/20/95	55.0	4	8/27/97	64.5	6 (5)	2
Male	6/7/95	36.5	1	2/17/97	47.7	3 (3)	2
Male	8/12/93	52.1	3	7/28/95	70.5	5 (7)	2
Male	6/11/93	72.3	7	8/24/95	83.0	9 (11)	2
Female	7/19/93	94.2	7	6/8/95	103.4	9 (8)	2
Female	8/27/91	83.7	6	7/4/93	98.7	8 (8)	2
Female	8/30/91	95.0	7	6/9/93	100.0	9 (8)	2
Female	7/28/95	78.0	5	6/10/97	99.5	7 (8)	2
Female	6/8/95	97.5	8	6/9/97	108.0	10 (9)	2
Female	3/15/96	82.5	6	3/25/98	93.0	8 (7)	2
Female	5/11/95	74.0	5	6/9/97	93.0	7 (7)	2
Female	6/8/95	69.5	4	9/12/97	100.0	6 (8)	2
Female	7/28/95	50.0	2	8/28/97	90.5	4 (7)	2
Female	8/13/92	85.4	6	6/14/94	94.6	8 (7)	2
Male	7/29/92	75.5	8	11/29/95	86.0	11 (12)	3
Male	7/10/92	72.2	7	6/8/95	80.5	10 (10)	3
Female	6/8/95	87.5	6	8/7/98	100.0	9 (8)	3
Female	7/12/93	58.3	3	9/13/96	104.5	6 (9)	3
Female	7/19/93	61.6	3	4/24/96	94.5	6 (7)	3
Female	9/9/92	23.8	YOY (0)	4/5/95	65.5	3* (4)	3
Male	8/12/92	63.8	5	6/19/96	77.5	9 (9)	4
Male	7/22/92	71.4	7	5/23/96	81.5	11 (10)	4
Male	8/12/92	48.8	3	6/5/96	69.0	7 (6)	4
Female	8/12/92	88.4	6	6/5/96	108.5	10 (9)	4
Female	8/27/92	66.6	4	11/19/96	109.0	8 (9)	4
Female	7/12/93	39.5	1	8/28/97	94.0	5 (7)	4
Female	7/29/92	51.1	2	8/15/96	101.5	6 (8)	4
Female	7/10/92	87.3	6	9/13/96	107.0	10 (9)	4
Male	7/30/92	68.7	6	8/22/97	83.5	11 (11)	5
Male	7/8/92	79.5	9	9/12/97	89.5	14 (14)	5
Male	8/18/92	53.0	3	9/12/97	74.0	8 (8)	5
Female	8/27/92	59.4	3	4/2/97	101.0	8 (8)	5
Female	9/4/92	63.0	3	6/9/97	104.0	8 (9)	5
Female	9/2/93	52.1	2	6/8/99	106.9	8 (9)	6

Chi-Square[1] = 5.5095
(P>0.999)

1 - Chi-Square calculated from age to the nearest hundredth of a year.

Table 4.6 – Estimated potential variability in female age at maturity based on juvenile growth rates and a size at maturity of 79.5 cm SVL. Minimum, maximum, and mean growth rates follow Table 4.4B. The number of years to reach maturity is corrected to include periods of no growth (i.e., winter or 120 days per year). The estimates of first year of reproduction are based on 1) minimum size at birth and minimum growth rate, 2) maximum size at birth and maximum growth rate, and 3) mean size at birth and mean juvenile growth rate.

Size at Birth (mm SVL)	Days/Years to Reach Maturity (795 cm SVL)			Possible Year of First Reproduction
	Min. Growth Rate	Max. Growth Rate	Mean Growth Rate	
200 (min.)	2324 d / 9.49 yr	719 d / 2.93 yr	1420 d / 5.80 yr	10th year
280 (max.)	2012 d / 8.21 yr	622 d / 2.54 yr	1229 d / 5.02 yr	4th year[1]
244 (mean)	2152 d / 8.79 yr	665 d / 2.72 yr	1315 d / 5.37 yr	6th year

1 – Assuming the female does not mate until she has reached 795 mm, which would be after mating season (March-early May) in her third year.

Table 4.7 – Size characteristics of living *Nerodia taxispilota* neonates from SRS, South Carolina from two data sets: females collected by Stevan Arnold (SA) and Mark Mills (MM). Means are followed by 2 SE.

Data Set – sex	N SVL	Mean SVL (cm) (Range)	N Mass	Mean Mass (g) (Range)
MM – males	87	23.03 ± 0.27 (19.2-25.5)	87	11.18 ± 0.36 (6.30-14.85)
MM – females	75	22.74 ± 0.26 (20.8-25.3)	75	10.93 ± 0.41 (7.40-14.63)
MM – total	185	22.66 ± 0.21	185	10.83 ± 0.27
SA – males	978	24.54 ± 0.09 (12.7-28.4)	980	10.68 ± 0.11 (1.77-17.75)
SA – females	971	24.51 ± 0.09 (16.1-28.0)	970	10.91 ± 0.11 (3.57-18.46)
SA – total	1958	24.53 ± 0.06	1961	10.80 ± 0.08
Combined – males	1065	24.42 ± 0.09 (12.7-28.4)	1067	10.72 ± 0.11 (1.77-17.75)
Combined – females	1046	24.38 ± 0.09 (16.1-28.0)	1045	10.91 ± 0.10 (3.57-18.46)
Combined – total**	2143	24.37 ± 0.06	2146	10.80 ± 0.08

** SVL and mass of neonates varied significantly between litters (P<0.0001).

Table 4.8 – Litter size (living neonates only) of *Nerodia taxispilota* split by capture site and year. Three litters of 0 (all stillborn) from the Savannah River were not included. Means are followed by 2 SE.

Site, Year	Number of Litters	Mean Litter Size	Range
Savannah River, 1990	17	18.5 ± 5.2	6-50
Savannah River, 1991	36	18.5 ± 2.3	4-37
Savannah River, 1992	21	16.7 ± 3.4	4-35
Savannah River, 1993	21	21.0 ± 2.8	9-34
Savannah River, 1996	9	15.4 ± 2.3	10-21
Savannah River, Total	104	18.4 ± 1.5	4-50
UTR Creek, 1990	1	36	
UTR Creek, 1991	2	12.5 ± 1.0	12-13
UTR Creek, 1995	2	11.5 ± 1.0	11-12
UTR Creek, Total	5	16.8 ± 9.6	11-36
Steel Creek, 1990	8	15.1 ± 3.5	9-24
Edisto River, 1990	1	32	
Total	118	18.2 ± 1.4	4-50

Table 4.9 – (A) Parturition dates recorded from the field[1] and laboratory[2], and (B) capture dates for potential YOY individuals less than 27.4 cm SVL (i.e., within 2 SD of the mean neonate SVL).

A

	April-May	June	July	August	Sept.	Oct.	Nov.
Not Gravid[1a]	75	51	40	41	24	4	0
Gravid[1]	4	36	26	23	6		
Postpartum[1]			1	2	11	32	2
SA - Lab[2]				2	81	27	
MM - Lab[2]					12		

a – Includes only those females > 77.5 cm (5 years or older)

B

SVL (cm)	Capture Date	Site	Sex	Comments
22.3	10-15-92	a	M	YOY
22.8	9-13-96	a	M	YOY; Umbilical scar
22.9	10-25-95	b	F	YOY
23.0	10-29-96	a	F	YOY; Recapture from 9/25 release
23.1	10-7-95	c	M	YOY; Recapture from 9/22 release
23.5	7-28-95	a	M	YOY ; Umbilical scar
23.8	9-9-92	a	F	YOY
24.1	5-12-94	a	F	From 1993
24.1	8-16-96	a2	M	YOY, or could be from 1995; pair of scars
24.2	3-21-96	a1	F	From 1995
24.5	5-10-96	a	M	From 1995
24.7	6-5-96	a	F	From 1995
25.0	9-13-96	a	M	YOY, or could be from 1995
25.2	10-30-96	c	M	YOY, or could be from 1995
25.3	10-15-92	a	F	YOY, or could be from 1991
25.5	8-18-92	a	F	YOY, or could be from 1991
25.5	7-28-97	a	F	YOY, or could be from 1996
25.7	5-3-96	c	F	From 1995
25.7	5-12-94	a	M	From 1993
25.8	5-12-95	a	M	From 1994
26.0	10-15-92	a	F	YOY, or could be from 1991
26.0	5-11-95	a1	M	From 1994; underwater
26.2	10-3-95	a	M	YOY, or could be from 1994
26.5	6-8-95	a	M	From 1994
26.5	6-9-93	a	F	From 1993
26.6	7-6-95	a	M	From 1994
26.6	6-8-95	a	F	From 1994
26.7	6-14-94	a	M	From 1993
26.9	3-14-98	e	M	From 1997
27.0	4-17-95	e	F	From 1994
27.1	6-14-94	a	F	From 1993
27.3	8-18-92	a	M	YOY, or could be from 1991
27.5	8-6-92	a	F	YOY, or could be from 1991
27.5	5-12-95	a	F	From 1994

Table 4.10 – Female and litter characteristics (living neonates only) from females collected in the Savannah River.

	N	Mean	Standard Deviation	Range
Female SVL (cm)	107	96.84	6.70	83.3-115.8
Female Mass[1] (g)	107	652.20	143.45	353.05-1000.20
Litter Size[2]	104	18.4	7.5	4-50
Mean Litter SVL (cm)	104	24.32	1.29	20.05-27.54
Mean Litter Mass (g)	104	10.80	1.67	6.14-17.45

1 – Postpartum mass

2 – Living neonates only; 3 litters consisting completely of stillborn snakes were removed from the analyses.

Table 4.11A – Relationships between female *Nerodia taxispilota* and their litters with a comparison of correlation tests. These correlations were calculated using all females and litters from all sites (n = 114). Body condition was calculated as the residuals from the regression of mass on SVL.

Female Characteristic	Litter Characteristic	Pearson Correlation Coefficient	Partial Correlation Coefficient[1]	Spearman Rank Correlation Coefficient
Length (SVL, cm)	litter size	0.572***	0.731**	0.522***
	mean SVL	0.006	-0.025	-0.020
	mean mass	0.021	0.221*	0.046
	RCM	0.203*	-0.577**	0.171 (P=0.06)
Mass (g)	litter size	0.548***	0.857**	0.522***
	mean SVL	0.091	-0.110	0.062
	mean mass	0.192*	0.556**	0.212*
	RCM	0.131	-0.782**	0.112
Body Condition	litter size	0.149	0.495**	0.156
	mean SVL	0.159	-0.094	0.143
	mean mass	0.321**	0.434**	0.317**
	RCM	-0.064	-0.486**	-0.030

* P≤0.05, **P≤0.001, ***P≤0.0001

Table 4.11B – Relationships between female *Nerodia taxispilota* and their litters with a comparison of correlation tests. In order to reduce the possible confounding effects of collection site (see text), these correlations were calculated using only those females and litters collected from the Savannah River (n = 104). Body condition was calculated as the residuals from the regression of mass on SVL.

Female Characteristic	Litter Characteristic	Pearson Correlation Coefficient	Partial Correlation Coefficient[1]	Spearman Rank Correlation Coefficient
Length (SVL, cm)	litter size	0.596***	0.727**	0.576***
	mean SVL	-0.014	-0.063	-0.047
	mean mass	0.008	0.222*	0.035
	RCM	0.239*	-0.554**	0.224*
Mass (g)	litter size	0.547***	0.843**	0.526***
	mean SVL	0.094	-0.122	0.062
	mean mass	0.191 (P=0.052)	0.539**	0.213*
	RCM	0.144	-0.763**	0.138
Body Condition	litter size	0.120	0.494**	0.147
	mean SVL	0.189 (P=0.054)	-0.068	0.166
	mean mass	0.330**	0.428**	0.333**
	RCM	-0.086	-0.503**	-0.047

* P≤0.05, **P≤0.001, ***P≤0.0001

1 – StatView® statistical software does not compute a separate P-value for partial correlations. Table B.16 in Zar (1984) was used to determine the P-values, but reports critical values to 0.001.

Table 4.12 – Relationships between reproductive parameters as determined by multiple regression. The multiple regression model with mean offspring SVL as the dependent variable was not significant (P=0.23) and was omitted from this table. All other regression models were significant (ANOVA, P< 0.01). Maternal body condition is calculated from the residuals of maternal mass regressed on maternal SVL.

Dependent Variable	Independent Variables	Standardized[a] Regression Coefficient	P-Value
Litter Size	Maternal SVL	0.592	<0.0001
	Maternal body condition	0.092	0.251
Mean Offspring Mass	Maternal SVL	0.010	0.933
	Maternal body condition	0.333	<0.001
	Litter size	-0.029	0.805
RCM	Maternal SVL	-0.388	<0.0001
	Maternal body condition	-0.304	<0.0001
	Litter size	1.071	<0.0001
	Mean offspring mass	0.328	<0.0001

a – Standardized partial regression coefficients better allow direct comparisons between coefficients within a model and indicate the relative importance of the various independent variable in determining the dependent variable. They correct for differences in the scale of the variables involved and because these coefficients are standardized they can be greater than 1 (e.g., litter size regressed on RCM).

Table 4.13 - Direct effects, indirect effects, and effect coefficients (sum of direct and indirect effects) relating female size and condition to reproductive variables in *Nerodia taxispilota*. The values in this table are derived from the path coefficients (standardized partial regression coefficients) in Fig. 4.12. SVL = snout-vent length (cm); neonate mass = mean mass of living offspring in the litter; maternal body condition = residual values of postpartum maternal mass regressed on SVL; RCM = total clutch mass (includes living and stillborn neonates plus unfertilized ova) / maternal postpartum mass.

	Litter Size	Neonate Mass	RCM
Effect of Maternal SVL			
Direct	0.592	0.010	-0.388
Through litter size		-0.017	0.634
Through neonate mass			0.003
Through litter size and neonate mass			-0.006
Effect Coefficient	0.592	-0.007	0.243
Effect of Maternal Body Condition			
Direct	0.092	0.333	-0.304
Through litter size		-0.003	0.099
Through neonate mass			0.109
Through litter size and neonate mass			-0.001
Effect Coefficient	0.092	0.330	-0.097

Table 4.14A - A comparison of the litters containing the greatest and least mean mass. For this comparison I chose those litters that were greater (N=11) or less than (N=13) mean neonate mass ± 1SD (10.80 ± 1.85g). Means are reported with ± SE (range). P-value is from a t-test or if parametric assumptions were not met, a Mann-Whitney U test*.

Trait	Lightest Litters n = 13	Heaviest Litters n = 11	P-Value[a]
Maternal SVL (cm)	95.98 ± 1.77 (83.3-108.0)	97.63 ± 2.25 (85.0-110.0)	0.57
Maternal Mass (g)	584.0 ± 43.7 (376.4-845.3)	719.9 ± 53.3 (391.6-955.3)	0.06
Maternal Body Condition[b]	-57.13 ± 20.94 (-157.68-84.75)	49.75 ± 21.44 (-56.73-168.51)	0.002
Litter Size	14.8 ± 2.7 (4-37)	16.2 ± 1.6 (7-25)	0.40*
Mean Offspring SVL	22.56 ± 0.29 (20.05-24.06)	25.89 ± 0.26 (24.28-27.54)	<0.0001
RCM	0.235 ± 0.031 (0.072-0.399)	0.308 ± 0.017 (0.207-0.384)	0.13*

a – The P-value is that of a t-test unless the assumptions of normality and equal variance were not met, in which cases a Mann-Whitney U test was used. Those values with an (*) are from the Mann-Whitney test.
b – Body condition is the residual from mass regressed on length.

Table 4.14B - A comparison of the females and their litters that contained combinations of <u>both</u> the greatest mean mass and mean SVL and the least mean mass and SVL. For this comparison I chose those litters from Table XA that contained combinations of both the greatest mean mass and SVL (n = 7) and the least mean mass and SVL (n = 8). Means are reported with ± SE (range). P-value is from a t-test or if parametric assumptions were not met, a Mann-Whitney U test*.

Trait	Light-Short Litters n = 8	Heavy-Long Litters n = 7	P-Value[a]
Maternal SVL (cm)	96.65 ± 1.91 (91.0-108.0)	96.87 ± 3.16 (85.0-110.0)	0.95
Maternal Mass (g)	583.9 ± 52.3 (430-805.3)	708.1 ± 79.4 (391.6-955.3)	0.20
Maternal Body Condition[b]	-69.09 ± 30.27 (-157.68-84.75)	51.25 ± 33.03 (-56.73-168.51)	0.02
Litter Size	16.5 ± 3.9 (4-37)	15.4 ± 2.1 (7-23)	0.82
RCM	0.263 ± 0.044 (0.072-0.399)	0.304 ± 0.016 (0.258-0.352)	0.73*

a – The P-value is that of a t-test unless the assumptions of normality and equal variance were not met, in which cases a Mann-Whitney U test was used. Those values with an (*) are from the Mann-Whitney test.
b – Body condition is the residual from mass regressed on length.

Table 4.15 – This table is modeled after Table 2 in Shine and Seigel (1996) and compares temporal variability in clutch-size variance within the Savannah River population of *N. taxispilota* (A) with other natricine populations included in their table, including data on *N. taxispilota* collected by R. Seigel in the early 1980's. CV = Shine and Seigel's (1996) "standardized deviation score" (see text for a full explanation). For comparative purposes, I also present the minimum and maximum residual values (indicated by an asterisk) for the regression of litter size on SVL (*N. taxispilota*-B). A one factor ANOVA (F) and the nonparametric Kruskal-Wallis (H) tests were used to test for differences between years.

Species	Number of Years	Maximum CV	Minimum CV	ANOVA & (Kruskal-Wallis) tests	P-Values F test (H test)	Source[1]
Nerodia taxispilota-A	5	174.7	1.1	$F_{4,99} = 1.22$ ($H_4 = 4.49$)	0.31 0.34	present study
N. taxispilota-B	5	18.45*	-19.14*	$F_{4,99} = 2.26$ ($H_4 = 8.73$)	0.07 0.07	present study
N. taxispilota	2	50.0	36.1	$F_{1,30} = 0.0$	1.00	R. Seigel, pers. obs.
Seminatrix pygaea	2	39.2	31.4	$F_{1,45} = 0.46$	0.50	R. Seigel & R. Loraine, unpubl.
Thamnophis sirtalis	9	47.8	25.5	$F_{8,157} = 1.23$	0.28	Seigel and Fitch (1985)
T. radix	3	34.0	7.9	$F_{2,51} = 1.44$	0.25	Seigel and Fitch (1985)

1 - I have provided the original citations; however, except for the first 2 rows, all data comes from Shine and Seigel (1996).

Table 4.16 – Correlations between measures of variation in litter size (CV, CV2, and Litter Residuals) and neonate size (mean, CV) for Savannah River populations of *Nerodia taxispilota*. Litter CV was calculated as in Shine and Seigel (1996) and Litter CV2 was calculated as the absolute value of the residuals from the regression of litter size on maternal length; CV values reported for neonate mass and SVL use the standard statistical definition of this measure of dispersion (SD/mean).

Measure 1	Measure 2	Pearson Correlation Coefficient	Partial Correlation Coefficient[1]	Spearman Rank Correlation
Litter CV	Mean – Neonate SVL	-0.198*	-0.025	-0.191 (P=.053)
	CV – Neonate SVL	0.117	-0.069	0.055
	Mean – Neonate Mass	-0.233*	-0.114	-0.202*
	CV – Neonate Mass	0.165	0.089	0.066
Litter CV2	Mean – Neonate SVL	-0.337**	-0.102	-0.266*
	CV – Neonate SVL	0.213*	-0.196*	0.061
	Mean – Neonate Mass	-0.340**	-0.098	-0.269*
	CV – Neonate Mass	0.322**	0.250*	0.161
Litter Residuals	Mean – Neonate SVL	-0.308*	-0.049	-0.262*
	CV – Neonate SVL	0.215*	-0.184	0.107
	Mean – Neonate Mass	-0.340**	-0.132	-0.272*
	CV – Neonate Mass	0.322**	0.246*	0.191 (P=.052)
Litter CV	Litter CV2	0.567***	-0.055	0.448***
	Litter Residuals	0.633***	0.345**	0.454***
Litter CV2	Litter Residuals	0.922***	0.884**	0.961***

* $P \leq 0.05$, ** $P \leq 0.001$, *** $P \leq 0.0001$

1 – StatView® statistical software does not compute a separate P-value for partial correlations. Table B.16 in Zar (1984) was used to determine the P-values, but does not report critical values less than 0.001.

Table 4.17A – Comparison of reproductive and demographic (life history) parameters in the genus *Nerodia*(there were no data available for *N.floridana*). All values refer to females and were taken directly from the original citation unless otherwise noted. Length is in mm and weight is in grams. Ro is net reproductive rate, Tc is mean cohort generation time in years, and % Gravid is averaged over all mature age/size classes.

Species	Location	Minimum Age (yrs) /SVL at Maturity	Long-evity	Mean Adult Survivorship (%)	Mean Litter Size (range)	Ro	Tc	% Gravid	RCM	Mean SVL of Mothers	Mean Off-spring SVL	Mean Off-spring Mass
N. cyclopion[6]	LA, USA	?/637			18.4			85				
N. erythrogaster[6]	LA, USA	?/734										
N. fasciata[6]	LA, USA	?/550										
N. floridana												
N. harteri[4]	TX, USA	?/460			11.1			85	0.46		175	3.8
N. rhombifer[7]	AR, USA	?/785			23.1			56-100	0.30	908	246	10.3
N. rhombifer[6]	LA, USA	?/688										
N. rhombifer[2]	MO, USA	3/?			37.1[a]							
N. sipedon[3b]	MI, USA	2-3/476	7	30	11.8	0.681	2.77	82.6		669	188	5
N. sipedon[1]	MO, USA	2-3/600										
N. sipedon[5]	OH, USA	3/590			22.9			77		821	181	4.8
N. taxispilota[8]	VA, USA	?/725			28.0[c]			82.1		905	185	
N. taxispilota[9]	SC, USA	5/795	6+	68	18.2			75.6	0.31	968	244	10.8

References: 1-(Bauman and Metter, 1977), 2-(Betz, 1963), 3-(Feaver, 1977), 4-(Greene et al., 1999), 5- (King, 1986), 6-(Kofron, 1979), 7-(Plummer, 1992), 8-(White et al., 1982), 9-Present study

a - Litter size taken from Table 2 in Betz (1963) and represents the combined mean of fetuses of pregnant females and corpora lutea of postpartum females, and therefore is probably a slight overestimate of actual litter size.

b – Data taken primarily from Table 15 and the text in Feaver (1977); mean survivorship was taken from Table 4.16. Mean SVL of mothers is the mean SVL of mature females, some of which may not have produced clutches.

c – This figure represents the number of living young rather than the reported 33.9 which was based on yolking follicles and embryos.

Table 4.17B – Comparison of mean litter size, mean proportion breeding, and the relationship between body size (SVL, cm) and clutch size in *Nerodia taxispilota* (table format after Table 8-2 in Seigel and Ford, 1987). Litter size was based on follicle or embryo number in Semlitsch and Gibbons (1982) and White et al. (1982).

					Regression Equation				
Mean Litter Size (Range)	Mean Female SVL (Range)	Gravid (%)	N	Location	Y-Intercept	Slope	r^2	N	Reference
		100	41	SC	-18.4	0.49	0.60	41	(Semlitsch and Gibbons, 1978)
28 (7-63)				SC	-6.03	0.38	0.44	51	(Semlitsch and Gibbons, 1982)
18.2 (4-50)	96.8 (79.5-130.5)	76		SC	-48.8	0.69	0.36	104	Present Study
33.9* (19-63)	90.5	82	28	VA	-51.8	0.93	0.62	23	(White et al., 1982)

*Mean litter size was based on yolking follicles or embryos. The mean number of full-term embryos was 28.0 (N=5).

Table 4.18 – Comparison of female length (SVL in mm), clutch sizes, and clutch size variability for various water snakes (Natricinae). I omitted fields in this table in cases where data was insufficient or confusing in the original source. n = number of litters. When possible, SD and CV were calculated if not reported in the original source.

Species	Mean SVL	CV of SVL	Mean Litter Size	SD of Litter Size	CV of Litter Size	N	Source
Nerodia harteri	477		14.5	4.31	30.32	12	Rose (1989)
N. harteri	596	12.36	12.2	4.5	36.89	27	Greene et al. (1999)
N. rhombifer	1129	9.71	37.1	8.6	23.15	20	Betz (1963)[c]
N. sipedon[1]	709	6.49	18.9	4.6	24.34	49	Weatherhead et al. (1999)
N. sipedon[2]	744	7.12	20.0	5.1	25.50	28	
N. sipedon	756	15.50	19.9	9.15	46.00	19	Fitch (1999)
N. sipedon	821		22.9			39	King (1986)
N. sipedon	774	1.64	28.5			24	Mitchell (1994)
N. taxispilota	936	14.74					Blem & Blem (1990)
N. taxispilota	968	6.92	18.4	7.53	40.99	104	Present Study
N. taxispilota	1059	10.52	31.8	12.53	39.71	32	Shine & Seigel (1996)
N. taxispilota[a]	905	10.93	33.9	12.2	35.99	23	White et al. (1982)
N. taxispilota[b]			28.0	10.6	37.86	5	White et al. (1982)
Regina grahami	598		11.6	3.06	26.40	11	Seigel (1992)
R. septemvittata	592	10.52	12.8	2.57	20.60	10	Branson & Baker (1974)
Seminatrix pygaea	328	11.12	8.1	2.87	35.59	47	Shine & Seigel (1996)

1- Free-living snakes
2- Captive snakes
a – includes yolking follicles and embryos
b – full-term embryos only
c – see footnote a under Table 4.17

Table 4.19 – A review of the correlations between litter size and offspring size in natricine snakes (Colubridae: Natricinae). “Not significant” can mean either no trade-off or that the trade-off could not be detected statistically. “Negative” signifies a negative correlation between litter size and offspring size; i.e., offspring were smaller in larger litters.

Species	Correlation	Source
Nerodia harteri	Not Significant	Greene et al. (1999)
N. sipedon	Not Significant	King (1993)
N. sipedon	Negative	Weatherhead et al. (1999)
N. rhombifer	Not Significant	Plummer (1992)
N. taxispilota	Not Significant	Present study
Regina septemvittata	Negative	Branson & Baker (1974)[b]
Storeria dekayi	Negative	King (1993)
Thamnophis butleri	Negative	Ford & Killebrew (1983)
T. elegans	Negative	Gregory & Skebo (1998)
T. gigas	Not Significant	Hanson & Hanson (1990) [b]
T. marcianus	Not Significant	Ford & Karges (1987)[a]
T. melanogaster	Not Significant	Ford & Ball (1977) [a]
T. sirtalis	Not Significant	Jayne and Bennett (1990)

a – from Ford and Seigel (1989)
b – from King (1993)

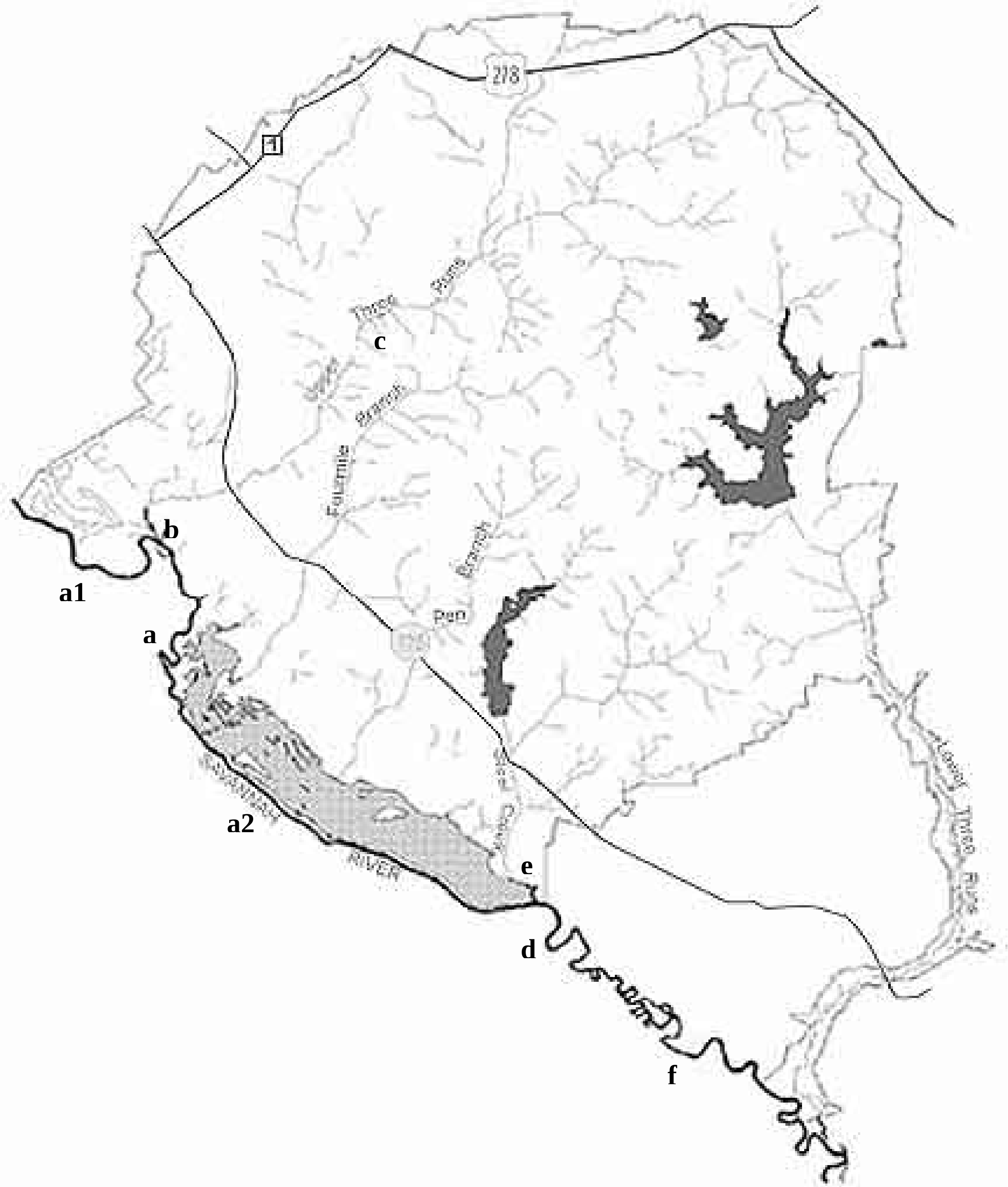


Figure 4.1 – The Savannah River Site in Aiken and Barnwell Counties, South Carolina. The primary study sites are indicated with letters. Site a (Savannah River) corresponds to the study site of Mills et al. (1995), and is the main focus of the present study.

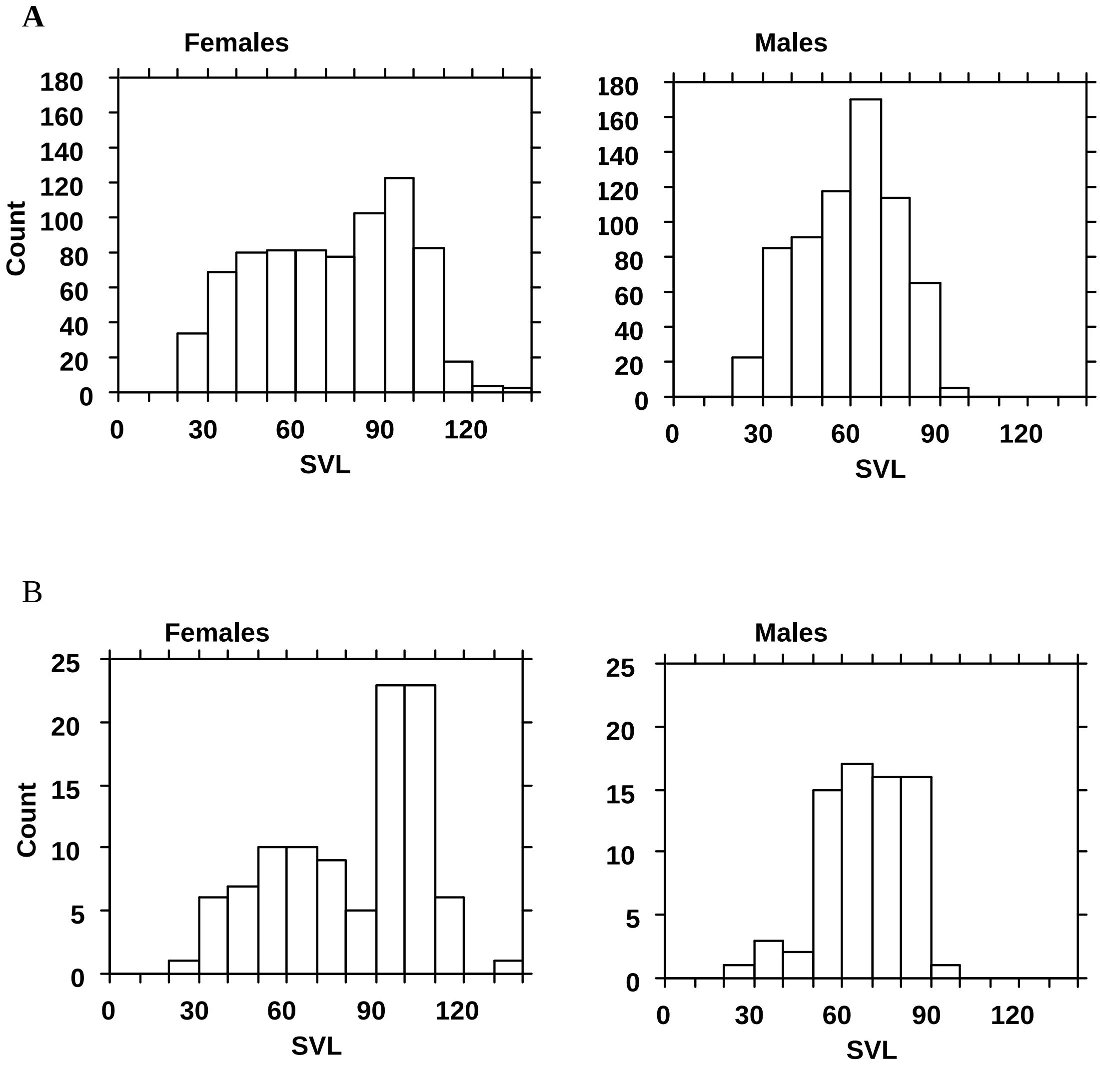


Figure 4.2 – Size frequency of all captured (A) and recaptured (B) *Nerodia taxispilota* on the SRS, South Carolina. Mean ± SD (range) SVL of original-capture females was 72.03 ± 25.12 cm (22.9-133.0 cm, n = 748) and males was 59.13 ± 16.10 cm (22.3-97.0 cm, n = 675). Recaptured females were an average of 81.05 ± 25.04 cm (23.0-133.0 cm, n = 99) and recaptured males were 68.02 ± 14.43 cm (23.1-94.8 cm, n = 73). This graph does not include neonates born and marked in the laboratory.

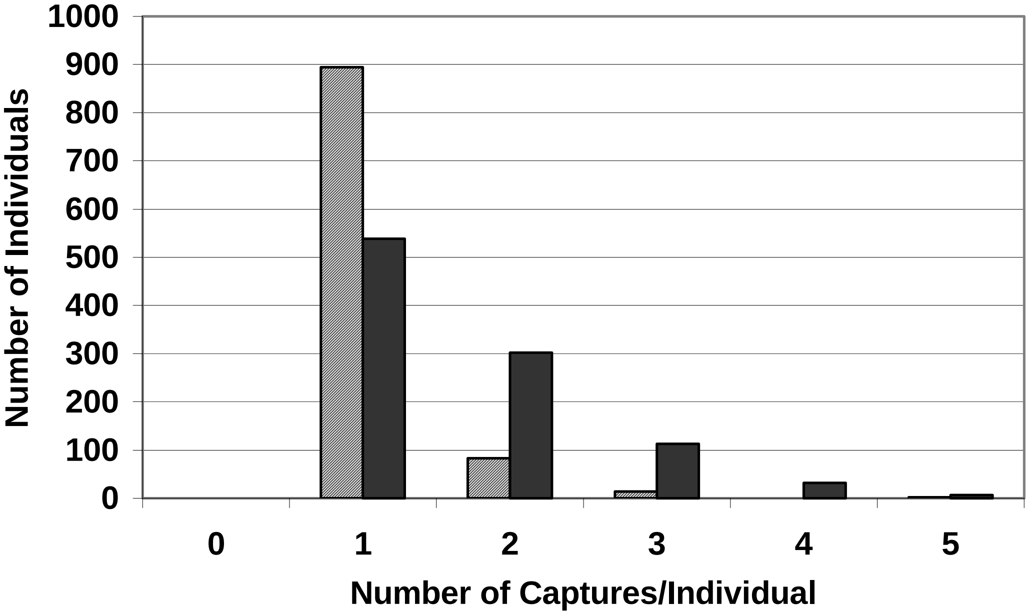


Figure 4.3 – Observed (hatched bars) versus expected (solid bars) number of recaptures per individual *Nerodia taxispilota* for Study Site a (Savannah River near UTR Creek). Expected numbers are based on a zero-truncated Poisson (random) distribution.

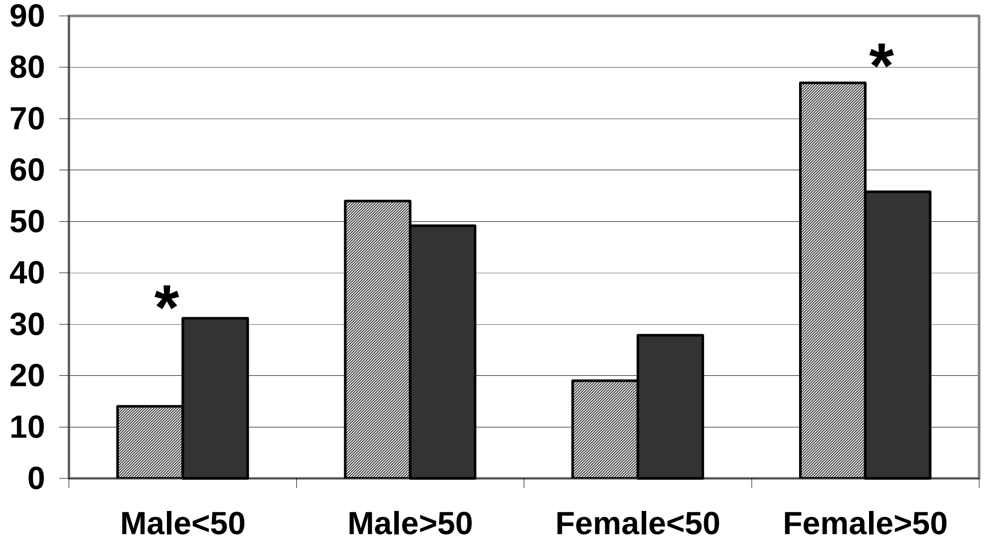


Figure 4.4 – Observed (hatched bars) versus expected (solid bars) number of recaptures in each of four size-sex categories of *Nerodia taxispilota*. The expected values are based on the proportion of original captures in each category. The asterisk indicates the categories that contribute the most to the Chi-square statistic (see text for explanation).

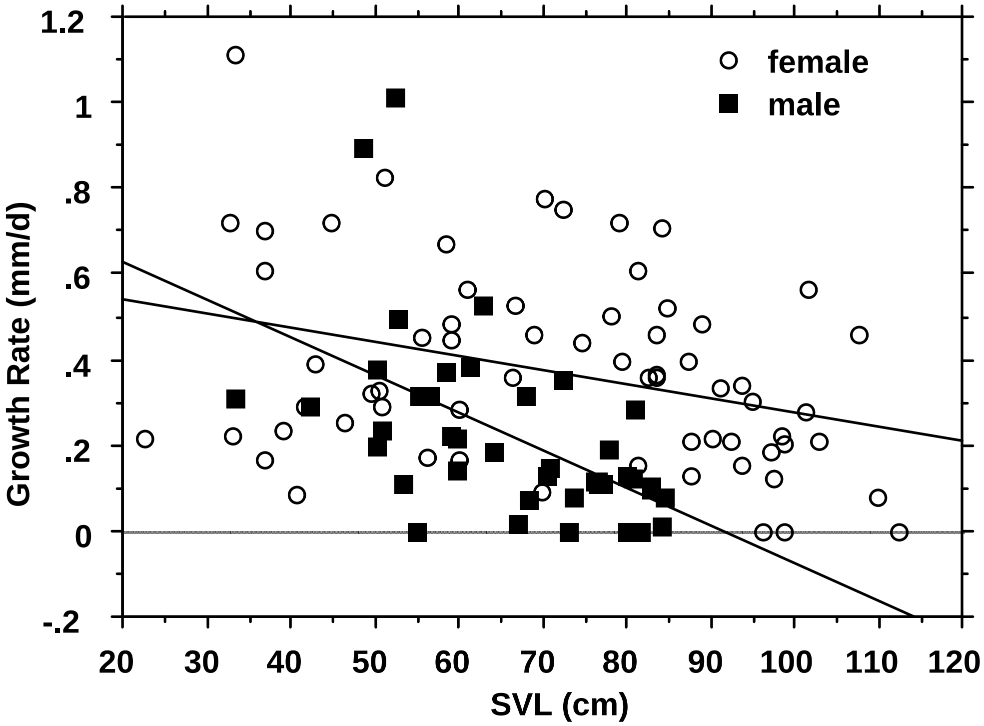


Figure 4.5 – Growth rate as a function of body size for male and female *Nerodia taxispilota*. The regression equations are as follows: male growth rate = 0.752 – 0.000757 * SVL, R2 = 0.206, P = 0.003; female growth rate = 0.519 – 0.000183 * SVL, R2 = 0.041, P = 0.105.

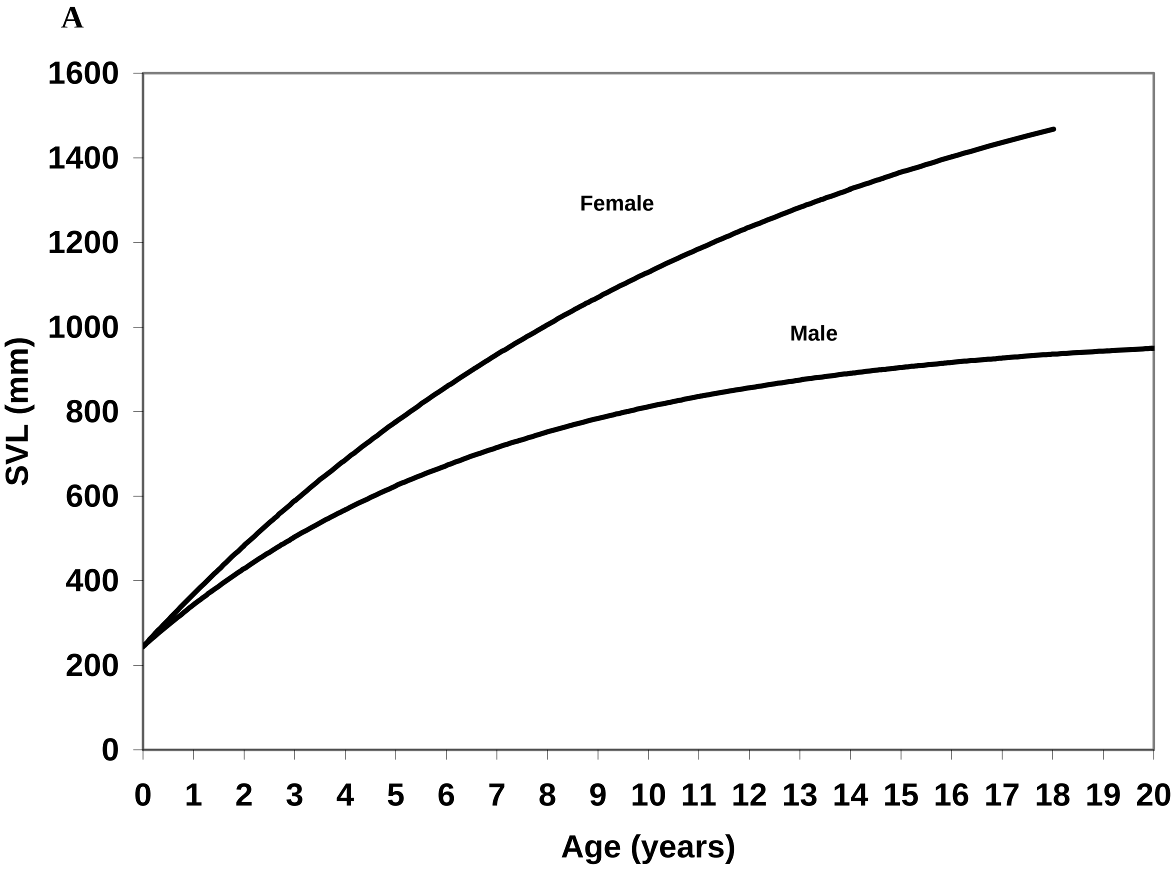


Figure 4.6 – A) Hypothesized age-length relationship of females and males based on growth of recaptured individuals fitted to the von Bertalanffy model (see text for fitted parameters of this model).

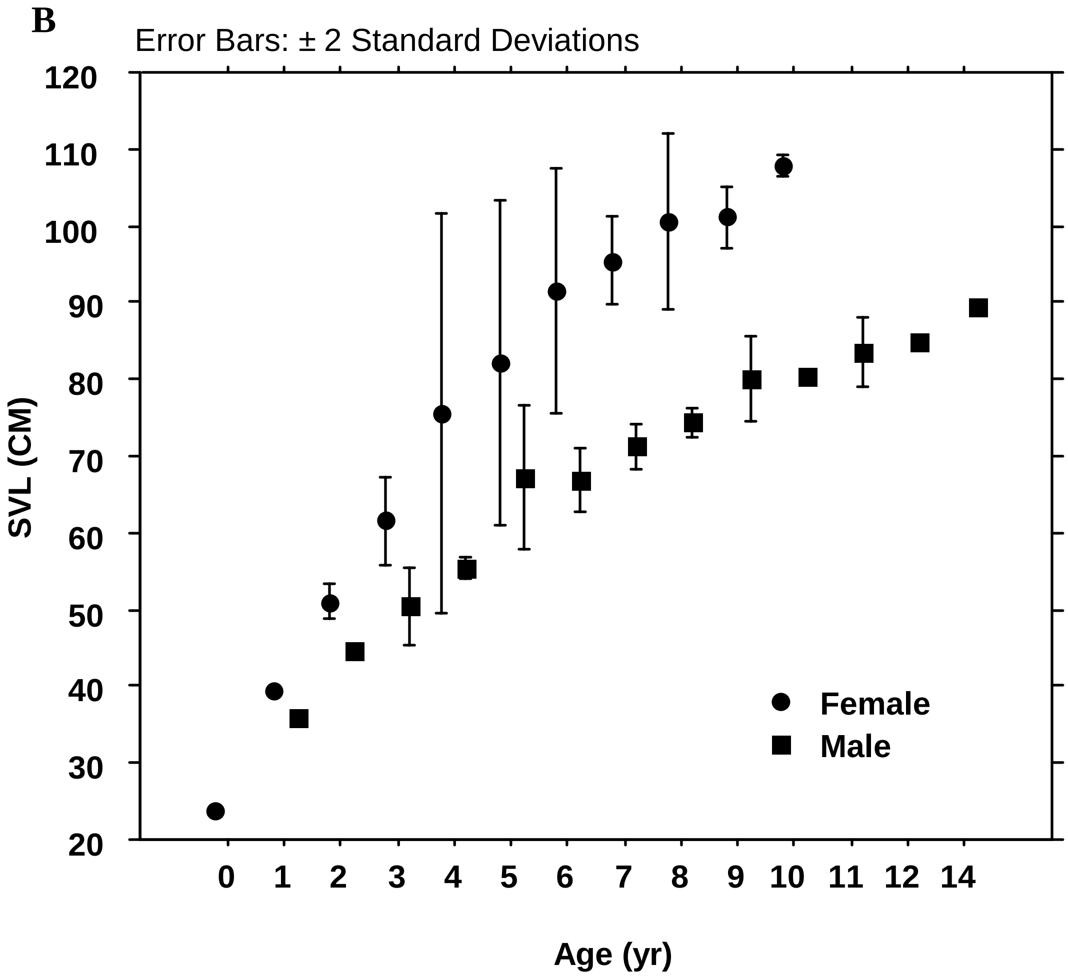


Figure 4.6 – B) Observed growth for individuals captured two or more years after their original capture (Table 6). Age at original capture was estimated using the von Bertalanffy growth curves and subsequent age was calculated from the time interval between captures. Symbols represent mean values for recaptured individuals and vertical bars are two standard deviations.

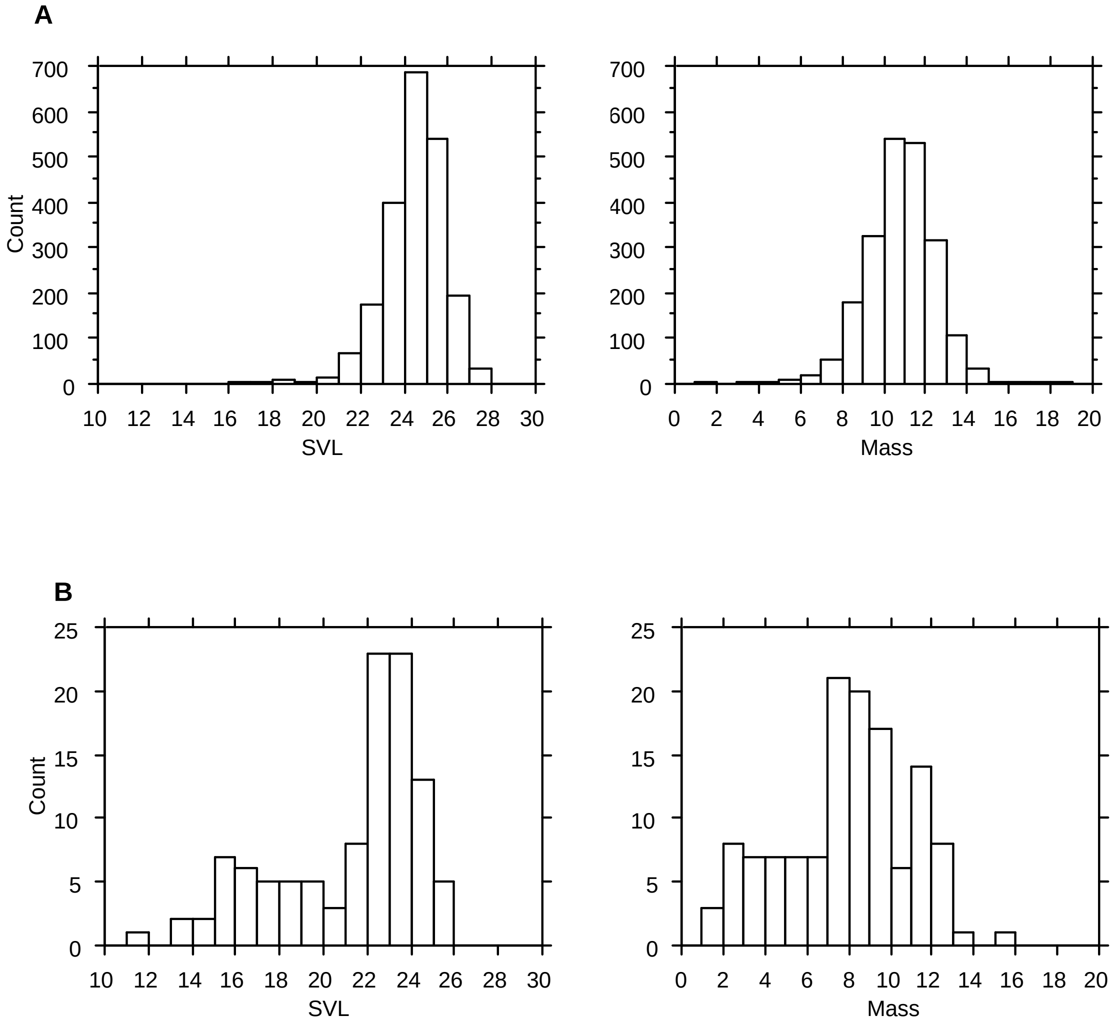


Figure 4.7 – Histograms of neonate *Nerodia taxispilota* SVL and mass based on A) living (top) and B) stillborn (bottom) neonates.

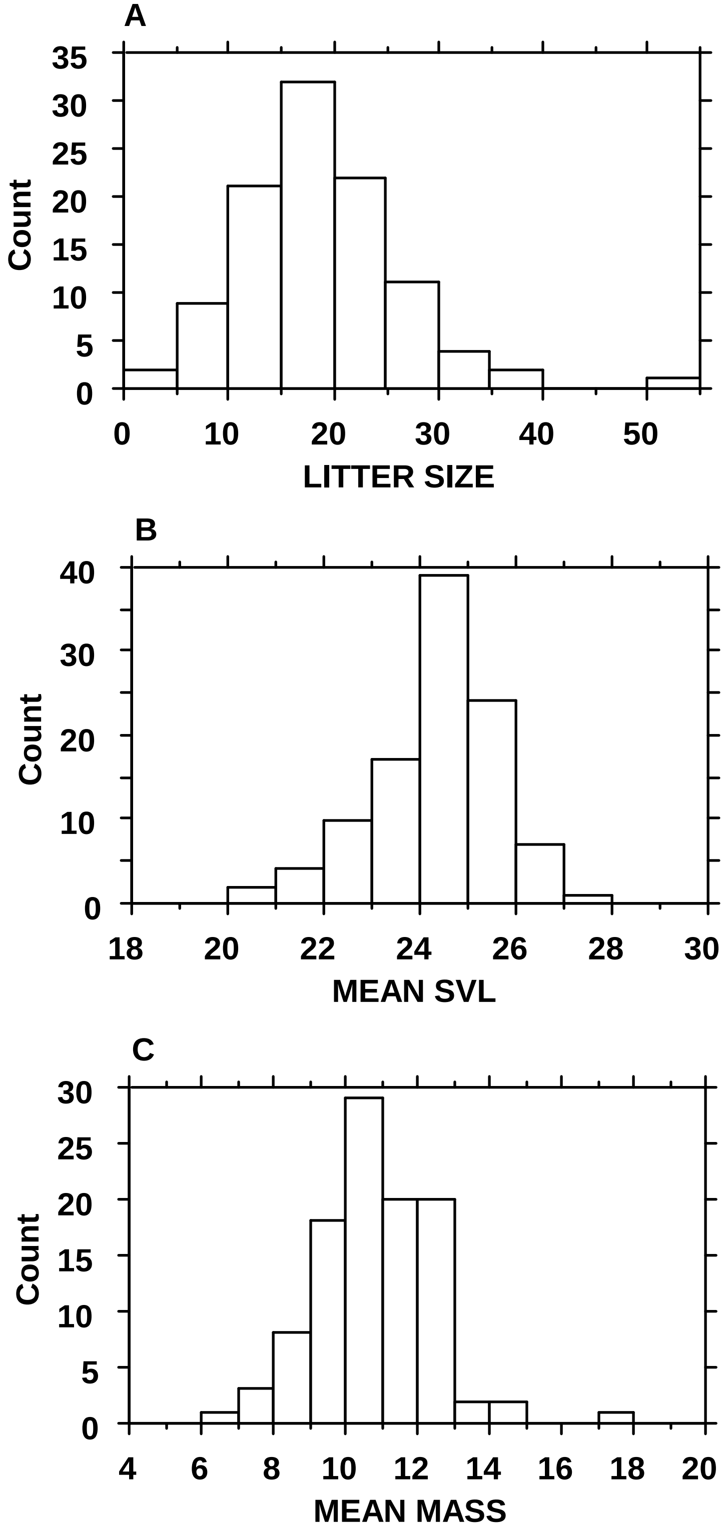


Figure 4.8 – Frequency histograms of A) litter sizes (n = 104), B) mean SVL (cm) of neonates (n = 104 litters), and C) mean mass (g) of neonates (n = 104 litters).

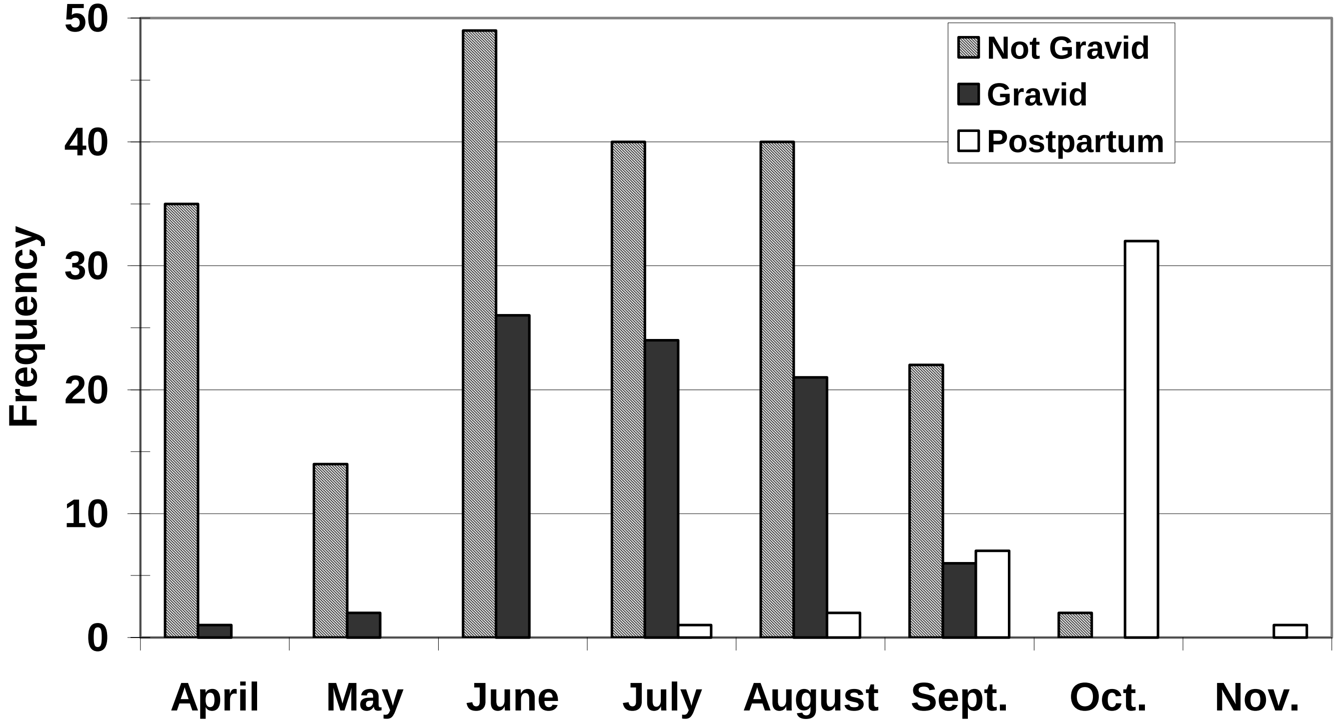


Figure 4.9 – Reproductive condition of mature (> 79.5 cm) wild-caught *Nerodia taxispilota* from April through November.

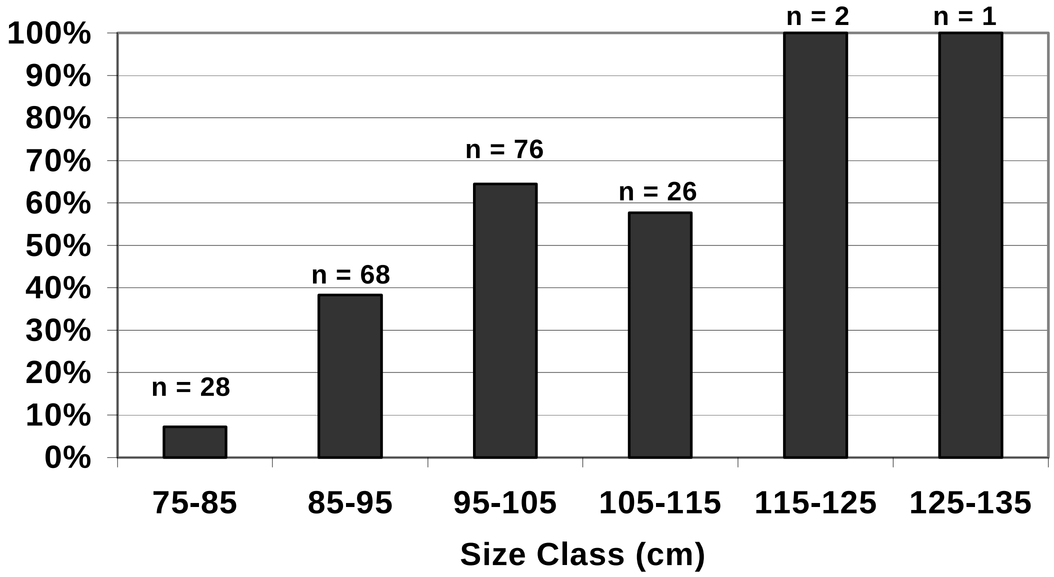
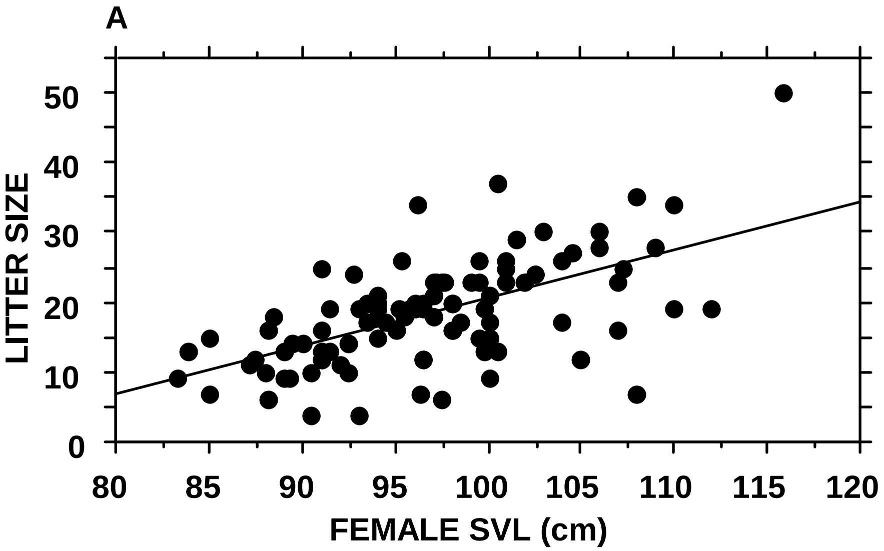
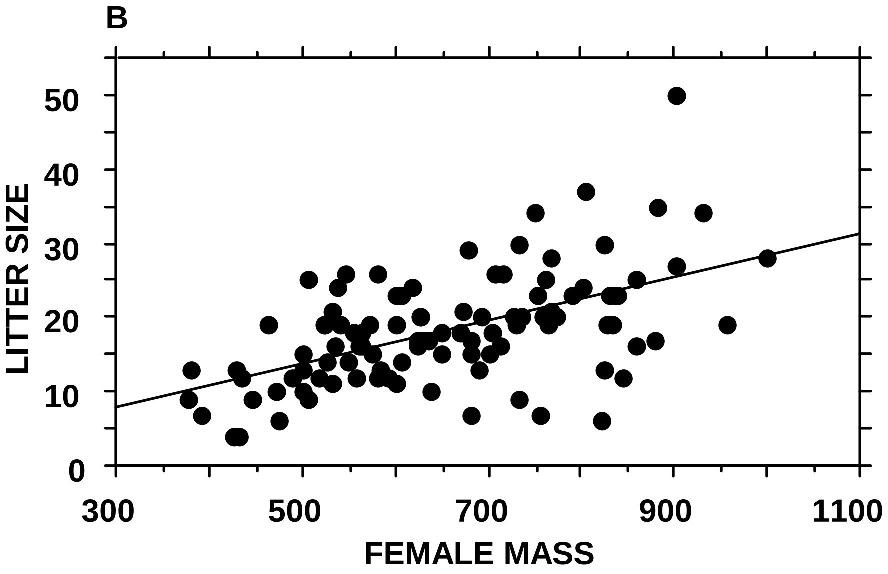


Figure 4.10 – Proportion of females in each size class that were gravid based on field observations after July 1.



LITTER SIZE = -48.823 + .694 * FEMALE SVL (cm); R^2 = .356



LITTER SIZE = -.619 + .029 * FEMALE MASS; R^2 = .299

Figure 4.11 – Litter size as a function of female A) length (cm), and B) mass (g). All regressions are significant ($P<0.0001$).

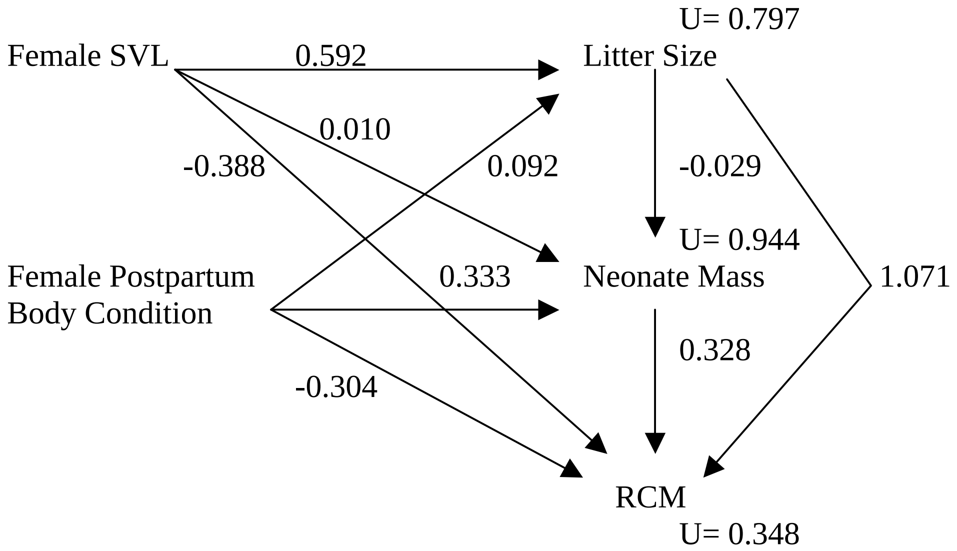
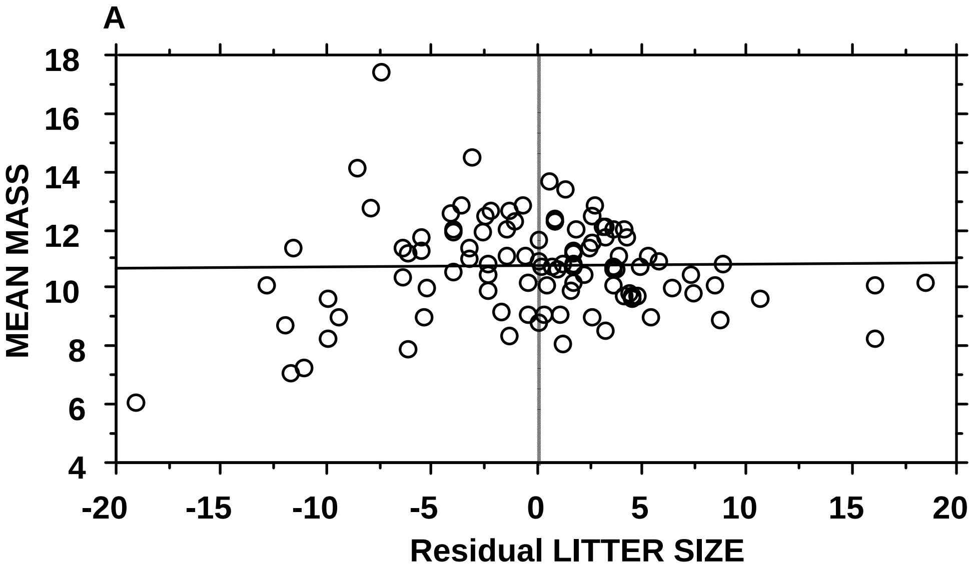
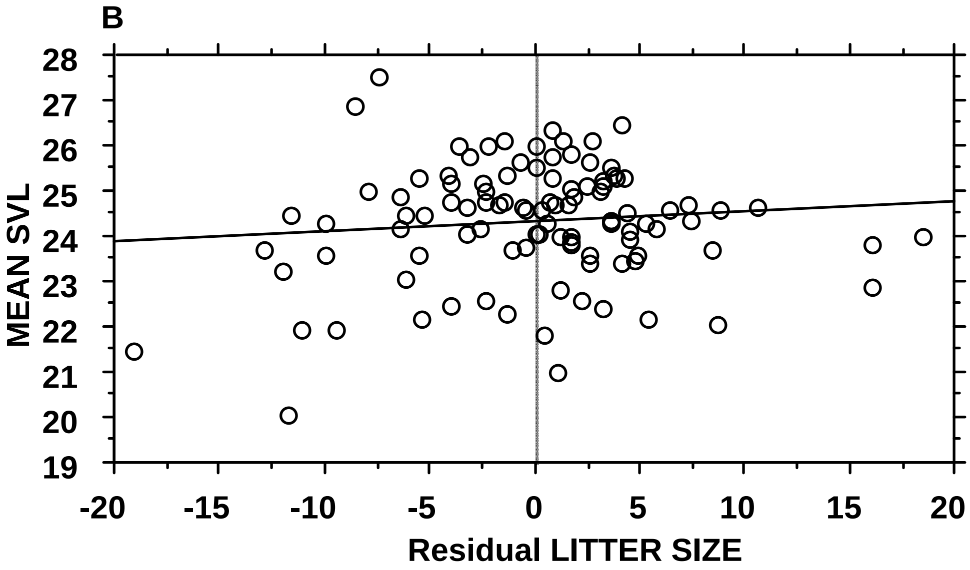


Figure 4.12 – Path diagram illustrating observed relationships among reproductive variables in *Nerodia taxispilota*. Path coefficients (standardized partial regression coefficients) were obtained from multiple regressions (Table 14). Unexplained variance (U) in the path diagram was calculated as $U = (1 - R^2)^{0.5}$, where R is the proportion of variation in the dependent variable that is explained by the regression model (King, 1993; Madsen and Shine, 1996).



MEAN MASS = 10.797 + .004 * Residual LITTER SIZE; R^2 = 2.099E-4



MEAN SVL = 24.322 + .021 * Residual LITTER SIZE; R^2 = .01

Figure 4.13 – The trade-off between relative litter size (residual litter size = residual score from the linear regression of litter size on maternal SVL) and A) mean offspring mass, and B) mean offspring SVL.

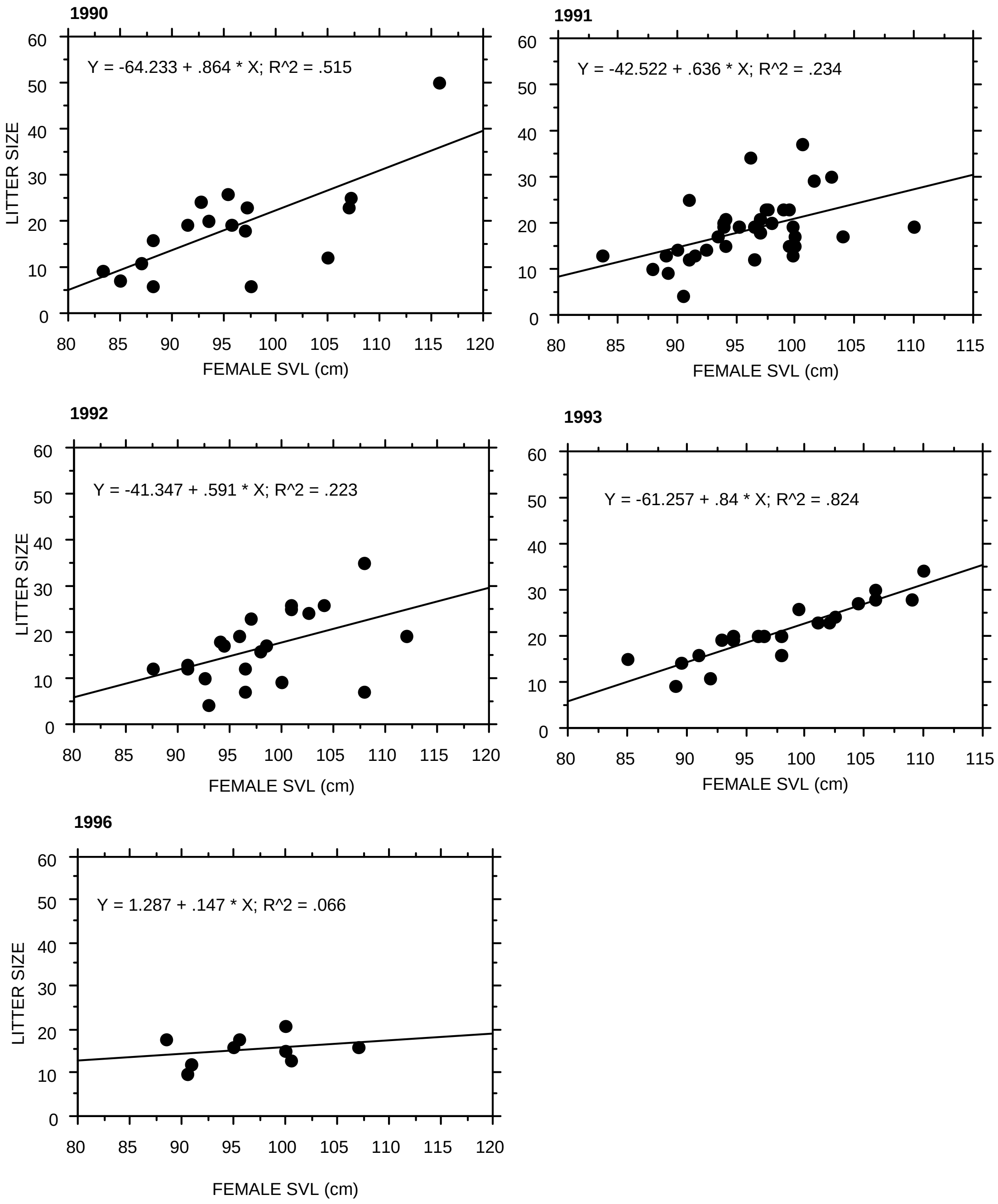


Figure 4.14 – Litter size as a function of female length (cm), separated by year.

CHAPTER 5

CONCLUSIONS

Over a period of almost eight years I observed, captured, and studied the brown water snake, *Nerodia taxispilota*, at the Savannah River Site (SRS), South Carolina, USA. My intended purpose for this research was to identify and fill in gaps in our knowledge and understanding of this species at the SRS in order to provide the solid background needed for future and ongoing studies in ecology, life history evolution, ecotoxicology, and other areas. Whereas I had hoped that the apparently high population densities, conspicuous basking behavior, and other traits of this snake would make this a model species for study, I was confronted with many of the same problems that have plagued other studies of snakes, including: low recapture rates (<10%), difficulties in sampling juveniles, highly variable growth rates, and an inability to accurately age individuals. Despite these problems, this dissertation represents the largest (> 1500 original captures; > 2200 neonates born in captivity), longest (8 yr), and most comprehensive study to date on *N. taxispilota*.

The brown water snake occurs in high densities (1 snake/5m of shoreline) on the Savannah River and its tributaries. These snakes are not randomly distributed along the river and were associated with the steep-banked outer bends of the river and areas within 200 m of tributaries, sloughs, and oxbow lakes. Whereas most individuals were recaptured near their previous capture site, several moved greater than 1 km.

Nerodia taxispilota is a piscivorous snake and greater than 60% of its diet consists of catfishes (Ictaluridae). Although the adults eat catfish almost exclusively, the young consume a greater variety of prey. Brown water snakes were observed using both sit-and-wait and active foraging to locate and capture their prey.

Brown water snakes are relatively large (often > 1m in body length), with females reaching larger maximum sizes than males. Growth is similar in juvenile males and females, but adult males grow more slowly than adult females. Males mature earlier than females, and combined with differences in growth rates this results in the observed sexual size dimorphism. Despite difficulties in accurately aging *N. taxispilota*, individuals appear to be relatively long-lived (> 6 yr) based on recaptures. Breeding takes place in the spring and parturition occurs from early August through October. Females are capable of annual reproduction, although not all females reproduce in a given year. Litter size was large (mean = 18.2), highly variable (4-50 offspring/litter), and positively correlated with female body size. No apparent trade-off exists between number and size of offspring; that is, offspring size remains relatively constant, independent of the number of young in the litter.

The present study represents a major advance in our knowledge and understanding of *N. taxispilota* and has offered research avenues for future work. For example, research is currently being conducted to study the role *N. taxispilota* has in the uptake and transport of toxins (e.g., mercury), and the potential for multiple paternity in this species is being evaluated using blood samples taken from females and their litters collected as part of the present study. I and others will continue to monitor this population to gain information on long-term survivorship and population structure of the brown water snake, *N. taxispilota*.