Chapter

Comparative Ecology of Two Species of Semiaquatic Snakes in Southeastern North America

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Abstract

The banded water snake (*Nerodia fasciata fasciata*) and the Eastern cottonmouth (*Agkistrodon piscivorus piscivorus*) were the focal species in a long-term mark and recapture study in the upper coastal plain of South Carolina, USA. Recapture rates were low for both species. Female *N. fasciata* were significantly larger than males. Male *A. piscivorus* were larger than females but not significantly. Age structure and sex ratios were determined for these populations. Recapture latency was greater for *A. piscivorus* than for *N. fasciata.* There was little dietary niche overlap between these two species. *Nerodia fasciata* ingested significantly more fish headfirst and more amphibians tail first. Growth rates were also calculated for both species. Litter size, offspring size, relative clutch mass and parturition dates were determined for *N. fasciata.*

Keywords: banded water snake, Eastern cottonmouth, reproduction, food habits, population ecology, sexual dimorphism

1. Introduction

Certain aspects of the life history of an organism can have important fitness consequences [1]. Snakes have lagged behind other groups of vertebrates in the understanding of life history traits due to difficulties in detection and sampling [2]. Successful reproduction is the primary measure of fitness but life history parameters such as foraging success, thermoregulation and habitat choice are important to survival and therefore a prerequisite to fitness increases [3, 4]. In an attempt to elucidate the importance of these ecological factors I studied two semiaquatic snake species on the coastal plain of southeastern North America.

The banded water snake (*Nerodia fasciata*) is a moderate sized (to 1524 mm total length) heavy bodied snake with a dorsal color pattern of brown to reddish-brown bands with grayish to brown pigment between the bands [5] (**Figure 1**). The labial scales bear dark bars at their margins and a dark stripe runs from the eye to the angle of the jaw. Larger specimens frequently lose much of the banding and are uniformly brown. This species occurs throughout the coastal plain of southeastern North America from the state of North Carolina south to Florida and west to Texas [6]. It can be found in almost any body of fresh water including streams, rivers, lakes, ponds, marshes, sloughs, canals and swamps. Life history data for this species has been summarized by [5, 6].

Figure 1.
Adult female banded water snake (Nerodia fasciata fasciata) from the study site. Note faint bands in upper left part of photograph.

The cottonmouth or water moccasin (*Agkistrodon piscivorus*) is a large (to 1890 mm total length) pitviper with a thick brown stripe on the side of the head that runs through the eye to the angle of the jaw (**Figure 2**). Pale lines both above and below border this stripe. The large triangular shaped head is distinctly wider than the neck and the pupil is vertically elliptical. The dorsal color pattern consists of wide dark brown bands with lighter centers that alternate with a lighter brown ground color. Many larger specimens have the banding pattern obscured and appear a uniform dark brown. The inside of the mouth is lined with white tissue and is used

Figure 2.
Adult male Eastern cottonmouth (Agkistrodon piscivorus piscivorus) from Clarendon County, South Carolina, USA. Note the gaping behavior that inspires the common name.

as a warning to potential predators [7]. Cottonmouths occur in many of the same habitats as banded water snakes [6]. One long term mark recapture study was published by [8] for a western population of this species. Other aspects of the biology of this species have been reviewed by [6, 9].

The objective of this long-term study was to compare the ecology of syntopic populations of these semiaquatic snakes that are distantly related and from different clades [10]. *Agkistrodon piscivorus* and *Nerodia fasciata* show striking similarities and marked differences in many of their life history traits [5, 6]. Both are live bearing but differ in that *Nerodia* are income breeders with larger litters of smaller offspring whereas *Agkistrodon* are capital breeders producing small litters of larger young [11]. Female water snakes usually breed annually whereas female cottonmouths do not. Even though both species consume similar prey they employ different foraging behaviors. *Nerodia* are active foragers whereas *A. piscivorus* use sit and wait or ambush foraging [5, 12].

2. Methods

2.1 Study site

The study site was the Pee Dee Research and Education Center (PDREC), a 972 ha experimental agricultural facility owned by Clemson University, located in the upper coastal plain of Darlington County, South Carolina, USA. A series of six ponds formed by damming a creek was sampled most intensively (**Figure 3B**), a larger pond nearby was also sampled (**Figure 3A**), and Back Swamp (**Figure 3C**) an undammed creek north of the other two sites was sampled as well. All three of these wetlands flow east into Dargan's Pond which is a man-made reservoir. The ponds were surrounded by mowed grass, old field or strips of woody vegetation consisting of alder (*Alnus* sp.), willow (*Salix* sp.), loblolly pine (*Pinus taeda*), bald cypress (*Taxodium distichum*), sweet gum (*Liquidamber styraciflua*) and oaks (*Quercus* sp.). The swamp contained riparian forest which includes the above-mentioned woody plants plus red maple (*Acer rubrum*), water tupelo (*Nyssa aquatica*) and tulip poplar (*Liriodendron tulipifera*). The littoral zone of all wetlands consisted of emergent vegetation that included water lilies (*Nuphar* sp., *Nymphaea* sp.), smart weed (*Polygonum* sp.), bur-reed (*Sparganium* sp.) and patches of penny wort (*Hydrocotyle* sp.). The climate of this region consists of hot humid summers (mean June–August high temperatures during 2002–2006 were 33°C) [13]. Precipitation averaged 14.5 cm per month during June–August 2002–2006 and the region has mild winters with the mean January high temperatures of 14°C during 2002–2006.

2.2 Data acquisition

Snakes were sampled most frequently using double ended funnel traps although opportunistic hand captures under artificial cover objects placed along the shoreline or on or near roads were used as well. Commercially available metal minnow traps (Cuba Specialty Manufacturing Co., Filmore, NY, USA) 42 × 22 cm, plastic funnel traps (model 700; N.A.S. Incorporated, Marblehead, Ohio, USA), vinyl coated wire funnel traps (Academy Sports + Outdoors) and funnel traps made from hardware cloth that were 41 × 22 cm with 5 cm funnel openings [14] were used to sample *Nerodia fasciata* and *Agkistrodon piscivorus.* Pre-manufactured metal traps had their funnel openings enlarged to approximately 3 cm with a rake handle. Traps were placed about 3 m apart in shallow water (water depth < trap diameter) along logs, in emergent vegetation and along short aluminum drift fences. The drift

Figure 3.
The Pee Dee Research and Education Center, Darlington County, South Carolina, USA. The property boundaries are outlined in black. (A) Pond near headquarters, (B) ponds where most data were collected, (C) back swamp. The Great Pee Dee River is on the upper right just outside the property boundaries. The scale bar in the lower left is 800 m.

fences consisted of 5 m lengths of aluminum flashing oriented perpendicular to the shoreline with two traps placed at each end. Due to low capture rates, 0.007 captures/trap day (1 trap day = one trap out over 1 night, hereafter TD) in 1998 to 0.011 captures/TD in 2002, traps were checked at 48 h intervals and were either disabled or not checked on weekends when PDREC was closed. From 2010 onward traps were checked daily and closed over weekends.

Sampling took place from 1998 to 2003, 2010–2011, 2014 and 2016. Data collection from *A. piscivorus* was not started until August 1999. Sampling occurred from July–October 1998 (960 TD), May–October 1999 (4108 TD), May–July 2000 (994 TD), April–June 2001 and 2002 (810, 994 TD respectively), and May–June 2003 (757 TD) [15]. Starting in 2010 multiple shorter sampling periods per season were introduced following the robust design of [16]. Sampling occurred for 7 days in March, 11 days in April, 9 days in May–June, 9 days in August and 14 days in September during 2010. In 2011 sampling occurred for 10 days in each of May and June. During 2014 snakes were sampled for 10 days in May, 6 days in June and 5 days in September. During 2016 sampling occurred for 7 days in May and 10 days in each of June and August. The number of traps used ranged from 97 to 140. From 2010 to 2016 trapping effort ranged from 665 to 1876 TD per trapping period.

Snakes were usually processed in the field. Snout to vent length (hereafter SVL) and tail length (TL) was measured to the nearest mm with a measuring tape for *Nerodia* and a squeeze box [17] was used to measure SVL, TL, head length and head width of *A.*

piscivorus. The squeeze box was a modified plastic toolbox 66 cm × 28 cm × 28 cm. Head length and width were measured to the nearest 0.1 mm with calipers for *N. fasciata*. Mass was measured with Pesola spring scales to the nearest 1 g. Except for *Nerodia* neonates, snakes were marked with passive integrated transponder (PIT) tags [18]. Newborn *Nerodia* were marked by clipping ventral scales [19]. Sex was determined by examination of the base of the tail or by probing the tail. Data were taken from recaptures only after a minimum of 14 days had elapsed since the previous capture.

Diets were studied by examining stomach contents. Prey were palpated from the stomachs of *Nerodia* and stomach contents were recovered from cloth bags or from traps for both species. Only prey from traps with evidence of ingestion (saliva, mucous, envenomation) were included in the analyses. Prey mass was measured to the nearest 0.1 g using an electronic balance. Prey length and width were measured to the nearest 0.1 mm with calipers. Prey were identified to species when possible. Prey availability was measured by counting all prey in all traps during one day of most sampling periods. Prey counts were conducted in May and August of 2010, May of 2011, May and September of 2014 and May, June, and August of 2016 (**Table 1**). Dietary niche overlap used the formula of [20].

Females were palpated for embryos when processed. In 1999 four gravid *N. fasciata* were kept in the lab until parturition. Pregnant females were given water and food ad libitum. Food consisted of frozen/thawed fish purchased alive from a bait store. Pregnant snakes were kept on a 12:12 light: dark cycle at approximately 27°C. One died about 1 week prior to giving birth. Young were weighed and measured and marked by scale clipping. They were released at the site of maternal capture. Clutch sizes were also reported from oviductal eggs of females that died in traps. Cloacal swabs were taken from both sexes of each species from 1999 to 2001 to look for the presence of sperm. The ductus deferens of one male of each species were also examined for the presence of sperm.

Growth rates were calculated from recaptures as the difference in SVL in mm divided by the number of days between captures. The active season was considered 15 April through 15 October which is 183 days per year. Even if active the animals were considered to not be feeding and therefore not growing before 15 April or after 15 October. Negative growth values were not used in calculating growth rates and were considered the result of measurement error.

2.3 Statistical analyses

Tests for normality utilized the Shapiro-Wilks test and visual examination of box plots and histograms. Homoscedasticity was examined using the F-test or Bartlett's test.

Date	Crayfish	Fishes	Amphibians	Turtles	Snakes
May 2010	26.6	53.8	19.4	0.3	0
August 2010	1.9	88	9.7	0	0.4
May 2011	20.5	40.5	38.8	0	0.2
May 2014	24.4	37.2	38.4	0	0
September 2014	1.6	72.1	26	0	0.3
May 2016	22.3	33.7	43.5	0	0
June 2016	10.8	28.4	60.6	0.2	0
August 2016	4	44.2	48.6	3.1	0

Table 1.
Prey availability in one pond where most snakes were sampled in this study. Numbers are percentages. See text for explanation of methods.

Due to correlation among response variables (mass, SVL, TL, head length, head width), a multivariate analysis of variance (MANOVA) was used to test for sexual differences. The Welch t-test was used to test differences between individual variables due to unequal variances. Means are followed by ±1 standard deviation (SD) and an $\alpha \leq 0.05$ is considered significant in all statistical tests. Statistical analyses were performed in R version 4.1.1 [21]. Due to heteroscedasticity some data were natural log transformed.

3. Results

3.1 Population structure

A total of 181 *N. fasciata* and 93 *A. piscivorus* were marked in this study. Because year was used as the sampling period in the early part of this study (1998–2003) and shorter periods during the latter part of the study (2010–2016) estimates of

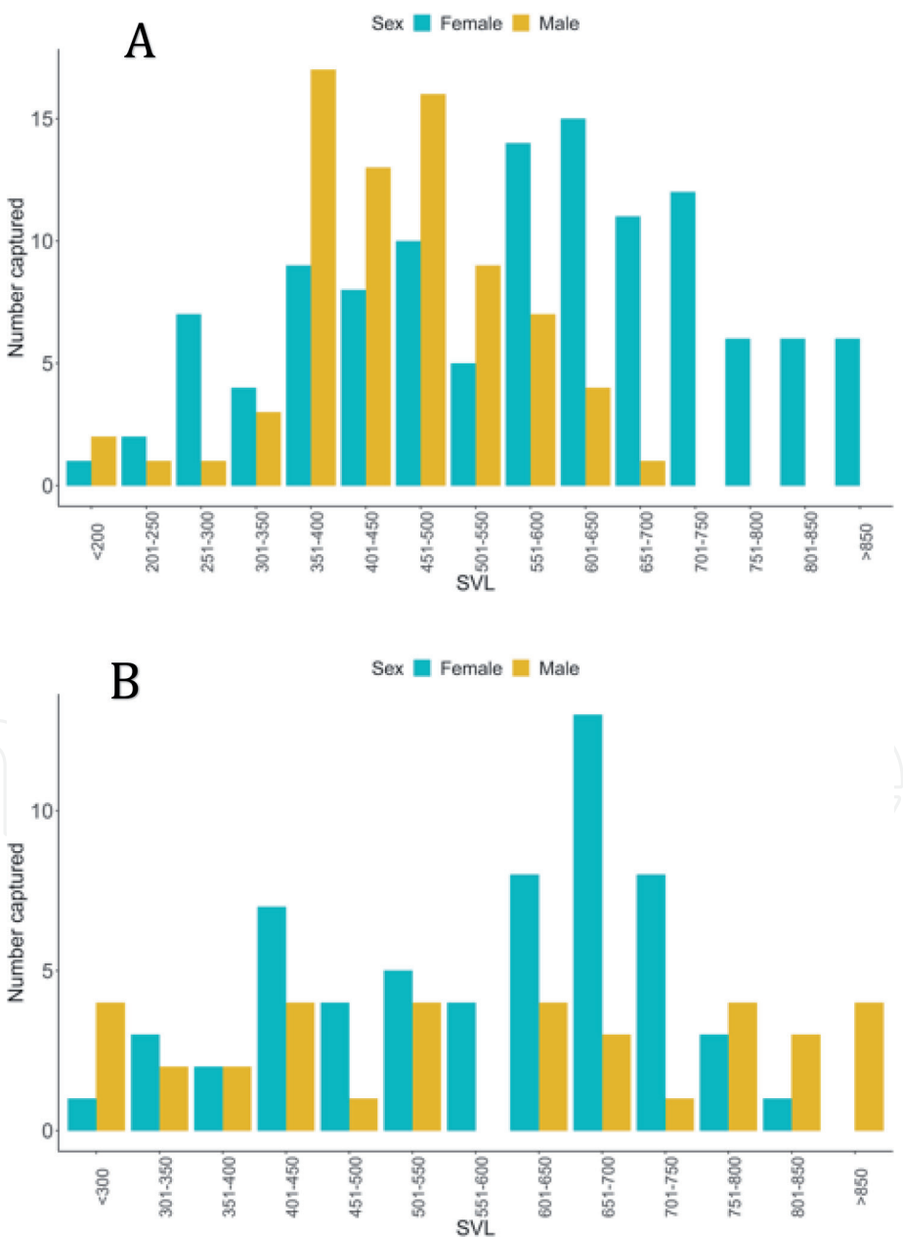

Figure 4.
Size distribution of captures of each sex of (A) Nerodia fasciata; (B) Agkistrodon piscivorus at the Pee Dee Research and Education Center, Darlington County, South Carolina, USA. The ordinate is the number of captures.

population size and survivorship could not be calculated. Recapture rates were higher for *N. fasciata* (31.5%) than for *A. piscivorus* (16%). Few neonates were captured with only 1.66% of the sample for banded water snakes and 6.45% for the cottonmouths. Subadults were defined as >1 year old but not sexually mature and made up a larger part of the sample for both species with 27% for *Nerodia* and 25.8% for *Agkistrodon*. **Figure 4A** indicates that most male *N. fasciata* were between 350 and 550 mm SVL whereas most adult females were between 550 and 750 mm SVL. There was a peak in adult female *A. piscivorus* from 600 to 750 mm SVL (**Figure 4B**). Captures of both sexes of *Nerodia* peaked in May and females showed a smaller peak in August (**Figure 5A**). Male captures gradually declined throughout the summer. Low numbers for July were due to lower trapping effort. Adult male cottonmouth captures peaked in May and declined throughout the summer (**Figure 5B**). Female captures peaked in June and showed a smaller peak in September. Sex ratios exhibited a female bias and were 1.4F:1M for each species. However, four litters of *N. fasciata* born in the lab had sex ratios that did not differ from 1:1 (X^2 = 4.934, df = 3, p = 0.084839).

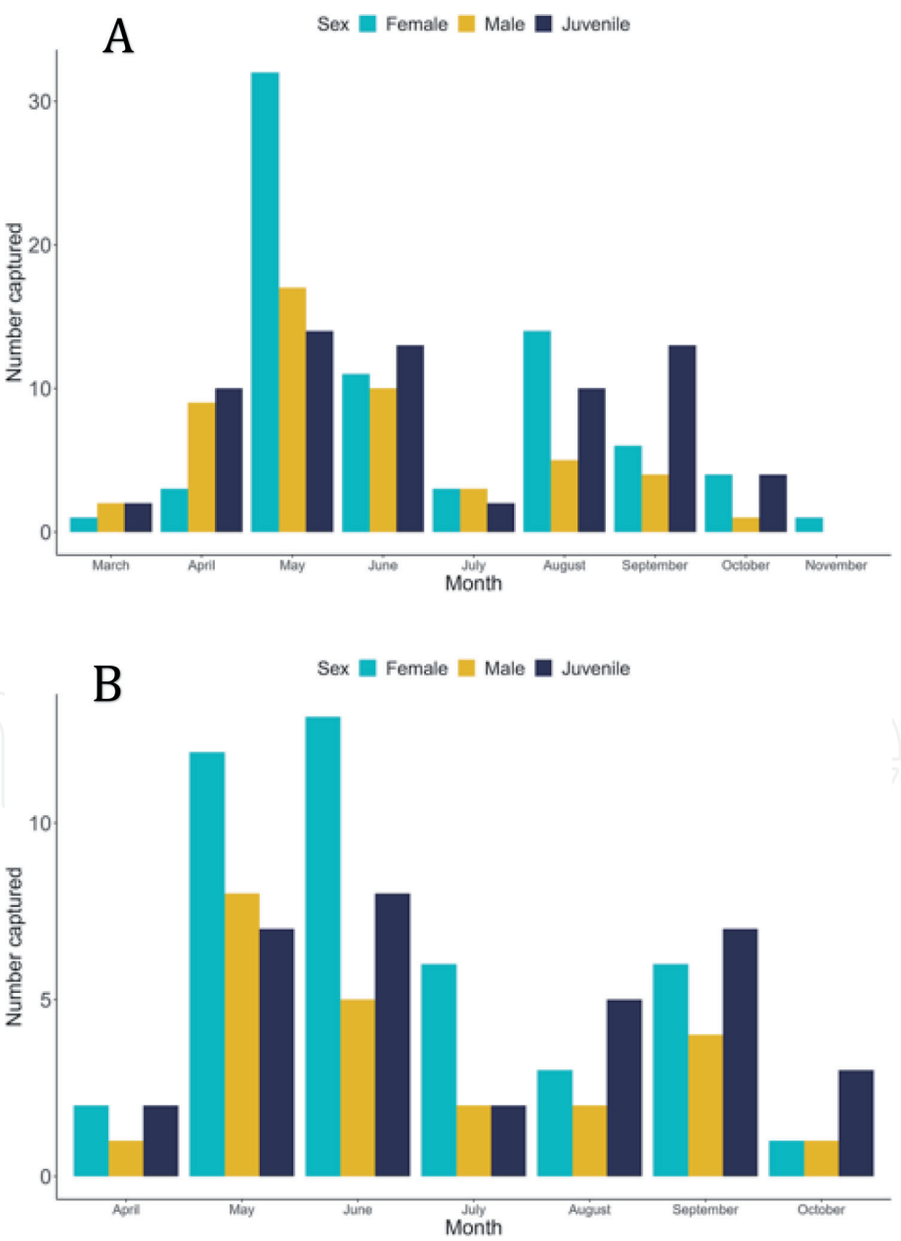

Figure 5.
Seasonal distribution of captures of (A) Nerodia fasciata; (B) Agkistrodon piscivorus at the Pee Dee Research and Education Center, Darlington County, South Carolina, USA. The ordinate is the number of captures.

Recapture latency or the time between captures in days for each species was calculated based upon an activity season from 25 March to 10 November which is 231 days per year. Mean days between captures for male *N. fasciata* were 116.5 ± 193.6 days (range 2–814 days) and for females it was 60.4 ± 58.1 days (range 4–233 days). These were not significantly different using a two-sample t-test with unequal variances ($t = -0.334$, $df = 23$, $p = 0.7415$). Mean recapture latency for both sexes combined was 80.7 ± 126.1 days (range 2–814 days). Mean recapture latency for *A. piscivorus* was 263.3 ± 575.4 days with a range of 12–2074 days. Although recapture latency was greater for *A. piscivorus* the difference was not significant ($t = -1.7025$, $df = 15.295$, $p = 0.1089$) with a two-sample t-test with unequal variances.

3.2 Sexual dimorphism

Nerodia fasciata and *Agkistrodon piscivorus* exhibit different patterns of sexual size dimorphism. Females are larger in *N. fasciata* whereas males are larger in *A. piscivorus* (**Table 2**). A multivariate analysis of variance (MANOVA) showed significant differences between the sexes for *N. fasciata* (Pillais' trace = 0.340, $F(1, 140) = 14.002$, $p < 0.001$) for the morphological variables in **Table 2** but not for *A. piscivorus* (Pillais' trace = 0.117, $F(1, 86) = 2.17$, $p = 0.065$). Female *N. fasciata* were significantly greater in mass ($t = 3.5508$, $p = 0.0005$), SVL ($t = 3.983$, $p = 0.0001$), head length ($t = 5.025$, $p < 0.001$) and head width ($t = 5.218$, $p < 0.001$). However, tail length was not significantly different ($t = 1.6743$, $p = 0.0963$) between males and females. Relative tail length (tail length/total length; hereafter RTL) was greater for males of both species. For *N. fasciata* mean male RTL = 0.262 ± 0.016 (0.197–0.286, N = 55) whereas females averaged 0.241 ± 0.014 (0.197–0.269, N = 87). Values

	Nerodia fasciata		*Agkistrodon piscivorus*	
	Males	**Females**	**Males**	**Females**
Mass (g)	129.3 ± 58.2	340.8 ± 165.7	518 ± 305	412.9 ± 147.3
Range	54–307	131–730	165–1316	125–814
N	42	55	22	36
Snout vent length (mm)	504.5 ± 73.9	670.1 ± 98	731.3 ± 139.6	650.5 ± 85.2
Range	397–655	505–915	500–980	490–848
N	42	57	22	36
Tail length (mm)	178.1 ± 25.4	210.4 ± 28.4	130.5 ± 26.9	116.6 ± 15.4
Range	143–230	163–266	96–175	80–151
N	31	36	20	35
Head length (mm)	28 ± 4.3	37.4 ± 5.5	43.9 ± 5.8	41.8 ± 4.9
Range	18.5–37.3	24.2–51.3	34–51.5	32–48
N	42	57	22	36
Head width (mm)	15.8 ± 3.4	22.7 ± 3.8	37 ± 5.9	37.3 ± 4.2
Range	10.8–29.5	15.7–31.5	25.1–48.5	27.9–44
N	42	57	22	36

Table 2.
Sexual dimorphism in body and head size of adult Nerodia fasciata and Agkistrodon piscivorus from South Carolina, USA. Numbers are means ±1 standard deviation.

for male *A. piscivorus* were 0.159 ± 0.019 (0.111–0.229, N = 33) and for females 0.153 ± 0.016 (0.110–0.197, N = 56). The sexual dichromatism with males retaining a bolder banding pattern was also observed in this population of *A. piscivorus* [22].

3.3 Growth rates

Growth rate estimates were available for 28 *N. fasciata* and 6 *A. piscivorus*. Growth rates (mean ± 1 SD) were 0.726 ± 0.626 mm/day (0–2.3 mm/day) for *N. fasciata* and 0.783 ± 1.26 mm/day (0.029–3.31 mm/day) for *A. piscivorus*. Mean female *N. fasciata* growth rates were almost twice that of males (female 0.824 ± 0.672 mm/day, 0–2.3 mm/day, N = 21; male 0.432 ± 0.353, 1–1.029 mm/day, N = 7). Small sample size precluded statistical analysis. One female *A. piscivorus* that was originally marked on 3 May 2001 was recaptured on 28 April 2010 and had grown only 52 mm in almost 9 years and had a growth rate of 0.0322 mm/day.

3.4 Food habits

Both species fed frequently upon fishes whereas banded water snakes ate amphibians frequently but not reptiles and cottonmouths consumed reptiles but few amphibians (**Table 3**). The number of prey per stomach ranged from 1 to 8 for *N. fasciata* and 1–5 for *A. piscivorus*. Multiple prey were found in 10 of 24 (41.7%) banded water snakes and 3 of 5 (60%) cottonmouths. One 715 mm SVL female *A. piscivorus* contained 1 catfish, 1 sunfish (*Lepomis* sp.), 1 pickerel (*Esox* sp.), 1 frog (*Lithobates* sp.) and one Eastern musk turtle (*Sternotherus odoratus*). All but the turtle was swallowed headfirst. Mass ratios (prey mass/snake mass) given as mean ± 1 standard deviation followed by the range was greater for *A. piscivorus* (0.159 ± 0.208, 0.186–0.526) than for *N. fasciata* (0.109 ± 0.083, 0.0096–0.3889). Banded water snake stomach contents were 44% fishes and 56% amphibians whereas cottonmouth stomach contents were 46% fishes, 50% reptiles and 4% amphibians. Only one *N. fasciata,* a female 380 mm SVL, had eaten one Eastern mosquito fish (*Gambusia holbrooki*). Larval anurans made up the largest proportion of amphibians, with metamorphosed anurans contributing 18.7% and salamanders only 1.7% of the total. The dietary niche overlap [20] was low between these two species (O = 0.01024). Only *A. piscivorus* more than 550 mm SVL included reptiles in their diets and *N. fasciata* over 750 mm SVL dropped amphibians from their diets. Banded water snakes did not swallow prey headfirst more frequently than tail first (X^2 = 0.34, df = 1, $p > 0.05$) however, fishes were swallowed headfirst significantly more often, and amphibians tail first (2 × 2 contingency table, X^2 = 17.049, df = 1, $p < 0.05$). Small sample sizes precluded statistical analysis of *A. piscivorus* stomach contents.

Prey availability was assessed by counting all potential prey in the traps during one day per sampling period. There were eight prey censuses during this study (**Table 1**). Crayfish decreased in abundance during the season. Fishes and amphibians varied between sampling dates but did not show any discernible trends. *Gambusia holbrooki* made up a mean of 11.13 ± 7.73% (1.6–23.7%) of the samples.

3.5 Reproduction

The smallest male *N. fasciata* with sperm in the cloaca was 397 mm SVL and was sampled on 24 September 1999. Because a specimen 395 mm SVL sampled on 28 June 1999 lacked cloacal sperm, 400 mm SVL was designated as adult size for male *N. fasciata*. Eight males contained sperm (397–600 mm SVL) and 8 others (320–655 mm SVL) did not. Two males with sperm were from May, 4 from June

Prey category	*Nerodia fasciata*	*Agkistrodon piscivorus*
	N (%)	N (%)
Cyprinidae	1 (1.7)	1 (4.3)
Cyprinella sp.		1 (4.3)
Ictaluridae	1 (1.7)	1 (4.3)
Noturus sp.	1 (1.7)	
Esocidae		
Esox americanus	2 (3.4)	
Esox niger		1 (4.3)
Esox sp.	3 (5.1)	3 (13)
Poeciliidae		
Gambusia holbrooki	1 (1.7)	
Centrarchidae	1 (1.7)	
Enneacanthus sp.	1 (1.7)	
Lepomis punctatus	1 (1.7)	
Lepomis sp.	7 (11.9)	2 (8.7)
Micropterus salmoides	1 (1.7)	
Unidentifiable fish	7 (11.9)	1 (4.3)
Sirenidae		
Siren intermedia	1 (1.7)	
Hylidae		
Hyla cinerea	1 (1.7)	
Ranidae		
Lithobates catesbeianus	5 (8.5)	
Lithobates sphenocephalus	1 (1.7)	
Lithobates sp.	4 (6.8)	1 (4.3)
Lithobates larvae	20 (33.9)	
Kinosternidae		
Sternotherus odoratus		1 (4.3)
Colubridae		
Nerodia fasciata		11 (47.8)
Total prey	59	23

Table 3.
Frequency of occurrence of prey found in 25 Nerodia fasciata and 14 Agkistrodon piscivorus from the Pee Dee Research and Education Center, Darlington County, South Carolina, USA. N is the number of prey items in the sample.

and 2 from September. The males lacking sperm included 4 from May, 1 from June, 2 from July and 1 from August. The smallest male *A. piscivorus* that had sperm in the ductus deferens was 500 mm SVL and was caught on 26 May 2000. Another male (863 mm SVL) had cloacal sperm on 23 May. Three males lacking sperm were 768–961 mm SVL and were sampled in May (2) and July.

The smallest gravid female *N. fasciata* was 575 mm SVL however 500 mm SVL was used as the size for sexual maturity in analyses [23]. In 2000 92% of females were gravid and 91% in 2006 indicating that most females probably reproduce

annually in this population. Only 58% of female *A. piscivorus* were gravid in 2000 indicating a likely biennial reproduction in females of this species. The smallest gravid female *A. piscivorus* was 660 mm SVL and 500 mm SVL was used as minimum adult size for females of this species as well [24]. During 1999 four gravid *N. fasciata* were brought into the lab until parturition. One specimen died on 13 August with embryos in developmental stage 36 [25]. Clutch sizes ranged from 12 to 28 (mean ± 1 SD) was 18.45 ± 5.24 (N = 11). There was a significant positive correlation between maternal SVL and clutch size (r = 0.723, p = 0.018, N = 10). Dates of parturition for females that gave birth in the lab were 5 and 23 August and 3 September. The earliest in the season that females were found to be pregnant was 17 May for *N. fasciata* and 18 May for *A. piscivorus*. Relative clutch mass (RCM) ranged from 0.19–0.478 (mean ± 1 SD) was 0.335 ± 0.119 (N = 4). Mean neonate mass from three litters born in the lab was 3.89 ± 0.51 g (3–5 g, N = 66) and the mean SVL for these same snakes was 153.72 ± 5.77 mm (133–166, N = 66). Data on size of oviductal eggs came from four females collected in late May and early June which were at a similar enough developmental stage to be lumped into a single data set. Mean oviductal egg length was 21.30 ± 5.01 mm (13.2–32.7 mm, N = 66 ova) and mean oviductal egg width for the same ova was 13.82 ± 3.99 mm (7.7–19.9 mm, N = 66). One 715 mm SVL *A. piscivorus* collected on 26 May 2000 contained five oviductal eggs with a mean length of 35.68 ± 1.63 mm (33.9–37.5 mm) and a mean width of 21.94 ± 0.82 mm (21.0–22.9 mm). Three *N. fasciata* with oviductal eggs had more in the right oviduct than in the left. Mean (± 1SD) for the right oviduct was 10.33 ± 1.15 (9–11) and for the left 7 ± 1 (6–8) but not significantly more (X^2 = 1.924, df 1, p > 0.05). No banded water snakes had more in the left oviduct and the one *A. piscivorus* had two in the right oviduct and three in the left.

Stub tails and body scars can give information on potential predation pressure on snakes [26]. Nineteen male *N. fasciata* exhibited stub tails (15) or body scarring (4) which was 35% of the sample. Female *N. fasciata* showed 37.6% injured snakes with 26 of 32 with stub tails and 6 with body scarring. Cottonmouths showed a much lower frequency of injuries with only 4 of 32 males (12.5%) showing injuries and only one with body scarring. Females had the same numbers of injuries which showed an 8.3% injury rate.

4. Discussion

4.1 Population structure

Because population sizes and survival rates could not be estimated the discussion of population structure will focus on age structure and sex ratios. Only 3 neonate *N. fasciata* and 6 neonate *A. piscivorus* were caught in this study. Under sampling of juvenile snakes is usually attributed to low survival rates [27] however it may also be from trapping bias as neonatal snakes can escape through the mesh of traps [28] which I think may have occurred in this study for *N. fasciata.* Neonatal *A. piscivorus* are too large to escape through the trap mesh. Captures of subadult snakes, defined as >1 year old but not sexually mature, were frequent for both species (**Figure 4**). This finding may indicate these populations have a relatively young age structure and therefor may be undergoing population growth [29].

Sex ratios for both species were skewed in favor of females which I think may be due to sampling bias. Primary sex ratios were not different from unity for *N. fasciata*. There was a secondary peak of captures of postparturent females in August (**Figure 4**). Sometimes the same females were caught in the same traps on consecutive days (J. Camper, unpublished observation) as found by [30] in another South

Carolina population. Female capture bias was shown by [31] for both focal species in Texas. In another study in Texas, using a different sampling method, [8] found a sex ratio not significantly different from one for *A. piscivorus*. Three other populations of this species were found to have slight male bias [22, 32, 33] as did one study of *N. fasciata* in another region of South Carolina [32].

4.2 Sexual dimorphism

I found that female *N. fasciata* were significantly greater in mass, SVL and head size than males whereas tail length was not significantly different. Similar results were found in another South Carolina *N. fasciata* population located about 180 km southwest of my study site [32]. The latter study did not examine head size, however. Patterns of sexual dimorphism in *A. piscivorus* contrasted with *N. fasciata* but were not statistically significant and in agreement with [22, 34]. Although head size was not significantly different between the sexes of cottonmouths [33] found that males had longer quadrate bones than females. The males in this population retain a bold banding pattern similar to juveniles that was first documented by [22]. Relative tail length averaged about 2% longer in males of *N. fasciata* but less than 1% longer in *A. piscivorus.* Similar findings for both species were published by [35] for specimens collected from throughout North Carolina. The values reported here were higher for *Nerodia* but close to those of *Agkistrodon* calculated by [34].

4.3 Growth rates

Growth rates have not been reported for *N. fasciata* so they will be compared to the closely related *Nerodia sipedon* [10]. Growth rates from this population were higher than the 0.12 mm/day mean for male and the 0.14 mm/day mean for female *N. sipedon* in Lake Erie [26]. The *N. sipedon* study was from a northern population with a much shorter growing season which could affect growth rates. Three neonate *N. fasciata* caught in August (1 snake) and September (2) averaged 173.67 ± 16.29 mm SVL. This was 20 mm longer than the mean for lab born snakes suggesting that growth may occur before their first winter. Cottonmouth growth rates reported here were also higher than reported for western populations of 0.210–0.280 mm/day [24] and 0.170–0.434 mm/day [8]. Because male *N. fasciata* mature at about 400 mm SVL (see below) they may reach sexual maturity by the end of their second year and mate the following spring. Females probably mature 1 year later when they surpass 500 mm SVL. Based upon these growth rates, male *A. piscivorus* may reach sexual maturity in about 2.5 years and females in about 4 years.

4.4 Food habits

These two species exhibited little dietary niche overlap which was probably due to *A. piscivorus* having few amphibians and many reptiles in its diet. The banded water snake diet documented in this population is similar to that found in other populations [5, 36] except that *G. holbrooki* was consumed only once by one juvenile banded water snake. In a study in Louisiana *N. fasciata* consumed 30.6% *G. holbrooki* and 11.2% amphibians [37]. *Nerodia fasciata* may be avoiding *G. holbrooki* at this study site because it appears to be an abundant species at this locality and only one specimen was found in the stomach contents. Banded water snakes ingested significantly more fish headfirst. This could be due to scales covering the fish. Snakes feeding on reptiles usually swallow prey headfirst and scales are used in prey orientation [38, 39]. *Agkistrodon piscivorus* is known for its broad diet that includes mammals, birds and their eggs, alligators and pit vipers in addition

to what was found in this study [6, 40]. Five different species of amphibians were found in North Carolina specimens [35]. There is geographic variation in the diet of this species also, as evidenced by [41] finding no amphibians in the diet to amphibians making a large proportion of the diet in other populations [24, 33]. No novel prey were found in the diet of *A. piscivorus* in this study but the lesser siren (*Siren intermedia*) is a newly documented prey species for *N. fasciata.* Larger mass ratios for *A. piscivorus* as compared to *N. fasciata* was not surprising given that the former have relatively larger heads and a greater gape [33].

Frequencies of stub tails and body scarring were more than 20% higher in *N. fasciata* than in *A. piscivorus* at my study site. Injury frequency may reflect predation intensity or predator efficiency [26]. I believe the former to be true in this study because of the relatively high frequency in *N. fasciata* and the lower frequency in *A. piscivorus*. Because the latter is a large pit viper with potent venom it probably experiences less predation pressure than *N. fasciata*. Injury frequency was about 15% higher for *N. fasciata* in this study when compared to another population about 180 km to the southwest [34].

4.5 Reproduction

Litter sizes documented here agree with what has been found in other populations of both species [24, 32, 35, 41–46]. The correlation of maternal SVL and litter size is well documented in snakes [47] and was found for another South Carolina population of *N. fasciata* [32]. The RCM found in this study is larger than the 0.201 reported for one specimen of *N. fasciata* [48]. Parturition dates for *N. fasciata* were like those in other populations [43, 45]. Neonate sizes reported here averaged 4 mm SVL longer than reported by [28] for another South Carolina population. Three neonates trapped in August and September were small enough to escape through the trap mesh [28]. The mean SVL for 6 neonate *A. piscivorus* trapped in this study was 277.67 ± 56.46 (215–344) which is larger than reported for other populations [8, 24, 42] but smaller than neonates from Florida [49]. The low proportion of pregnant female *A. piscivorus* found here suggests that females give birth biennially in this population. Most populations of cottonmouths reproduce biennially [8, 24, 49, 50]. However, some populations may have annual reproduction [23, 42]. All three gravid female banded water snakes had more ova in the right oviduct which was also reported by [51] for one Texas specimen. More embryos in the right oviduct of *A. piscivorus* were also reported by [44, 46] unlike what was found here.

5. Conclusions

Two common snake species, the banded water snake (*Nerodia fasciata*) and the Eastern cottonmouth (*Agkistrodon piscivorus*) were studied on the coastal plain of southeastern North America. This long-term mark-recapture study used funnel traps to sample the snakes. Approximately 180 *N. fasciata* and 93 *A. piscivorus* were marked in this study. Recapture frequencies were low and population size estimates and survival rates could not be calculated.

Sexual size dimorphism favors females in *N. fasciata* which were significantly larger in mass, SVL and head size than males. Males were the larger sex for *A. piscivorus* but this was not significant. Growth rates were 0.726 ± 0.626 mm/day (0–2.3 mm/day) for *N. fasciata* and 0.783 ± 1.26 mm/day (0.029–3.31 mm/day) for *A. piscivorus*. Both species exhibited female biased secondary sex ratios which may be due to sampling bias. Primary sex ratios of four litters of *N. fasciata* were not significantly different from one.

Male *N. fasciata* reach sexual maturity at about 400 mm SVL and females at about 500 mm SVL. Males may be able to reach this length in about 2 years and females in 3 years. Male *A. piscivorus* reach maturity at 450 to 500 mm SVL which takes about 3 years. Female *A. piscivorus* mature at about 500 to 550 mm SVL which probably takes 3–4 years.

Both species fed upon fish and *N. fasciata* included many amphibians in its diet whereas *A. piscivorus* ate reptiles but few amphibians. Fish prey were swallowed headfirst and amphibian prey usually tail first. Female banded water snakes appear to breed annually whereas female cottonmouths probably breed every other year. Clutch sizes ranged from 12 to 28 with a mean of 18.45 ± 5.24 (N = 11) for *N. fasciata*. There was a significant positive correlation between maternal SVL and clutch size. One female *A. piscivorus* contained 5 oviductal eggs. Clearly more work is needed on these populations to determine population size estimates, survivorship and to elucidate the reproductive biology of *A. piscivorus.*

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