

Ambush site selection and ontogenetic shifts in foraging strategy in a semi-aquatic pit viper, the Eastern cottonmouth

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Abstract

Although habitat selection has been studied in a variety of snake taxa, little is known about habitat selection in aquatic snake species. Additionally, due to their small size and secretive nature, juvenile snakes are seldom included in habitat selection studies. The Eastern cottonmouth *Agkistrodon piscivorus* is a semi-aquatic pit viper known to use ambush, sit-and-wait foraging strategies. Ambush hunters are likely to select habitats that increase opportunity for successful prey capture while minimizing predation risk and maintaining appropriate thermal and hydric conditions. We characterized the foraging strategy and microhabitat use of cottonmouths at Ellenton Bay, an isolated Carolina bay freshwater wetland on the Savannah River Site in SC, USA. We measured habitat characteristics of 55 ambush sites used by 51 individual cottonmouths located during nighttime visual surveys, as well as 225 randomly selected sites within our search area. Cottonmouths exhibited an ontogenetic shift in foraging strategy with juveniles using predominately ambush foraging around the edge of the wetland while adults were most often encountered actively moving within the wetland. Principal components analysis revealed that juveniles selected foraging microhabitats that were different from random and consisted of mud substrate with sparse vegetation, whereas adults occupied a greater variety of microhabitats that did not differ from random. Concomitantly, free-ranging cottonmouths exhibited ontogenetic shifts in diet: juveniles consumed mostly salamanders, while adults ate a greater variety of prey including other snakes and birds. Our results highlight the importance of understanding how ontogenetic changes in coloration, diet and predation risk influence foraging strategy and microhabitat selection in snakes.

Introduction

Understanding the spatial distribution of organisms has long been a central focus in ecology (Thorpe, 1945; Turner, 1989). An organism's distribution can be viewed in terms of habitat choice, and the habitat of a given species may be described as the range of environments in which an animal lives, with this space defined by numerous habitat characteristics (Whittaker, Levin & Root, 1973). The habitat an animal selects must meet its physiological needs while maximizing the abundance of prey and minimizing exposure to predators and potential competitors. Thus, habitat use can shed light on the ecological requirements of a species and observations on habitat use have been instrumental in developing ideas about the evolution of species, the maintenance of species diversity and the organization of community structure (Reinert, 1993).

Snakes have received particular attention in the area of habitat use since the groundbreaking telemetry work by Reinert (1984a,b), and most studies have found that snakes

select habitats to satisfy physiological needs (e.g. Reinert, 1984b; Robertson & Weatherhead, 1992; Blouin-Demers & Weatherhead, 2002; Pearson, Shine & Williams, 2003) and/or to encounter prey (e.g. Hebrard & Mushinsky, 1978; Reinert, Cundall & Bushar, 1984; Madsen & Shine, 1996; Shine & Sun, 2002). Habitat use in pit vipers has received particular attention because they are large-bodied (which facilitates transmitter implantation) and often use sit-and-wait foraging strategies, which presumably require careful selection of microhabitats. Additionally, ambush predators are known to maximize foraging success by selecting ambush sites based on chemical cues left by potential prey items (Roth, May & Farrell, 1999; Clark, 2004). Habitat selection in terrestrial (e.g. Semlitsch, Brown & Caldwell, 1981; Reinert, 1984a; Burger & Zappalorti, 1989) and arboreal (e.g. Shine & Sun, 2002; Shine *et al.*, 2002) snake species has been relatively well studied. Studies of aquatic or semi-aquatic species have generally focused on habitat use at relatively large spatial scales (e.g. Scott *et al.*, 1989; Whiting, Dixon & Greene, 1997; Roe, Kingsbury & Herbert, 2003) or have focused on interspecific comparisons

(e.g. Hebrard & Mushinsky, 1978; Keck, 1998) and detailed intraspecific studies of microhabitat selection in aquatic snake species are limited (but see Lind & Welsh Jr, 1994).

Ontogenetic shifts occur in many important life-history characteristics of snakes. Ontogenetic changes in diet, specifically, have been observed in snakes, with many species exhibiting shifts in prey type (Mushinsky, Hebrard & Vodopich, 1982) or prey size (usually larger) as they grow (Godley, 1980; Lind & Welsh Jr, 1990; Arnold, 1993; Lind & Welsh Jr, 1994). The propensity for larger snakes to consume larger prey can result in different foraging strategies between adult and juvenile snakes (e.g. Lind & Welsh Jr, 1994; Savitzky & Burghardt, 2000; Welsh Jr & Lind, 2000). Many snake species also exhibit ontogenetic shifts in morphology or coloration that may influence prey capture or habitat use. For example, juveniles of some pit viper species, including several within the genus *Agkistrodon*, possess yellow tail tips that can be used to attract prey in a display known as caudal luring (Wharton, 1960; Carpenter & Gillingham, 1990; Gloyd & Conant, 1990). Most pit vipers lose their yellow tail coloration as they grow, presumably reflecting a shift from prey that respond strongly to luring (e.g. amphibians and lizards) to those that do not (e.g. mammals and birds; Heatwole & Davison, 1976). Because many snake species show ontogenetic shifts in diet and foraging strategy, changes in the habitats necessary to accommodate these behaviors may be expected.

Most field studies of habitat use in snakes have relied on radiotelemetry, which allows for a comprehensive study of larger individuals; however, the technique usually prohibits studies of ontogenetic shifts in habitat use since transmitters historically have been too large to implant within neonates and juveniles of most species. Prompted by the lack of data on ontogenetic shifts in habitat use in snakes, and on habitat use in aquatic snakes in general, we conducted a comprehensive habitat selection study of the Eastern cottonmouth *Agkistrodon piscivorus*. Being both semi-aquatic and venomous, the cottonmouth is unique among its sympatric species (mostly natricine watersnakes) and offers an opportunity for observation of potentially complex foraging and ambush site selection behaviors. Additionally, cottonmouths are often abundant and conspicuous, making them relatively easy to capture using visual encounter surveys, which in turn allow for sampling of all size/age classes within the population.

In this study we characterized foraging strategies used by cottonmouths within an isolated wetland and the microhabitats that cottonmouths used as foraging sites in comparison with available habitats. Specifically, we aimed to address the following questions: (1) Do cottonmouths select microhabitat-specific ambush sites or are they foraging at random? (2) Is there an ontogenetic shift in foraging strategy that could, in turn, influence habitat choice? (3) What factors (morphological, physiological and dietary) are involved in this shift in foraging strategy if indeed it does exist?

Methods and materials

Study site

Ellenton Bay is a large isolated freshwater wetland located on the US Department of Energy's Savannah River Site in Aiken County, SC, USA. Water levels are extremely variable (Willson *et al.*, 2006; Winne, Willson & Gibbons, 2006b), but Ellenton Bay typically holds water year-round and when full covers *c.* 10 ha. Owing to low precipitation during 2006, the total surface area of water at Ellenton Bay was *c.* 5.4 ha throughout our study. The water is generally shallow (<1 m deep) and is dominated by relatively uniform expanses of emergent grasses (predominantly *Panicum* sp.) with smaller patches of water lilies *Nymphaea odorata* and water-shields *Brasenia schreberi*. As a result of severe droughts, Ellenton Bay has dried completely on at least three occasions in the past three decades, most recently during 1987–1990 and 2000–2003. Thus, Ellenton Bay is devoid of fish (*Gambusia holbrooki* were present until a severe drought in 1987; Seigel, Gibbons & Lynch, 1995), crayfish, and large aquatic salamanders (*Siren* sp. and *Amphiuma means*). The upland habitat surrounding Ellenton Bay is forested with mixed hardwoods, loblolly and slash pines (*Pinus taeda* and *Pinus elliottii*), but the wetland itself is free of canopy cover. A 10-m-wide dike, covered by early successional vegetation, bisects the wetland, splitting it into a smaller portion to the north and a larger one to the south. Further details of the study site can be found in Gibbons (1990) and Gibbons *et al.* (2006).

Snake collection and processing

On 10 nights between 11 June and 19 July 2006, we conducted time-constrained visual encounter surveys along transects following the margin of the wetland and across the interior of the wetland (Fig. 1a). We systematically altered our starting location and direction (clockwise vs. counter-clockwise) among nights. We conducted all surveys between 21:00 and 24:00 hours, using three to six observers on each night. While walking each transect, we searched all microhabitats equally and thoroughly by having observers walk parallel to each other along the same transect. We invested a total of 76 person-hours performing surveys and recorded all transects using GPS units (Trimble GeoXT or ProXRS).

For each snake encounter, we recorded the snake's exact location and body posture (tightly coiled vs. active). Because cottonmouth foraging is primarily nocturnal in the summer in our region (Dorcas & Gibbons, 2008), we assumed that juvenile snakes we encountered were foraging. Therefore, we categorized tightly coiled juveniles as sit-and-wait ambush foragers and outstretched (crawling or swimming) individuals as active. Adult cottonmouths encountered during our searches may have been involved in other activities, such as mate-searching, but most or all of the adult snakes we observed were likely also foraging.

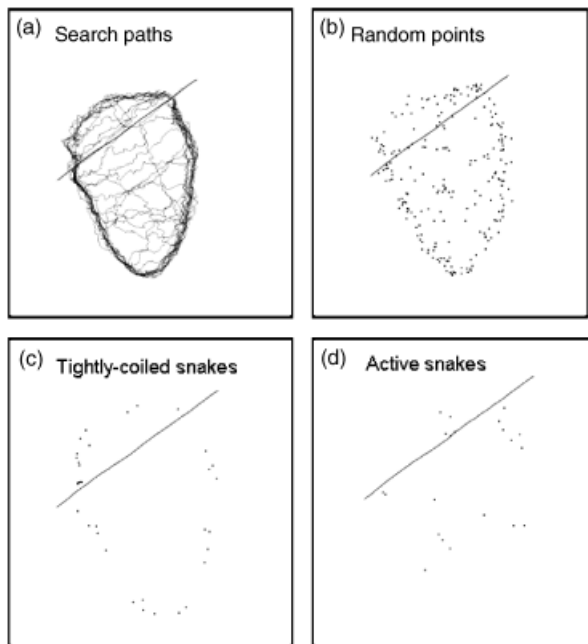


Figure 1 Maps of search paths walked (a), randomly generated habitat points that were quantified (b), locations of cottonmouths *Agkistrodon piscivorus* encountered in a tightly coiled ambush posture (c) and cottonmouths encountered while active (d) at Ellenton Bay on the Savannah River Site, SC, USA. In all maps the diagonal line represents the middle of a dike, which bisects the bay.

We attempted to capture each snake, and upon returning to the laboratory we determined the mass (electronic balance), snout-to-vent length [SVL; using a squeeze box (Quinn & Jones, 1974)], sex (by probing) and reproductive condition (pregnant vs. non-pregnant and number of follicles or embryos by palpation) of each. To determine ontogenetic shifts in diet, we induced regurgitation (Fitch, 1987) of all *A. piscivorus* captured at Ellenton Bay from 2003 to 2006 that contained palpable prey items. We marked all snakes individually by heat-branding ventral and lateral scales (Winne *et al.*, 2006a). We released all snakes near their initial capture location within 2 days.

Microhabitat assessment

Following each night of visual searching, we used ArcGIS (Environmental Systems Research Institute Inc., Redlands, CA, USA) software to create a buffer around our search path, which approximated our search area. We set the width of the buffer to 7.6 m for nights when three people searched and we added an additional 1.5 m for each additional person searching. For each night, we randomly selected 25 points within our total search area, using ArcGIS. These points served as our reference to compare with the specific locations of observed cottonmouths.

We measured the distance of each snake from the wetland edge, assigning positive values to snakes outside the wetland perimeter and negative values to those inside the wetland

perimeter. Additionally, we quantified 10 characteristics of the microhabitat occupied by each snake for use in a principal components analysis (PCA). We estimated most microhabitat characteristics using a 0.75×0.75 m quadrat (evenly divided into 25 smaller squares) that we centered on each snake's location. We estimated the per cent of substrate that was land (as opposed to water) within the quadrat. We estimated the per cent cover found in the quadrat to the nearest 4%. Categories of cover included open water, open mud, dense grass, sparse grass and lily pads. We measured the height of the tallest vegetation in each quadrat. We determined the distance of each snake to the closest area of open water and recorded water depth if the snake was found in water. If the snake was found on land, we measured mud viscosity by dropping a steel ball weighing 222.22 g from a height of 50 cm onto the snake's location (method adapted from Burger & Zappalorti, 1986). The mud viscosity measurement was the distance the ball penetrated into the mud. Thus, a hard surface that the ball did not penetrate received a mud viscosity measurement of zero.

We quantified the microhabitats of random points following the same procedures used for snakes, with both the microhabitat itself and the middle 'snake point' chosen randomly. After navigating to a randomly generated point within our search area, we laid down the quadrat and then centered the quadrat on the 'snake point' which was selected randomly.

Statistical analyses

We used the χ^2 test of independence (Sokal & Rohlf, 1995) to determine if juvenile *A. piscivorus* were more likely than adults to be found in ambush foraging postures. We did not find any adults using ambush foraging postures; therefore, we used Yates' correction for small expected values during this analysis (Sokal & Rohlf, 1995). To characterize the multivariate habitat dimensions used by adult and juvenile *A. piscivorus* and to characterize the microhabitat dimensions that were available to them, we used a PCA. PCA is advantageous because it reduces the dimensionality of the habitat variables to the core two or three summary variables that explain the majority of the variation in the dataset (Reinert, 1992). Before performing the PCA, we tested all habitat variables for normality and we transformed all variables that were not normally distributed in their original scale to meet this assumption. Finally, we used analysis of variance (ANOVA) to determine if snakes in ambush posture were more likely than active snakes to be found closer to the edge of the wetland.

Results

During 10 nights of visual searching we identified 55 locations of 51 individual *A. piscivorus*. We gathered physical measurements from the 45 snakes that we were able to capture. Additionally, we sampled a total of 225 randomly selected locations from our search area (Fig. 1).

For comparisons of foraging strategy, we classified individuals >500 mm SVL as adults, which approximately reflects maturation size (Burkett, 1966; Glaudas, Winne & Fedewa, 2006). Of the snakes captured, eight were adults and 37 were juveniles. The 500 mm SVL cutoff also represents a size at which most snakes no longer had yellow coloration on their tail (Fig. 2). We found a significant difference between foraging strategies used by adults and juveniles, with juveniles using tightly coiled ambush postures more frequently than adults ($\chi^2 = 14.38$; $P < 0.001$; Fig. 3).

We used a PCA to evaluate microhabitat selection of cottonmouths in relation to available habitats. The first three principal components explained 73.5% of the variation in the 10 habitat characteristics (Table 1). Positive values of PC1 indicate that the snake or random point was closer to water and that the microhabitat contained more water substrate, was deeper, and that the coverage was

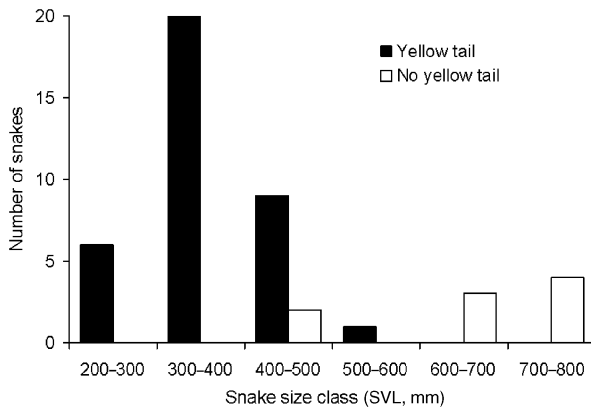


Figure 2 Size frequency distribution of cottonmouths *Agkistrodon piscivorus* captured from Ellenton Bay that had their tail color categorized ($n=45$). Snakes with no yellow in their tail tips can first be seen in the 400–500 mm snout–vent length (SVL) range and all individuals >600 mm SVL do not have any yellow on their tail.

Table 1 Principal components analysis (PCA) of microhabitat variables for cottonmouths *Agkistrodon piscivorus* at Ellenton Bay

Eigenvectors	PCA 1	PCA 2	PCA 3
Distance to water	-0.805	-0.077	-0.115
Water depth	0.853	-0.344	-0.128
Mud viscosity	-0.136	0.759	0.364
Per cent land	-0.899	0.186	-0.021
Per cent water	0.711	-0.086	-0.130
Per cent mud	-0.261	0.816	0.156
Per cent dense grass	-0.546	-0.727	0.326
Per cent sparse grass	-0.340	0.230	-0.839
Per cent lily pads	0.673	0.282	0.228
Tallest vegetation	-0.468	-0.570	0.172
Per cent variation explained	38.6	23.9	10.9

Data represent the contribution of eigenvectors to the first three PCA factors. Bold emphasis indicates eigenvectors that contributed significantly to PCA factors.

generally open (i.e. fewer grasses) and dominated by lily pads. Positive values of PC2 indicate that the microhabitat was predominantly composed of less viscous mud (i.e. more fluid mud) and that the coverage was relatively open and composed of less dense and shorter grass. Positive values of PC3 indicate coverage containing fewer sparse grass clumps and more fluid mud.

Snakes that were found in coiled ambush postures occupied distinct microhabitats and were tightly clustered in the PCA relative to active snakes and randomly generated locations. Tightly coiled snakes were generally found farther from open water, in open, mucky (i.e. fluid mud) microhabitats with fewer lilies and grasses (Fig. 4). In contrast, active snakes did not cluster into a tight group

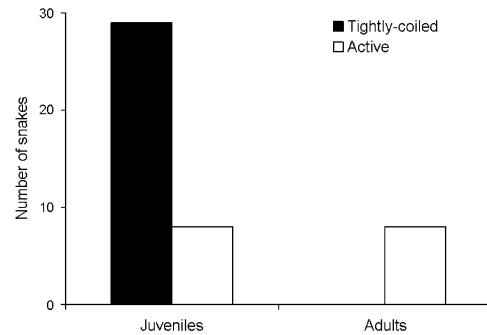


Figure 3 Foraging strategies of juvenile and adult cottonmouths *Agkistrodon piscivorus* found at Ellenton Bay. Adults are defined as any snake with a snout–vent length (SVL) >500 mm. Juveniles were more likely to be found in tightly coiled postures whereas adults were only found outstretched or actively moving.

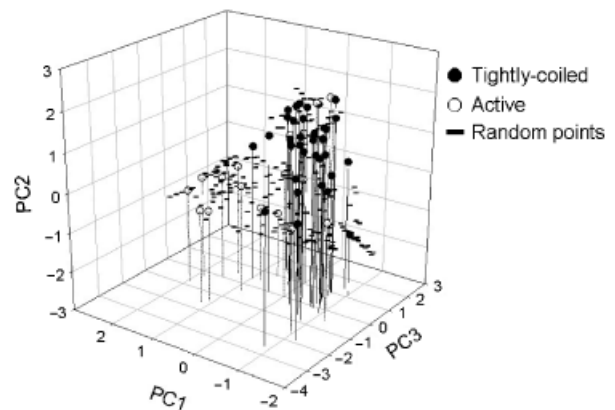


Figure 4 Results of a principal components analysis of habitat data. Positive values of PC1 indicate that the microhabitat was closer to water and that it contained more water substrate, deeper water and coverage that was generally open (i.e. fewer grasses) and dominated by water lilies. Positive values of PC2 indicate that the microhabitat was predominantly composed of less viscous mud (i.e. more fluid mud) and that the coverage was relatively open and composed of less dense and shorter grass. Positive values of PC3 indicate coverage containing fewer sparse grass clumps and more fluid mud.

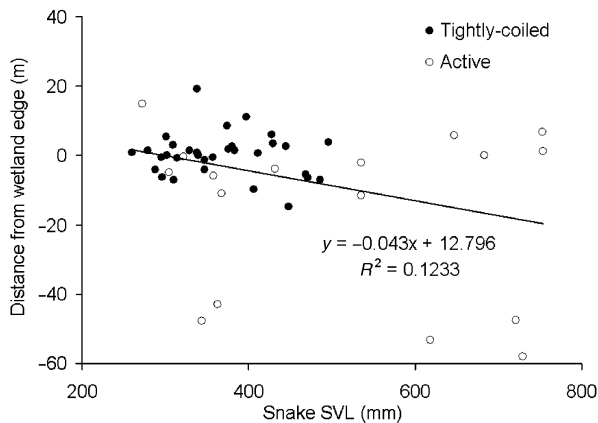


Figure 5 Distances from bay edge for tightly coiled and active cottonmouths *Agkistrodon piscivorus* found at Ellenton Bay. A distance of '0' represents a habitat point exactly at the edge of the bay while a negative number represents a distance inside the bay (in the water) and a positive number represents a distance outside of the bay. Tightly coiled snakes exhibited a smaller variance in distance to wetland edge when compared with actively foraging snakes, which were often found well within the wetland. Overall, larger snakes were found closer to the center of the wetland than smaller snakes, as indicated by a significant negative correlation between body size (snout-vent length) and distance to bay edge (solid line, $P = 0.013$).

but instead were found scattered throughout the three habitat dimensions delineated by the PCA, and they did not appear to differ from random locations (Fig. 4). Active snakes used a broad range of microhabitat types including dryer microhabitats with little vegetative cover, aquatic microhabitats with extensive vegetative cover and relatively open water.

Overall, larger snakes were found closer to the center of the wetland than smaller snakes, as indicated by a significant negative correlation between body size (SVL) and distance to bay edge ($r^2 = 0.123$; $P = 0.013$; Fig. 5). On average, snakes in ambush posture were found closer to the edge of the wetland than were actively foraging snakes (ANOVA; $F_{1,47} = 12.0$; $P = 0.001$; Fig. 1, Fig. 5). Active snakes exhibited significantly greater variation in the distance at which they were found from the wetland edge, compared with snakes in ambush posture (Levene's test for homogeneity of variances; $F_{1,47} = 46.9$; $P < 0.001$; Fig. 5). Consequently, we reanalyzed the data using a non-parametric statistical procedure, the Kruskal-Wallis ANOVA, and we found similar support for our results ($\chi^2 = 3.99$; $P = 0.046$).

Analysis of prey data revealed ontogenetic differences in diet (Fig. 6). Sixty-eight per cent of the juveniles that contained food items had consumed salamanders (predominately paedomorphic and newly metamorphosed mole salamanders *Ambystoma talpoideum*), making it the most numerous prey type for that demographic. Adults, however, showed an expanded range of prey items that included

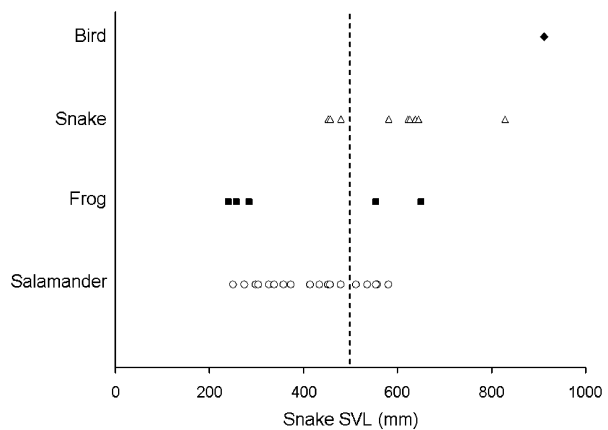


Figure 6 Diet composition of adult and juvenile cottonmouths *Agkistrodon piscivorus* captured at Ellenton Bay between 2003 and 2007. Juveniles consumed mostly salamanders while snakes began to become present in the diet at about the 500 mm snout-vent length (SVL) mark, the size at which maturity was defined in this study (dashed line).

snakes (*Nerodia fasciata* and *Nerodia erythrogaster*), frogs (several species of *Rana* and *Hyla*) and birds and a decreased reliance on salamanders as food items.

Discussion

We found evidence of ontogenetic shifts in foraging strategy and microhabitat selection in cottonmouths at Ellenton Bay. Juvenile cottonmouths were found to hunt using tightly coiled postures along the edge of the wetland in specific microhabitats. Conversely, all adults were found outstretched or active in a variety of microhabitats, including deep water. Our results mirror those found in other studies of ontogenetic shifts in foraging strategy (Savitzky, 1992; Lind & Welsh Jr, 1994; Savitzky & Burghardt, 2000). For example, Lind & Welsh Jr (1994) observed ontogenetic shifts in the foraging patterns of Oregon garter snakes *Thamnophis atratus hydrophilus* in a stream habitat. Neonates and juveniles fed on smaller prey along the stream margins, often employing ambush foraging strategies and lingual luring (Welsh Jr & Lind, 2000), whereas adults foraged widely over a greater variety of habitats in search of larger prey. Lind & Welsh Jr (1994) proposed differential prey availability, predation, morphology and physiological constraints (e.g. decreased capacity for sustained activity in smaller snakes; Pough, 1978) between age classes as the primary factors causing ontogenetic shifts in foraging strategies and habitat use in Oregon garter snakes. We suspect these same factors may be responsible for the ontogenetic differences we observed in cottonmouths.

Although few studies have quantified predation risk in snakes, juvenile snakes generally have lower survivorship than adults (Parker & Plummer, 1987; Brown, Kéry & Hines, 2007). For example, in a population of copperheads

Agkistrodon contortrix annual survivorship of juveniles was 30% compared with 71% for adults (Fitch, 1960; Parker & Plummer, 1987). Increased predation risk alone could influence the juvenile choice of a foraging strategy that minimizes energy expenditure while maximizing concealment from predators. Young cottonmouths gain an additional advantage from a sit-and-wait, ambush foraging strategy because of their tail coloration, which is adapted to caudal luring (Wharton, 1960). Allen (1949) made observations on the feeding behaviors of juvenile cantils *Agkistrodon bilineatus*, a close relative of the cottonmouth. The juvenile cantils effectively used caudal luring to attract and kill a variety of prey including frogs (*Hyla* sp.) and toads (*Bufo* sp.). At Ellenton Bay the size at which snakes shifted from ambush foraging to active behaviors coincided with the size at which snakes lost yellow coloration on their tail tips, supporting the idea that juvenile snakes may use caudal luring to ambush amphibians around the edge of the wetland. In contrast, large adult snakes might gain an advantage by foraging actively in a greater variety of habitats, including deep water where they can encounter larger prey such as watersnakes (*Nerodia* sp.) but where coiled postures and caudal luring may not be effective strategies. Cottonmouths are known to feed on a variety of prey including amphibians, fish, mammals and other snakes (Kofron, 1978; Blem & Blem, 1995; Vincent, Herrel & Irschick, 2004), and observations have been made of adult cottonmouths successfully capturing fish while actively foraging (Bothner, 1974). The prey data collected from cottonmouths at Ellenton Bay show an ontogenetic shift in prey consumption, with the adults eating a wider variety of prey, including a large proportion of other snakes. The capture of these prey items, which are found in a variety of microhabitats, would seem to suggest that adult cottonmouths forage widely and possibly actively in their environment.

We found that juvenile snakes in ambush postures selected microhabitats close to the margin of the wetland that contained relatively sparse vegetation and less viscous mud than randomly selected locations. Active snakes were found more often in the water, up to 58 m from shore, and the PCA analysis showed them randomly distributed among available microhabitats. These results support the conclusion that larger snakes forage widely, but often in the more aquatic microhabitats. Juveniles, conversely, selected sites with a higher proportion of land, presumably to allow tight coiling and ambush hunting in habitats where smaller prey items (frogs and salamanders) are abundant. Also, juveniles were commonly found in habitats with more open mud than either random locations or actively foraging snakes. Although ambush hunting can provide an advantage against predators because an animal can lie cryptic and immobile, waiting for prey, prey still must be encountered. The more open habitat used by tightly coiled snakes would presumably facilitate chemical detection of prey, provide greater visibility for caudal luring, and allow for an unobstructed strike. Chiszar *et al.* (1986) found that cottonmouths have strong chemoreceptive abilities, which would allow them to detect prey items from a considerable dis-

tance. Additionally, the relatively open habitat around the bay edge favored by juvenile cottonmouths would likely contain high abundances of migrating amphibian prey, providing an optimal foraging site for juveniles whose diet consists largely of salamanders. Finally, the juvenile preference for less viscous (i.e. more fluid) mud may stem from a physiological origin. Recent studies have found that cottonmouths are more affected by evaporative water loss than was previously thought (Moen, Winne & Reed, 2005). Smaller snakes have higher surface area to volume ratios than larger ones and hence lose relatively more water through evaporative water loss; thus, for juvenile snakes, selecting a foraging site that provides ample moisture for them, as well as their amphibian prey, could be a priority.

In conclusion, we observed significant ontogenetic shifts in habitat use, diet and foraging strategies in *A. piscivorus*. The larger adult snakes ranged actively over a wide array of microhabitats and consumed a wide variety of prey, while juveniles selected specific microhabitats and used tightly coiled, ambush foraging to capture mostly small amphibian prey. The patterns we observed likely reflected ontogenetic shifts in tail coloration, body size, physiology, susceptibility to predation and/or prey availability. However, cottonmouths are known to consume a wide variety of prey taxa (Kofron, 1978; Blem & Blem, 1995; Vincent *et al.*, 2004) and their diet may be site-specific (Wharton, 1966). The large abundances of amphibian prey available to cottonmouths in our system are both season- and system-dependent (Todd & Winne, 2006), and therefore we suspect that cottonmouths may exhibit foraging strategies that shift across seasons or habitats. Consequently, cottonmouths may be ideal study organisms for investigations focusing on complex foraging behaviors in a variety of habitats.

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