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Front cover:
Eastern cottonmouth,
Agkistrodon piscivorus.
Photo: John D. Willson

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Migration patterns in a population of cottonmouths (*Agkistrodon piscivorus*) inhabiting an isolated wetland

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Abstract

Few studies have examined the spatial and temporal migration patterns of snakes to and from active-season habitats. We conducted a year-long population-level analysis of cottonmouth *Agkistrodon piscivorus* migration patterns by monitoring snakes entering and leaving a Carolina bay wetland that was encircled by a continuous terrestrial drift fence. Cottonmouths used the wetland during the active season and left the bay in the fall to overwinter in other habitats. Adults and juveniles did not differ in time of arrival at the bay but juveniles left the bay earlier than adults. Spatially, captures of adult cottonmouths entering and leaving the bay were distributed non-randomly, with capture peaks corresponding to the directions to the nearest permanent aquatic habitats. Juveniles' immigration patterns in the spring were biased in the same directions as those of the adults, but they left non-directionally in the fall. This suggests that neonates do not rely on adult scent trailing to locate hibernacula, and that in a region with moderate winter temperatures, suitable overwintering sites may not be a limited resource. Additionally, our study demonstrates that cottonmouths make extensive use of upland habitats and underscores the importance of both critical upland habitat and forested corridors between wetlands and hibernacula for the conservation of wetlands herpetofauna.

Introduction

Large-scale movements in animals often occur in response to temporal and spatial variation in resource availability (Gregory, 1982; Sinclair, 1983; Larsen, 1987). In ectotherms, reliance on external environmental conditions to maintain adequate body temperatures often induces seasonal shifts in habitat use (e.g. hibernacula vs. summer feeding/reproductive habitats) and spatial separation of such habitats results in pronounced seasonal migrations (Gregory, 1982). Accordingly, movements to and from overwintering sites are among the most apparent seasonal activity patterns in temperate snakes (Gibbons & Semlitsch, 1987).

Studies of seasonal migration in reptiles have generally focused on arrival to and departure from hibernacula because these patterns are most easily observed at communal dens (Gregory, 1982). Such studies have revealed that arrival and departure vary temporally among and within species (for a review, see Gregory, 1982) and that some species of snakes exhibit directionality of movement indicating complex orientational capabilities (Hirth *et al.*, 1969; Gregory & Stewart, 1975; Larsen, 1987; Lawson, 1989, 1994). However, data on migration to active-season habitats are sparse, possibly due to a lack of summer habitat centers where snake arrival and departure can be thoroughly monitored. Consequently, our understanding of migration patterns to and from summer habitats is limited.

Carolina bays, ovoid isolated wetlands located within the Coastal Plain of the south-eastern United States, are among the most productive and species-rich habitats in the region (Sharitz, 2003). Many reptiles use Carolina bays extensively during the active season, but rely on upland habitats for hibernacula in the winter (Gibbons, 2003). Our study site, a large Carolina bay completely encircled by a drift fence, provided an opportunity to conduct a population-level analysis of temporal and spatial movement patterns of a semi-aquatic viperid snake, the cottonmouth *Agkistrodon piscivorus*, to and from its summer habitat.

Our study has two important implications. First, we have little information regarding the movement ecology of cottonmouths other than habitat use (Roth, 2005*a,b*). More generally, our understanding of snake spatial ecology is still in its infancy (Diffendorfer *et al.*, 2005), and the development of a theoretical framework for movement patterns requires investigation of a wide variety of taxa (Gregory, Macartney & Larsen, 1987). Second, isolated wetlands (i.e. those not connected to navigable waterways) are directly threatened by the Solid Waste Agency of Northern Cook County versus US Army Corps of Engineers decision (Zedler *et al.*, 2001), and lack of baseline knowledge about organisms inhabiting these habitats may preclude reasoned conservation decisions (Greene, 2005). Cottonmouths are top predators and thus may be of particular conservation concern in wetland ecosystems.

Our objective in this study was to identify temporal and spatial migration patterns of cottonmouths at a highly productive summer habitat. Specifically, we investigated the following questions: (1) When and to what extent do cottonmouths enter and leave the wetland? (2) Do cottonmouths arrive at and depart from the bay through distinct corridors or in a random fashion? (3) Are there associations between individual attributes (e.g. body size, sex) and timing or direction of movement? Finally, we discuss our results in the light of other studies and implications of our findings for wetland conservation.

Materials and methods

Study site

Ellenton Bay (33°13′N, 81°45′W) is a Carolina bay located on the Department of Energy's Savannah River Site (SRS) in the upper Coastal Plain of South Carolina, USA, and covers up to 10 ha at maximum water level. Although water levels at Ellenton Bay are extremely variable, the bay generally holds water year round at a maximum depth of over 2 m. Ellenton Bay is currently fish free and harbors a diverse assemblage of semi-aquatic species of amphibians ($n = 24$) and reptiles ($n = 18$; Gibbons & Semlitsch, 1991). The habitat within Ellenton Bay is open, devoid of large trees and is dominated by extensive areas of thick emergent vegetation, particularly *Panicum* spp. The surrounding terrestrial habitat is a mosaic of old fields in various stages of succession and second-growth mixed pine-hardwood forest. The south-eastern United States has experienced two major droughts in the past two decades (1987–1990 and 1999–2003); each left Ellenton Bay completely dry for over 2 years (Gibbons *et al.*, in press; Willson *et al.*, in press). The initiation of the present study (February 2003) coincided with the end of the most recent drought.

Collection methods

We captured all snakes by hand or in traps along a drift fence (Gibbons & Semlitsch, 1982) that completely encircled Ellenton Bay from 1 February 2003 to 31 January 2004. The 1230-m-long, 40-cm-high fence was made of aluminum flashing and extended 6–10 cm below ground. We installed 41 pairs of 19-L pitfall traps (plastic buckets) at 30-m intervals along the fence, with one trap on each side of the fence. Beginning 27 February 2003, we placed 20 pairs of wooden box funnel traps along the drift fence between every other pair of buckets at 60-m intervals. Box traps were rectangular ($92.5 \times 32.5 \times 28.5$ cm) with treated plywood sides and hardware cloth (0.6 cm) funnels, extending 28 cm into the trap, with a square funnel opening (3.5×3.5 cm) and were similar to those used by Himes (2000) and Zappalorti & Torocco (2002). We removed funnel traps for several nights in May to avoid mortality of tens of thousands of metamorphosing amphibians emigrating from the bay (Gibbons *et al.*, in press).

We categorized captured snakes as entering or leaving the bay based on the side of the fence where they were captured

(Seigel, Gibbons & Lynch, 1995). We checked pitfall and funnel traps a minimum of once daily (07:00–09:00 h). On days warm enough for snakes to be active, we checked traps an additional time in the late afternoon (17:00–20:00 h).

Snake data collection

We returned all cottonmouths to the laboratory, where we measured their total length (nearest millimeter) using a 'squeeze box' (Quinn & Jones, 1974). We used plastic tubes to confine snakes and safely measure tail length (nearest millimeter), which was then subtracted from total length to obtain snout–vent length (SVL). Subsequently, we recorded sex (by probing) and mass (nearest gram using an electronic balance) for each individual. Each snake was given an individual mark by heat branding a unique combination of ventral scales with a medical cautery unit (Winne *et al.*, 2006). We released all snakes within 3 days of capture on the side of the drift fence directly opposite the capture location. We defined snakes greater than 450 mm SVL as mature individuals (Burkett, 1966).

Data analyses

Temporal movement patterns

We included only individuals captured during months of net immigration (March–May) for arrival data and net emigration (October–November) for departure data in our statistical analysis, but present capture distributions that include the entire activity season (March–November) in Fig. 1. Months of net immigration and emigration are more likely to depict the general movement patterns (i.e. migration events) pertinent to the objectives of this study. When an individual was captured multiple times entering or leaving the bay, we included only its first entrance and last exit in the analyses.

To analyze temporal patterns, we used one-way ANOVAs and linear regressions when the data met assumptions of both normality and homoscedasticity, and alternatively used non-parametric tests (Kruskal–Wallis test, Spearman's rank order correlation) when the data did not. Statistical significance was recognized at $P \leq 0.05$. We performed all statistical tests using Statistica' 6.0 software (StatSoft 2000, Tulsa, OK, USA).

Spatial movement patterns

We analyzed distributions of captures around Ellenton Bay for directionality using the first entry into and the last exit out of the bay for each individual. To maximize statistical power, we included entrance and departure of individuals throughout the year [including only snakes captured during peak movement periods (i.e. March–May, October–November) yielded similar trends, and thus would not alter our results or conclusions]. We acquired coordinates for all snake capture locations at the drift fence using a Trimble ProXR GPS unit (Trimble Navigation Limited, Sunnyvale,
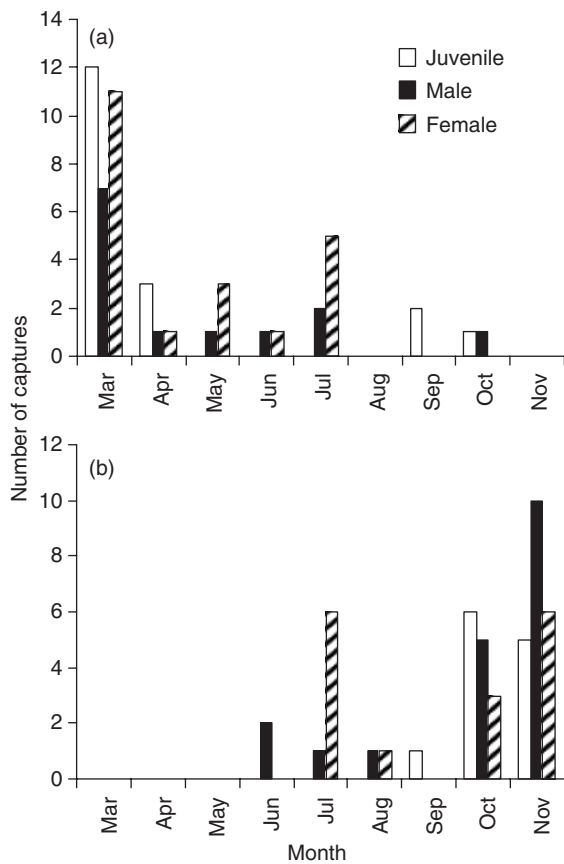
Figure 1 Monthly captures of cottonmouths *Agkistrodon piscivorus* (a) entering and (b) leaving Ellenton Bay in 2003.

CA, USA). We then imported these coordinates into Arc-View 3.3 [Environmental Systems Research Institute Inc. (ESRI), Redlands, CA, USA] to convert them to angles. We used Rayleigh's test for randomness (circular statistics, Oriana Version 2.01b, Kovach Computing Services, 2004, Anglesey, Wales, UK) to test for directionality of immigration and emigration for adult females, adult males, juveniles and all snakes combined. We treated bimodal data as axial data and analyzed for multi-directionality. Additionally, we performed Watson's U^2 test for differences in distribution or mean direction for (1) adult males and females and (2) adults and juveniles. We used the Mardia–Watson–Wheeler non-parametric test (i.e. uniform scores test) to perform a three-way pairwise comparison between adult males, adult females and juveniles. Lastly, we obtained an aerial photograph (US Forest Service, 2001, SRS, Aiken, SC, USA) to assess the landscape surrounding Ellenton Bay as it related to directionality of cottonmouth movement patterns.

Results

Temporal movement patterns

We captured a total of 52 individual cottonmouths entering Ellenton Bay from 5 March 2003 to 17 October 2003

(Fig. 1a). Most juveniles (83%, $n = 18$) entered the bay during the first 2 months of the active season (March–April). Adults showed a higher variance in time of arrival (58.8% of 34 arrived in March and April), primarily due to a secondary peak of female arrivals in July ($n = 5$ vs. 2 males). Snake body size (linear regression: $r^2 = 0.001$, $P = 0.8$) and sex (Kruskal–Wallis test: $H_{[1,24]} = 1.73$, $P = 0.18$; adults only) did not affect date of arrival.

Overall, we captured 47 cottonmouths leaving Ellenton Bay from 8 June 2003 to 28 November 2003 (Fig. 1b), and most (74.4%) left in October and November. We observed a peak departure in the summer (18.9%, $n = 37$) of mostly adult females ($n = 6$ vs. 1 male). Only 45.4% ($n = 11$) of the juveniles left the bay in November compared with 66.6% ($n = 24$) of the adults. Consequently, we detected a significant positive correlation between SVL and time of departure [Spearman's rank order correlation: $r = 0.407$, $t(33) = 2.56$, $P = 0.01$]. We did not detect any effect of sex in adults on time of departure (ANOVA: $F_{[1,22]} = 0.12$, $P = 0.73$).

Spatial movement patterns

We created circular rose diagrams to visualize spatial patterns of cottonmouth captures for all snakes (Fig. 2a and b), adult males (Fig. 2c and d), adult females (Fig. 2e and f) and juveniles (Fig. 2g and h) in relation to the surrounding landscape. Overall, snake captures were distributed in a significantly non-random pattern for both entering and leaving ($P < 0.001$; Fig. 2a and b). Most captures were located on the south-western side of the bay, corresponding with the direction of the Savannah River floodplain (seasonally flooded cypress forest) located *c*. 1.5 km away.

Immigrating snakes exhibited a bimodal pattern with an additional peak of captures from the north-east (Rayleigh's test: $Z = 10.257$, $P < 0.001$; Fig. 2a), corresponding with the direction to Bulldog Bay (a permanent man-made pond) *c*. 1 km away. In contrast, emigrating snakes departed unimodally in the south-westerly direction toward the floodplain ($Z = 7.467$, $P < 0.001$; Fig. 2b). Adult male captures were non-randomly distributed, with most captures in the direction of the river floodplain for both arrivals ($Z = 3.541$, $P = 0.02$; Fig. 2c) and departures ($Z = 5.643$, $P = 0.002$; Fig. 2d). Adult females also exhibited significant directionality in capture distributions: arrivals were bidirectional from the north-east and south-west ($Z = 6.842$, $P < 0.001$; Fig. 2e); departures were unidirectional toward the southwest ($Z = 4.412$, $P = 0.01$; Fig. 2f). In contrast to adults, juveniles exhibited directionality in arrival ($Z = 2.933$, $P = 0.05$; Fig. 2g) but left the bay randomly ($Z = 1.560$, $P = 0.21$; Fig. 2h).

When compared with Watson's U^2 test, adult males and females were not significantly different for mean direction or distribution for either immigration (Watson's U^2 test: $U^2 = 0.08$, $P = 0.21$) or emigration ($U^2 = 0.031$, $P = 0.50$). Additionally, adults and juveniles were not different in arrival patterns ($U^2 = 0.145$, $P = 0.10$), but differed in departure trends ($U^2 = 0.188$, $P < 0.05$). The Mardia–Watson–Wheeler test more specifically detected an overall
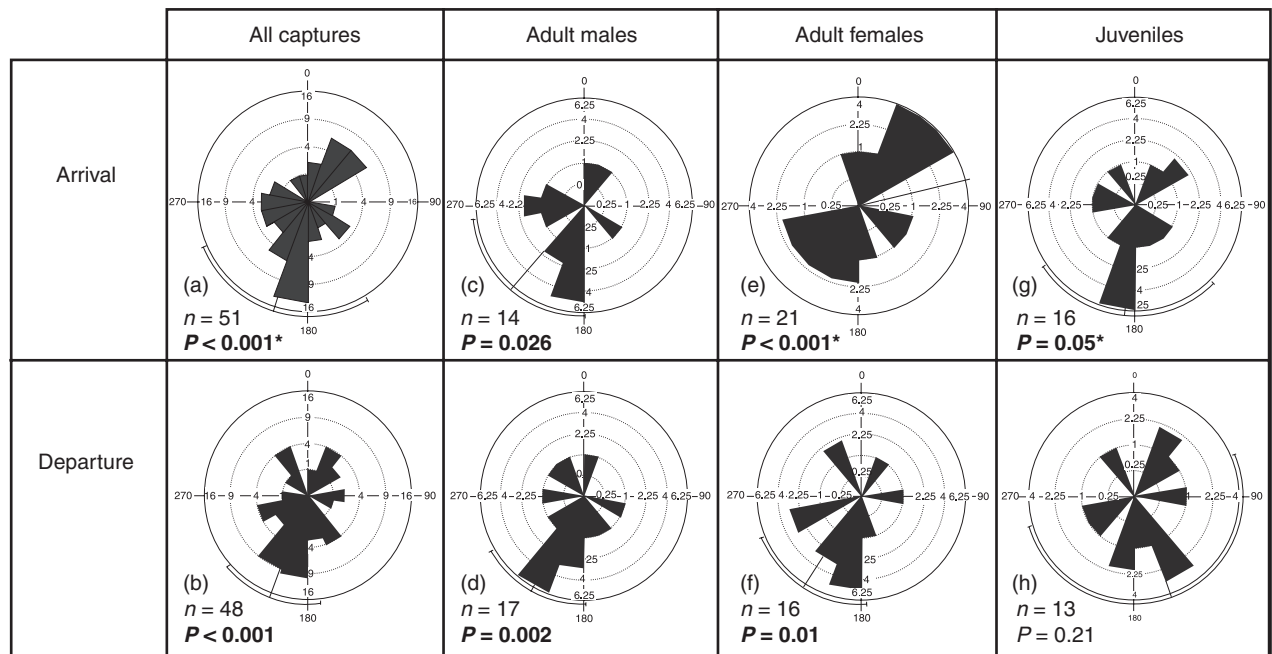
Figure 2 Circular rose plots of arrival and departure distributions and mean directions for all cottonmouth *Agkistrodon piscivorus* captures (a, b), adult males (c, d), adult females (e, f), and juveniles (g, h). Bold *P*-values indicate distributions that are significantly non-random ($P < 0.05$). Asterisks indicate bimodal distributions that were analyzed as axial data but are presented here uncorrected.

difference between adult males and juveniles for both immigration and emigration distribution (Mardia–Watson–Wheeler test: $W = 11.315$, $P = 0.003$).

Discussion

Immigration of cottonmouths to Ellenton Bay was highly synchronized, with most individuals arriving in March and April. Presumably, many of these snakes arrived at the wetland after crossing forested habitats from upland areas where cottonmouths are known to hibernate elsewhere in their range (Barbour, 1956; Smith, 1961). Adult males and juveniles arrived in early spring in contrast to females, which exhibited a bimodal pattern of arrival, with peaks in the spring and summer. Recrudescence of activity by females during the summer has been observed in several snake species (for a review see Gibbons & Semlitsch, 1987). At least two reasons can explain this pattern: (1) females may prospect for parturition sites (Parker & Brown, 1980); (2) some females (e.g. gravid females?) disperse from overwintering sites at a slower rate (Phelps, 1978). However, in our study, this peak of activity was unlikely due to some females dispersing from hibernacula at a slower rate because we observed a similarly high number of females leaving the bay in the summer (see below).

In his early study on cottonmouths, Barbour (1956) reported that 'youngsters' left hibernating habitats (wooded hillsides) later than adults. Our analysis revealed no significant relationship between SVL and arrival date during the immigration period, and this observation raises an interesting question: how do naïve cottonmouths [i.e. young-of-year snakes (YOY)] locate optimal habitats? Several studies have shown that certain snake species follow conspecific scent trails to locate dens or summer grounds (Brown & MacLean, 1983; Costanzo, 1989). Although our data do not allow us to test this hypothesis directly, the fact that the immigration patterns of both juveniles and adults were biased in the same directions indicates that YOY possibly use adult scent trails. This is particularly likely considering that the experience of YOY likely did not play a significant role in locating Ellenton Bay. That is, YOY captured entering Ellenton Bay in 2003 were probably not born there, due to the previous prolonged drought (i.e. 2.5 years; Gibbons *et al.*, in press; Willson *et al.*, in press). Alternatively, YOY may search for these habitats in a haphazard fashion.

Spatially, snake arrivals were highly directional, with peaks from the south-westerly and north-easterly directions. All directionality analyses, particularly those for adult males, were correlated with the direction of the Savannah River floodplain. An additional north-easterly peak consisted primarily of adult females and juveniles and likely represents snakes returning to Ellenton Bay from the vicinity of the nearest permanent water body, Bulldog Bay, which held water throughout the drought (J. L. Greene, pers. comm.). This bidirectional arrival occurred only with immigrating females and juveniles, suggesting intraspecific variation in response to drought, as observed in other snake species (Seigel *et al.*, 1995).

Cottonmouths left Ellenton Bay in a synchronized fashion, with most departures occurring in October and

November. As noted for arriving individuals, adult males and juveniles displayed a unimodal temporal departure pattern in the fall whereas adult females exhibited a bimodal pattern, with an additional movement peak in July. In addition, juveniles left the bay earlier than adults. Obviously, movement patterns in and out of the bay are affected by multiple biotic and abiotic factors (e.g. Gibbons & Semlitsch, 1987), and the motivation underlying these early departures is still unknown. However, we propose two possible explanations for the early departure of juvenile cottonmouths relative to adults. First, because environmental temperatures decline seasonally, the basking time required in order to maintain optimal body temperatures likely increases in the fall. As basking exposes snakes to predators (Webb & Whiting, 2005), selection may favor early departure to hibernacula in relatively more vulnerable, smaller snakes. Second, naïve YOY may leave the wetland earlier because they lack information about the surrounding landscape, which necessitates a greater time investment in locating suitable hibernacula.

In contrast to arrivals, which were bidirectional, adult cottonmouths predominantly left the bay through the south-west corridor. Juveniles (mostly naïve YOY) showed no directionality. The early and non-directional departure of juveniles from the bay suggests that conspecific scent trailing by juveniles does not play a significant role in locating hibernacula in this population, in contrast to snake species inhabiting less thermally favorable habitats (Brown & MacLean, 1983). Because of the relatively mild winter temperatures in our region, 'high-quality' hibernacula are likely not a limited resource. Additionally, as cottonmouths are known to be cannibalistic (Vincent, Herrel & Irschick, 2004), juveniles may benefit from not denning communally with larger, potentially dangerous adults.

In summary, we observed highly coordinated seasonal migrations by cottonmouths at Ellenton Bay. We detected intraspecific variation in spatial and temporal movement patterns, with (1) females and juveniles – but not males – exhibiting bidirectional arrival to the bay, and (2) naive snakes leaving the bay earlier than adults. The early fall departure and the lack of directionality exhibited by emigrating juveniles relative to adults indicate that in a region with moderate winter temperatures suitable overwintering sites may not be a limited resource, particularly in protected habitats (e.g. SRS). Our findings also suggest that locating optimal summer and winter habitats in naïve snakes may be mediated by different mechanisms.

Finally, our findings demonstrate that cottonmouths make extensive use of terrestrial habitats outside the wetland. The reliance of semi-aquatic organisms on terrestrial habitats around wetlands has been noted for a variety of taxa, including pond-breeding salamanders (Semlitsch, 1998), anurans (Richter *et al.*, 2001), freshwater turtles (Burke & Gibbons, 1995; Buhlmann & Gibbons, 2001) and natricine watersnakes (Roe, Kingsbury & Herbert, 2003). Roth (2005*b*) demonstrated that cottonmouths inhabiting riparian habitats (specifically gravid females) make extensive use of terrestrial habitats around the stream edges, and protection of riparian buffers may be critical for conservation of this species. Our study adds to Roth's (2005*b*) findings by demonstrating that cottonmouths also use distinct migration corridors when moving between overwintering and summer habitats. Thus, conservation of cottonmouths and other organisms relying on isolated wetlands may require protection of both critical upland habitat and forested corridors between wetlands and overwintering habitats.

Acknowledgements

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