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## SEASONAL VARIATION IN THE SPATIAL ECOLOGY OF THE BANDED WATERSNAKE (*NERODIA FASCIATA FASCIATA*)

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**ABSTRACT:** We used radiotelemetry to study the movements and habitat use in a population of *Nerodia fasciata fasciata* in the upper coastal plain of South Carolina from 2002 to 2006. Snakes that were surgically implanted with radiotransmitters were tracked during late spring of each year and located most days until the onset of hibernation in mid-November. Data were divided into summer and fall for seasonal analysis. Most home-range estimates and associated measures were significantly smaller during fall. Banded watersnakes used shoreline and littoral zone habitats in excess of their availability and used open water and terrestrial habitats relatively infrequently. Shoreline habitats were used more often during the fall, whereas littoral zone habitats were used more in the summer. Movement frequency was high relative to what has been reported for other *Nerodia* species. Females used shoreline habitats more than males, whereas males used littoral zone habitats more frequently.

**Key words:** Habitat use; Home range; Movements; *Nerodia fasciata*; Seasonal variation; Spatial ecology

THE SPATIAL ecology of an organism is an important aspect of its life history that allows biologists and land managers to assess how much and what habitats are needed to maintain viable populations of species in protected areas (Dodds, 1993). Seasonal changes in temperature and precipitation patterns may cause animals to change their activity patterns (Brown and Weatherhead, 2000; Madsen and Shine, 1996; Shine and Lambeck, 1985). Animals may move in response to a number of environmental cues (Gregory et al., 1987). For secretive, patchily distributed species, such as snakes, seasonal changes in activity can be difficult to document without the use of radiotelemetry (Reinert, 1992). The advent of this technique has allowed ecologists to gather these types of data for many animal groups and may help close the information gap that persists between snakes and other vertebrate groups (Seigel, 1993). Radiotelemetry is also useful in allowing the generation of spatial use estimates for snakes, which is necessary for conservation purposes.

Many management strategies focus on the protection of isolated wetlands and their resident species. While these practices are pertinent to conservation, they may not

recognize the importance of the surrounding terrestrial habitat (Roe and Georges, 2007). Sufficient terrestrial habitat surrounding these wetlands is integral to the health of an ecosystem. For species that utilize multiple, diverse wetlands, terrestrial landscapes connecting these wetland reserves are equally important for ecosystem conservation (Roe and Georges, 2007). These terrestrial buffer zones could encompass areas available for breeding and foraging, as well as facilitate movement between wetlands, which can be important for gene flow and metapopulation dynamics (Semlitsch and Bodie, 2003); however, they are often overlooked because of the lack of information on terrestrial habitat use by wetland species. While complete spatial data (i.e., seasonal, sex, and reproductive differences) are available for many species of herpetofauna, little information exists for snakes with regards to this topic. However, some studies have indicated that some snake and turtle species may require a substantial amount of terrestrial habitat around the wetlands they inhabit (Burke and Gibbons, 1995; Camper, 2009; Roe and Georges, 2007; Roe et al., 2003, 2004; Roth, 2005; Semlitsch and Bodie, 2003). One species that has received scant attention is the banded watersnake, *Nerodia fasciata*. We chose to study this species because it is an abundant and important predator in a variety of wetlands in the coastal plain of southeastern North

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America (Gibbons and Dorcas, 2004). Therefore, the terrestrial habitat requirements of this species ought to be incorporated into any freshwater wetland management plan within southeastern North America.

*Nerodia fasciata* is abundant and widespread throughout the coastal plain of the southeastern United States (Gibbons and Dorcas, 2004). It ranges from the Atlantic Coastal Plain of the Carolinas west along the Gulf of Mexico Coastal Plain into eastern Texas, extending northward along the Mississippi River into the southern tip of Illinois. The nominate subspecies, *Nerodia fasciata fasciata*, occurs east of the state of Mississippi and up the Atlantic coastal plain to northern North Carolina, exclusive of the Florida peninsula (Gibbons and Dorcas, 2004). Banded watersnakes occur in a number of aquatic habitats, including swamps, ponds, rivers, marshes, flooded ditches, and lakes. Despite the abundance of this snake, relatively little published information exists concerning its ecology and habitat use. *Nerodia fasciata* feeds largely on fish as well as adult and larval frogs (Kofron, 1978; Mushinsky and Hebrard, 1977). Hebrard and Mushinsky (1978) studied a population in Louisiana and reported that this species was seldom found out of water. However, individuals of *N. fasciata* will leave wetlands and travel overland in response to drought (Siegel et al., 1995; Willson et al., 2006) and have been reported to use ponds in a reclaimed strip mine in Texas (Keck, 1998). We predicted that *N. fasciata* will be more closely tied to aquatic habitats and therefore significantly less terrestrial than *Nerodia erythrogaster* (Camper, 2009; Roe et al., 2003), requiring less terrestrial core habitat around wetlands. The objectives of this study were to examine habitat use, calculate estimates of spatial use (e.g., home range), determine movement distance, rate, and frequency, and to test our prediction about the amount of terrestrial core habitat around wetlands that *N. fasciata* uses compared to *N. erythrogaster*.

## MATERIALS AND METHODS

### *Study Site*

The Pee Dee Research and Education Center (PDREC) is an experimental agricul-

tural facility owned by Clemson University in the upper coastal plain of South Carolina in southeastern Darlington County (Fig. 1). The site is 972 ha, with about 1/3 planted in row crops. Nonagricultural habitats at PDREC include pine forest, southern mixed hardwood forest (SMHF), riparian deciduous forest, pine plantations, clear cuts, old fields, mowed fields, artificial ponds, a swamp, and a lake (Dargan's Pond). The climate of this region consists of hot (mean June–August high temperatures during 2002–2006 were 33 °C) humid summers averaging 14.6 cm of rainfall per month (June–August of 2002–2006) and mild winters (January 2002–2006 average high temperature 14 °C; Weather Warehouse, 2010). Snakes were studied in a series of artificial ponds (Fig. 1) created from damming two streams. Six ponds, impounded on their east or downstream sides by earthen dikes, ranging in surface area from 0.09–1.9 ha, were used by all but two snakes during this study (Fig. 1A). One of these ponds dries each summer. A second pond was dry during 2002 due to a severe drought. It refilled in 2003 when the drought ended, and held water for the remainder of the study. The six ponds in Fig. 1A had gently sloping shorelines with clear water and muddy bottoms underlain by sand. The littoral zone of these ponds was dominated by water lilies (*Nuphar* sp., *Nymphaea* sp.) and contained patches of water penny wort (*Hydrocotyle* sp.), smart weed (*Polygonum* sp.), and bur-reed (*Sparganium* sp.). The largest pond used by snakes in this study (Fig. 1B) was 3.7 ha in surface area and was partially covered by the John B. Pitner Center building (white rectangle spanning the pond). This pond was relatively steep sided, with tall herbaceous vegetation along the water's edge, clear water, and a muddy bottom. Only one snake (a female) used area B exclusively, and one other female used both areas A and B. In the drainage shown in Fig. 1A one male used a basin 114 m west of Dargan's Pond. In this basin the dams of two ponds had been breached and small beaver ponds remained. The ponds at PDREC were bordered by mowed field, old field, SMHF, clear cut, and agricultural fields. These ponds differed from natural undammed creeks in the Atlantic coastal plain, which typically consist



FIG. 1.—Pee Dee Research and Education Center, Darlington Co., South Carolina, bordered by the heavy black line. Animals were radiotracked in two areas. Area A is a sequence of six artificial ponds and area B is two artificial ponds. The white rectangle spanning the pond in area B is the John B. Pitner Center building that is above the water. Only one snake used area B exclusively and one used both areas A and B. The bar in the lower left-hand corner is 800 m. The lake to the right is Dargan's Pond and the Great Pee Dee River borders PDREC on the upper right.

of swamp forest with very little open water (Rohde et al., 2009), by having a much larger surface area and substantially less swamp forest along their margins.

#### *Radiotelemetry*

We captured snakes in April to June of 2002–2006 with the use of aquatic minnow traps, hardware cloth funnel traps (Fitch, 1987), metal coverboards and by hand in and around the ponds. Although reproductive condition could not be determined for every female at the time of transmitter implantation, all but one female were presumed to be gravid during this study. Radio transmitters were surgically implanted into the body cavity following the method of Reinert and Cundall (1982). Animals were anesthetized with the

use of isoflurane that was administered in a clear plastic tube. We used radio transmitter model SB-2 (5.1 g, 10-month battery life) from Holohil Systems Limited (Carp, Ontario, Canada) for most snakes and during all years of the study. During 2004 two snakes (one male, one female) were equipped with AWE-RS transmitters (American Wildlife Enterprises, Monticello, Florida, USA) which weigh 5.5 g and have a 10-mo battery life. During 2006 three males were implanted with BD-2T Holohil transmitters (1.8 g, 6-mo battery life). Transmitters weighed from 0.7 to 3.8% ( $\bar{X} = 1.7 \pm 0.8\%$ ,  $n = 16$  females) and 1.1 to 4.9% ( $\bar{X} = 3.1 \pm 1.4\%$ ,  $n = 6$  males) of the snake's mass. Passive integrated transponder (PIT) tags (AVID, Norco, California, USA) were implanted in the snakes for identification in

case of transmitter failure. Snakes were released at their capture site 1–3 days after surgery.

We implanted radio transmitters in 22 adult *N. f. fasciata*, 16 females and 6 males, during this study. Females averaged  $680 \pm 93.11$  mm snout–vent length (SVL) and ranged from 530–860 mm SVL, whereas the mean SVL for males was  $501.33 \pm 53.13$  mm (range 443–590 mm SVL). Female mass averaged  $353.81 \pm 158.64$  g and ranged from 134–730 g, whereas mean male mass was  $113.50 \pm 33.04$  g (range 75–160 g). Fewer males could be used because most were too small to accommodate a transmitter (Camper, 2005; Semlitsch and Gibbons, 1982). Analyses used a maximum of 15 females and 5 males. Because of transmitter failure and predation, seasonal analyses used only 14 snakes (13 females, 1 male). Five females were radiotracked for 2 years but, to avoid problems with statistical independence, only a single year of data were used for each of these snakes in all analyses. The year that contained the most data was chosen for analysis. Based on the 20 animals used in the analyses, 2 snakes (1 of each sex) were tracked in 2002; in 2003 5 snakes (4 female, 1 male); in 2004 2 snakes (1 of each sex); in 2005 5 females; and in 2006 6 snakes were tracked (4 females, 2 males).

Snakes were located 3–5 days per week from the release date in the spring until late August. From late August until mid-November animals were located two–four times per week. Each snake location was marked with flagging tape and latitude and longitude coordinates (decimal degrees), time, macro-habitat type, and any behavioral observations were recorded. Snakes were tracked with the use of a Yagi antenna and an R-1000 receiver (Communications Specialists Inc., Orange, California, USA) during 2002–2003 or a TR-4 receiver (Telonics, Inc., Mesa, Arizona, USA) during 2004–2006. Global positioning system coordinates were detected with a Garmin GPS III plus (2002–2003) or a Garmin GPS V during 2004–2006 (Garmin International Inc., Olathe, Kansas, USA). Because visual observations of the snakes were rare 0–18.9% per snake ( $\bar{X} = 4.1 \pm 4.5\%$ ,  $n = 20$  snakes) few behavioral observations were made.

Stomach contents were palpated from *Nerodia fasciata* captured from the area in Fig. 1A from 1998 to 2001. Prey were identified to species whenever possible. None of the snakes yielding stomach content data were used in this study. Prey available to the snakes in these ponds included fishes in the genera *Esox*, *Gambusia*, *Lepomis* and *Micropterus* as well as anurans (both adults and larvae) of *Acris*, *Anaxyrus*, *Hyla* and *Lithobates*.

#### *Home Range, Habitat, and Movement Analyses*

Latitude and longitude coordinates were plotted on digitized topographic maps and digital orthophoto quarter quadrangle aerial photographs using Arcview 3.2 GIS software (ESRI, Redlands, California, USA). All movement distances and distances from wetlands were measured as straight-line distances with the use of Arcview. Movement distances less than 6 m were not included in movement analyses. Each animal's overall movement rate (OMR) and actual movement rate (AMR) were calculated according to Charland and Gregory (1995) for the summer (June–August) and fall (September–November). Overall Movement Rate is the sum of distance moved/total number of days in a time interval and AMR is sum of distance moved/number of days in which movement occurred.

Both 95% minimum convex polygon (MCP) and 95% kernel home range (95% KHR) analyses were conducted with the use of the animal movement analysis extension of Arcview 3.2 (Hooge and Eichenlaub, 1997). The harmonic mean method was used to identify and remove the 5% outliers prior to MCP calculation (Hooge and Eichenlaub, 1997). Fixed kernel 95% KHR estimates (hereafter 95% KHR) with the use of least-squares cross validation to calculate the smoothing parameter were used because of previously demonstrated reliable results (Seaman and Powell, 1996). The 50% kernel home range estimates (hereafter core area) were defined as the core area of the home range and were considered areas of intense use (Rodriguez-Robles, 2003).

For habitat analysis, snakes were scored as being in shoreline, littoral zone, pelagic zone, or terrestrial at each location. Shoreline is defined as being out of the water but along the

pond edge, littoral as in shallow water (<1 m deep), usually with emergent vegetation, and pelagic as out in the pond where GPS coordinates were not obtained, due to equipment constraints. Terrestrial was defined as out of the water and at least 5 m from the shoreline. We tested for differences in the width of the terrestrial buffer zone between *N. erythrogaster* and *N. fasciata* with the use of a Mann-Whitney test on the mean distance of terrestrial locations from wetlands. We decided not to use compositional analysis because the snakes were selecting habitat strips (shoreline and littoral zone) and we felt that calculating the area of linear habitat strips was too inaccurate (Harmata and Montopoli, 2001). Habitat availability was estimated by measuring the area of contiguous habitat (terrestrial and pelagic habitats only) within the MCP of each snake with the use of Arcview 3.2.

#### *Statistical Analysis*

Data were tested for normality with the use of the Shapiro-Wilk test ( $n \leq 50$ ) or the Kolmogorov-Smirnov test for larger sample sizes. Tests for homoscedasticity used the variance ratio test (Zar, 1984). Data were log transformed prior to statistical analysis if they did not meet the assumptions of normality. Nonparametric tests were used when transformed data did not conform to the assumptions of normality and homoscedasticity. We used SPSS version 15 (SPSS Inc., 2008) and GraphPad Prism 4 (GraphPad Software, Inc., 2009) for all statistical analyses. Means are reported with one standard deviation.

Tests for seasonal differences combined the sexes and compared only summer to fall because there were too few data for spring and the snakes rarely moved during winter. Seasonal comparisons used either a paired-sample *t*-test, if variables were correlated, or a two-sample *t*-test when variables were not correlated (Zar, 1984). The two-sample *t*-test was used to test for seasonal differences in the following variables; MCP, 95% KHR, core areas, and core area as a percentage of the entire home range. Paired-sample *t*-tests were used to test for seasonal differences in the following correlated variables; mean distance

per move, AMR, OMR, and movement frequency. Seasonal differences in range length, the two locations farthest apart within the home range of each animal, were tested with a Wilcoxon paired-sample test and for differences in total distance moved per season with the Mann-Whitney *U* test. Tests for differences in seasonal use of shoreline and littoral zone habitats used the  $\chi^2$  test with the number of observations in each habitat type used as the variable analyzed.

Tests for differences between the sexes used data from summer and fall combined. The two-sample *t*-test was used to test for differences in the means between males and females for the following variables; MCP, 95% KHR, core areas, core area as a percentage of the entire home range, distance per move, AMR, OMR, range length, and the number of locations in shoreline versus littoral zone habitats. The Mann-Whitney *U* test was used to test for sex differences in total distance moved. Tests for differences in MCP versus 95% KHR and MCP versus core area size utilized the Wilcoxon paired-sample test with the sexes and seasons combined. Analyses of habitat use employed Kruskal-Wallis test and Dunn's multiple-comparison test on the number of locations in each habitat category. We used the Spearman rho statistic to test for correlations between MCP size and the number of locations for each animal, snake snout-to-vent length (SVL) and home-range size, and SVL and movement distance and movement rate variables.

## RESULTS

### *Home Range and Movement*

Mean 95% KHR was significantly greater than mean 95% MCP (Table 1, Wilcoxon Paired Sample test,  $P = 0.0002$ ). Mean 95% MCP was significantly greater than core areas (Wilcoxon Paired Sample test, sexes pooled,  $P = 0.0158$ ). Mean summer estimates were greater for all home range variables calculated except 95% MCP (Table 1). Mean summer 95% KHR were 1.9 times the size of the fall kernels (Fig. 2) and mean summer core areas were 2.6 times the area of fall estimates. There was extensive overlap between summer and fall 95% KHR, indicating an activity range

TABLE 1.—Spatial use estimates for banded water snakes in the upper coastal plain of South Carolina studied from 2002 to 2006. Core areas are 50% kernel home ranges. Ranges appear under mean  $\pm$  1 SD. All data, except percent of total core area, were log transformed prior to seasonal analyses.

Estimate	95% minimum convex polygon (ha)	Range length (m)	95% kernel home range (ha)	Core area (ha)	Percent of total used as core
All snakes ( $n = 20$ )	3.54 $\pm$ 1.75 (1.26–8.28)	404 $\pm$ 114 (185–602)	10.95 $\pm$ 10.03 (1.84–39.98)	2.95 $\pm$ 3.78 (0.26–16.57)	22.26 $\pm$ 7.82 (10.47–41.45)
Summer ( $n = 13$ )	2.45 $\pm$ 1.51 (0.85–6.32)	355 $\pm$ 145 (145–671)	6.44 $\pm$ 5.18 (1.77–21.25)	1.62 $\pm$ 1.59 (0.34–6.26)	23.45 $\pm$ 6.24 (13.61–35.73)
Fall ( $n = 13$ )	1.60 $\pm$ 0.79 (0.34–3.24)	274 $\pm$ 56 (169–355)	3.41 $\pm$ 2.16 (0.94–8.10)	0.62 $\pm$ 0.58 (0.16–2.24)	16.65 $\pm$ 4.93 (10.09–27.65)
$P$	0.0847	0.0479*	0.0305*	0.0067*	0.0051*

\* significant at  $\alpha = 0.05$ .

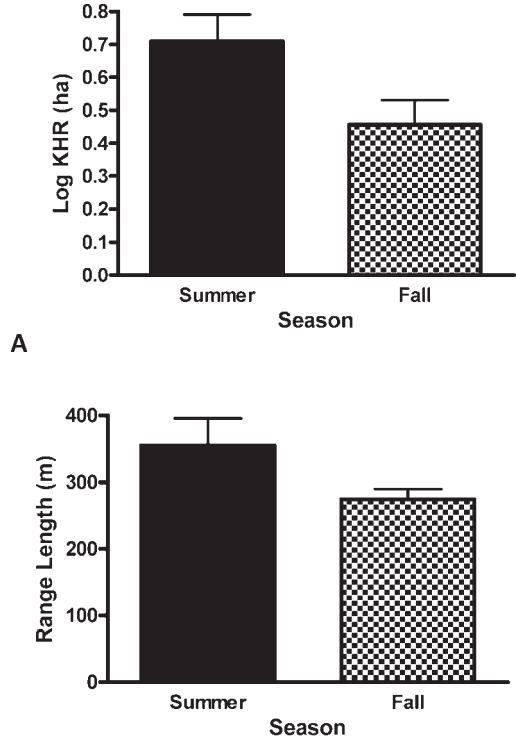


FIG. 2.—Seasonal differences in 95% kernel home range (KHR) in A and range length of 95% minimum convex polygon (MCP) in B for 13 *Nerodia fasciata* (12 females, 1 male). Error bars are one standard error (SE) of the mean.

contraction and not a spatial shift in activity range in the fall. The mean overlap between summer and fall was  $77 \pm 27\%$  (range 24–100%). Only three snakes had seasonal overlap of 95% KHR of less than 50% and three had 100% overlap. The latter had the entire fall 95% KHR completely enclosed within the summer polygon. Only one snake, a female, had a fall 95% KHR (7.1 ha) substantially larger than the summer estimate (1.77 ha). Males had a larger, but not significant, mean 95% MCP ( $\bar{X} = 4.14 \pm 2.49$  ha, 2.03–8.28 ha) than females ( $\bar{X} = 3.34 \pm 1.49$  ha, range = 1.26–6.24 ha; seasons pooled, two-sample  $t$ -test,  $t = 0.869$ ,  $df = 18$ ,  $P = 0.396$ ). On average, spatial use estimates were only slightly greater for males than for females; 95% KHR (males,  $\bar{X} = 13.12 \pm 10.22$  ha, 4.15–25.35 ha) and females ( $\bar{X} = 10.21 \pm 10.22$  ha, 1.05–39.98 ha; two-sample

*t*-test, seasons combined,  $t = 0.551$ ,  $df = 18$ ,  $P = 0.589$ ), core area (males  $\bar{X} = 3.10 \pm 2.72$  ha, 0.68–6.65 ha) versus females ( $\bar{X} = 2.89 \pm 4.15$  ha, 0.11–16.57 ha; seasons combined,  $t = 0.105$ ,  $df = 18$ ,  $P = 0.917$ ), and range length of 95% MCPs (males  $\bar{X} = 433 \pm 109$  m, 315–591 m) versus females ( $\bar{X} = 394 \pm 118$  m, 185–602 m; seasons combined,  $t = 0.648$ ,  $df = 18$ ,  $P = 0.525$ ). Twelve of 15 females and 1 of 5 males had core areas, for the entire active season, broken into more than one region. One female had three separate regions to her core area. Because MCPs have been shown to be dependent upon the number of locations of an animal (Worton, 1987), correlation analysis was conducted and no significant correlations between 95% MCP size and number of locations per animal ( $r = 0.008$ ,  $P = 0.975$ ) were found. Body size (SVL) was not correlated with either 95% MCP ( $r = 0.008$ ,  $P = 0.972$ ) or MCP range length ( $r = 0.065$ ,  $P = 0.786$ ).

Mean distance per move was not significantly greater for males ( $\bar{X} = 69.05 \pm 16.21$  m, range 54.49–95.61 m) than for females ( $\bar{X} = 64.71 \pm 14.02$  m, 44.20–89.38 m; two sample *t*-test, seasons pooled,  $t = 0.579$ ,  $df = 18$ ,  $P = 0.570$ ) and did not differ between seasons (Table 2). Mean total distance moved per season was significantly greater for summer than for fall but did not differ significantly between the sexes (males  $\bar{X} = 2617 \pm 1554$  m, range 1323–5138 m, females  $\bar{X} = 3036 \pm 585$  m, 1887–3783 m, seasons combined, Mann-Whitney test,  $U = 24$ ,  $P = 0.257$ ). Both AMR and OMR were greater in the summer than in the fall but not significantly so (Table 2). Mean male AMR was  $\bar{X} = 68.99 \pm 16.21$  m/day (range 54.49–95.61) and was not significantly greater than mean female AMR ( $\bar{X} = 64.00 \pm 14.08$  m/day, 43.42–89.88; seasons pooled,  $t = 0.662$ ,  $df = 18$ ,  $P = 0.516$ ). Mean male OMR was  $\bar{X} = 51.31 \pm 12.58$  m/day (39.89–70.73 m/day) and was not significantly greater than mean female OMR ( $\bar{X} = 44.86 \pm 10.95$  m/day, 27.89–63.63 m/day; seasons combined,  $t = 1.10$ ,  $df = 18$ ,  $P = 0.284$ ). Body size (SVL) was not correlated with mean distance per move ( $r = -0.018$ ,  $P = 0.940$ ), total distance moved ( $r = 0.046$ ,  $P = 0.848$ ), AMR ( $r = -0.026$ ,  $P = 0.915$ ), or OMR ( $r = -0.193$ ,  $P = 0.414$ ).

TABLE 2.—Movement statistics for banded water snakes ( $n = 20$ ) in the upper coastal plain of South Carolina studied from 2002 to 2006. AMR is actual movement rate and OMR is overall movement rate. Ranges appear under mean  $\pm 1$  SD. Total distance and OMR data were log transformed prior to seasonal analyses.

Estimate	Mean distance/move (m)	AMR (m/day)	OMR (m/day)	Total distance (m)
All snakes ( $n = 20$ )	65.80 $\pm$ 14.25 (44.20–95.61)	65.25 $\pm$ 14.36 (43.42–95.61)	46.47 $\pm$ 11.39 (27.89–70.73)	2932 $\pm$ 892 (1323–5138)
Summer ( $n = 14$ )	66.87 $\pm$ 21.90 (23.08–107.90)	68.34 $\pm$ 22.61 (24.00–111.48)	32.47 $\pm$ 25.40 (6.67–107.19)	1976 $\pm$ 906 (600–3426)
Fall ( $n = 14$ )	64.89 $\pm$ 22.16 (30.13–106.69)	63.45 $\pm$ 22.21 (30.13–106.69)	23.65 $\pm$ 21.51 (4.97–8.80)	1125 $\pm$ 441 (452–1906)
<i>P</i>	0.8108	0.7401	0.1171	0.0366*

\* Significant at  $\alpha = 0.05$ .



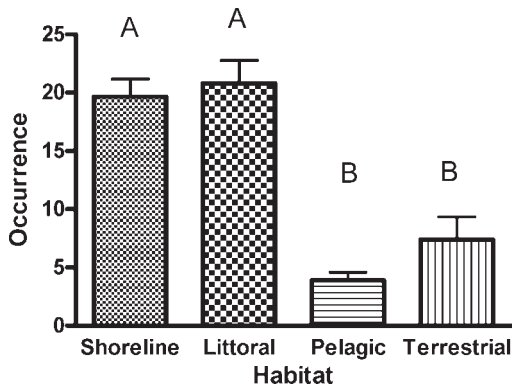
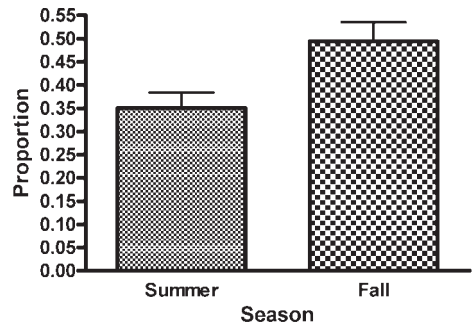


FIG. 3.—Habitat use by 20 *Nerodia fasciata fasciata* at PDREC. Different letters indicate significant differences with the use of a Dunn's multiple-comparison test. Error bars are one standard error (SE) of the mean.

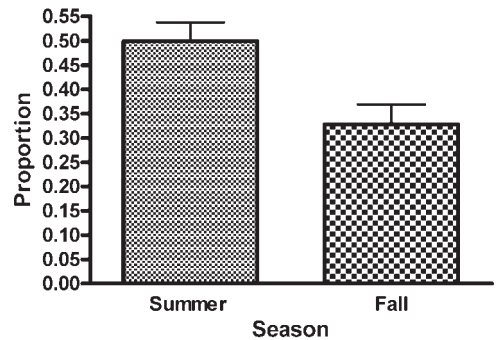
Snakes moved to new locations frequently with a mean of  $\bar{X} = 77.4 \pm 6.6\%$  (35–74%) new locations. Males ( $\bar{X} = 78.6 \pm 8.2\%$ , 52–74% locations new) did not move to new locations more often than females ( $\bar{X} = 77.0 \pm 6.2\%$ , 35–67%; seasons combined,  $t = 0.463$ ,  $df = 18$ ,  $P = 0.649$ ). *Nerodia f. fasciata* did not move to new locations significantly more often in the summer ( $\bar{X} = 80.3 \pm 11.7\%$ , 59–96%) than during the fall ( $\bar{X} = 77.0 \pm 14.3\%$ , 52–97%; paired  $t = 0.533$ ,  $df = 13$ ,  $P = 0.603$ ).

#### Habitat Use and Overwintering

Snakes did not use habitats in accordance with availability and were found in shoreline and littoral zone habitats significantly more often than in pelagic or terrestrial habitats (Kruskal-Wallis test,  $P < 0.0001$ , Fig. 3). Dunn's Multiple Comparison test showed that littoral and shoreline habitat use were not significantly different from each other nor was pelagic habitat use significantly different from terrestrial. These results strongly suggest habitat preference for littoral and shoreline habitats because pelagic habitat averaged  $19 \pm 13\%$  (range 0–54%) and terrestrial habitat averaged  $56 \pm 23\%$  (13–88%) of MCP home ranges, respectively. The littoral zone was used significantly more during the summer ( $\chi^2 = 63.92$ ,  $df = 1$ ,  $P < 0.05$ ) whereas the shoreline was used more frequently, but marginally non significant, during fall ( $\chi^2 = 3.82$ ,  $df = 1$ ,  $P > 0.05$ ; Fig. 4). This habitat



A



B

FIG. 4.—Seasonal differences in habitat use for shoreline (A) and littoral (B) habitats at PDREC for 14 *Nerodia fasciata fasciata* (13 females, 1 male). Error bars are one standard error (SE) of the mean.

preference may be due to prey availability (Table 3). *Nerodia fasciata* in this population fed exclusively on fishes and amphibians. Even though prey availability was not measured during this study, prey appeared to be abundant, perhaps even concentrated, in the littoral zone of the ponds (J. D. Camper, personal observation). Females used shoreline habitat significantly more often than males ( $\bar{X} = 19.7 \pm 6.8$  locations per snake for females versus  $\bar{X} = 13.6 \pm 5.1$  locations per snake for males, seasons pooled,  $t = 2.66$ ,  $df = 18$ ,  $P = 0.0161$ ).

Nine female snakes were found at terrestrial localities from 2 to 12 times per snake during this study yielding only 14.3% of localities in terrestrial habitats, indicating a high level of preference for aquatic environments. Straight-line distances from ponds

TABLE 3.—Prey items from *Nerodia fasciata fasciata* ( $n = 13$  snakes) collected during 1998–2001 from the Pee Dee Research and Education Center in Darlington County, South Carolina. Prey were palpated from snakes or voluntarily regurgitated by snakes.

Amphibians		Fishes	
Prey species	Number (%)	Prey species	Number (%)
<i>Siren intermedia</i>	1 (3.6)	Cyprinidae	1 (3.6)
<i>Lithobates catesbeiana</i>	4 (14.3)	<i>Esox</i> spp.	3 (10.7)
<i>Lithobates sphenoccephala</i>	1 (3.6)	<i>Enneacanthus</i> spp.	1 (3.6)
<i>Lithobates</i> larvae	1 (3.6)	<i>Lepomis punctatus</i>	1 (3.6)
<i>Lithobates</i> spp.	3 (10.7)	<i>Lepomis</i> spp.	4 (14.3)
<i>Hyla cinerea</i>	1 (3.6)	Centrarchidae	1 (3.6)
		<i>Noturus</i> spp.	1 (3.6)
		Ictaluridae	1 (3.6)
		Unidentified	4 (14.3)
Total	11 (39.3)	Total	17 (60.7)

were  $\bar{X} = 45.39 \pm 45.37$  m (range 6–213 m,  $n = 46$  locations) from nine snakes. Most (72%) terrestrial sites were <50 m from wetlands and only 13% were >100 m from wetland edges. Mean distance from wetlands for *N. fasciata* was significantly less than what was found for *N. erythrogaster* at this site ( $\bar{X} = 156.60 \pm 132.73$  m, Mann-Whitney test,  $U = 613$ ,  $P < 0.05$ ), supporting our prediction about *N. fasciata* using a smaller amount of terrestrial core habitat around wetlands than *N. erythrogaster* (Camper, 2009). Wetlands (pond, stream, seep, ditch, swamp, marsh) made up a large proportion of most of the snakes core areas ( $\bar{X} = 38.76 \pm 19.59\%$  wetland; range 7.2–89.9%) from  $n = 20$  snakes. A distance of 133 m of terrestrial habitat is needed to encompass 95% of the terrestrial localities recorded in this study.

Snakes typically ceased moving by early to mid-November as environmental temperatures decreased. Data for overwintering behaviors were available for 11 female snakes. Overwintering females were inactive for  $\bar{X} = 18.09 \pm 2.25$  wk (range 15.1–22.3 wk). During this period, occasional movements occurred. Only three did not move at all and from 0–9 moves ( $\bar{X} = 2.27 \pm 2.90$ ) occurred per snake. Winter movement distances averaged  $24.4 \pm 14.6$  m (range 9–49 m,  $n = 12$  moves). One snake was observed out of a hibernaculum during the winter. It was a female basking in a wax myrtle (*Myrica cerifera*) bush about 30 cm above the pond surface on 1 December, when ambient air temperature was approximately 6 °C. Overwintering sites were all right along (<1 m) the edges of ponds (seven snakes),

swamp (two snakes), stream (one snake) and ditch (one snake).

## DISCUSSION

### *Home Range and Movement*

Because of their ecological similarity (i.e., strong ties to water) and close phylogenetic relationship (Mebert, 2008), we expected *Nerodia fasciata* spatial ecology to be more similar to that of *N. sipedon* than other watersnake species. Home-range estimates (95% MCP) reported here for *N. f. fasciata* are comparable to those of *N. sipedon* from Ohio and Michigan (Roe et al., 2004) but larger than those of *N. sipedon* from Ontario (Brown and Weatherhead, 1999) and Pennsylvania (Pattishall and Cundall, 2008). Kernel estimates reported here are 2.5 to 3.75 times larger than found in two populations of *N. sipedon* (Roe et al., 2004; Roth and Greene, 2006). *Nerodia f. fasciata* had MCP home ranges approximately 4.5 times smaller than a syntopic population of *Nerodia erythrogaster erythrogaster* (Camper, 2009) and a northern population of *Nerodia erythrogaster neglecta* (Roe et al., 2004).

Summer home-range estimates were significantly greater than fall estimates for all measures except for 95% MCP, although it was only marginally non-significant (Table 1). Although the reasons for the seasonal differences are unclear, the high degree of overlap of seasonal home ranges indicates a contraction rather than a spatial shift in activity center. Others have reported seasonal shifts in spatial use by snakes based upon the use of

particular resources (Brito, 2003; Heard et al., 2004; Madsen and Shine, 1996; Shine and Lambeck, 1985). However, a contraction of the home range seems much less common in snakes. Further evidence supporting a home-range contraction during fall is that the mean total distance moved was less in fall than during summer (Table 2). Seasonal contraction of activity centers occurred for *N. sipedon* in Missouri (Roth and Greene, 2006). The reason for the apparent decrease in movement in fall may be due to reduced activity with more time spent thermoregulating and less time foraging (Brown and Weatherhead, 2000).

Mean distance per move was comparable to findings by Roth and Greene (2006) for *N. sipedon* in Missouri, however the total distance moved by *N. f. fasciata* was greater than in Midwestern *N. sipedon* (Roe et al., 2004) and considerably less than *N. sipedon* in Missouri (Roth and Greene, 2006). The OMR reported here was similar to that of *N. sipedon* in the Midwest (Roe et al., 2004) and comparable to *N. sipedon* in Missouri (Roth and Greene, 2006). Movement frequency (77%) was comparable to what Roth and Greene (2006) found for *N. sipedon* (71%) but much higher than the 27% that has been reported for *N. sipedon* in both Pennsylvania and Wisconsin, respectively (Pattishall and Cundall, 2008; Tiebout and Cary, 1987).

#### *Habitat Use and Overwintering*

*Nerodia f. fasciata* showed preference for shallow littoral and shoreline habitats (out of the water but along the pond edge). Relatively few locations occurred at distances in excess of 50 m from water or out in the middle of the ponds. This habitat preference may be due to the presence of prey (fish, amphibians) in littoral habitats (Table 3). Similar results were found by Hebrard and Mushinsky (1978) in Louisiana bayous where *N. fasciata* was found mainly in littoral and shoreline habitats. Tiebout and Cary (1987) found that *N. sipedon* used open water and terrestrial sites relatively infrequently, but used the shoreline and emergent vegetation most often.

*Nerodia f. fasciata* were found out of water along the shoreline more often in the fall than during summer (Fig. 4A). This may be

attributable to more basking in the fall as temperatures decrease. Brown and Weatherhead (2000) found that *N. sipedon* thermoregulate more later in the activity season in a population from Ontario. Females spent more time out of water along the shoreline than males. This habitat difference may be due to females thermoregulating more frequently during gestation as shown by Brown and Weatherhead (2000) for *N. sipedon*. Mushinsky et al. (1980) reported higher body temperatures for female *N. fasciata* in Louisiana than for males. Although reproductive condition could not be determined for every female at the time of transmitter implantation, all but one female were presumed to be gravid during this study.

Reptiles tend to travel across terrestrial landscapes more frequently and over greater distances than most amphibian species, however management practices often overlook this aspect of their life history (Gibbons et al., 2000). Species dispersal and abundance are both significantly affected by the characteristics of landscapes bordering wetland habitat (Roe and Georges, 2007). Our results support the prediction of strong ties to aquatic habitats for *N. fasciata*. The 133 m needed to encompass 95% of the terrestrial sites found in this study is well within the amount of terrestrial core habitat recommendations (Roe and Georges, 2007; Semlitsch and Bodie, 2003). This is higher than reported for *N. sipedon* by Roe et al. (2003) who found that 30 m included 95% of the upland sites used by their population. They found that *N. sipedon* used upland localities less (2.5%) as compared to 14.3% in this study for *N. fasciata*. Nine of 20 (45%) individuals were found to move out of wetlands by crossing old fields, wooded areas, and roads, indicating that although *N. fasciata* are highly associated with aquatic environments, they may temporarily use terrestrial habitats for travel corridors. By including these areas in protected wetlands, we may be able to buffer against potential local extinctions of metapopulations.

The limited amount of winter activity found in this study has been seen in Louisiana populations of this species (Kofron, 1978; Tinkle, 1959). Both authors indicate that *N. fasciata* was active almost until December and

became active again in February and March. The natricine *Thamnophis sirtalis* also exhibits some winter activity in South Carolina (Gibbons and Semlitsch, 1987). The limited amount of spring data from this population indicates that activity does not begin until March. Snakes hibernated singly and at lowland sites immediately adjacent to wetlands in this study. Hibernating in lowland habitats adjacent to water has been shown for *N. fasciata* in Louisiana (Kofron, 1978), *N. sipedon* in Pennsylvania (Pattishall and Cundall, 2008), *N. erythrogaster* (J. D. Camper, unpublished data; Kingsbury and Coppola, 2000) and *N. taxispilota* (Wright and Wright, 1957). However, Roe et al. (2003) reported that *N. erythrogaster* and *N. sipedon* used crayfish burrows in upland habitats to overwinter. None of the hibernacula observed in this study appeared to be crayfish burrows. The data presented here should help increase our understanding of the ecology of this important wetland predator. It is only when we understand the entire life history of an organism, including the amount of space it requires, its habitat use, and hibernation sites, that we will have enough information available to maintain viable populations of species in their native habitats.

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#### LITERATURE CITED

- BRITO, J. C. 2003. Seasonal variation in movements, home range and habitat use by male *Vipera latastei* in northern Portugal. *Journal of Herpetology* 37:155–160.
- BROWN, G. P., AND P. J. WEATHERHEAD. 1999. Female distribution affects mate searching and sexual selection in male northern water snakes (*Nerodia sipedon*). *Behavioral Ecology and Sociobiology* 47:9–16.
- BROWN, G. P., AND P. J. WEATHERHEAD. 2000. Thermal ecology and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Ecological Monographs* 70: 311–330.
- BURKE, V. J., AND J. W. GIBBONS. 1995. Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina Bay. *Conservation Biology* 6:1365–1369.
- CAMPER, J. D. 2005. Observations on problems with using funnel traps to sample semi-aquatic snakes. *Herpetological Review* 36:288–290.
- CAMPER, J. D. 2009. Core terrestrial habitat around wetlands: contributions from the spatial ecology of the Redbelly Watersnake (*Nerodia erythrogaster erythrogaster*). *Copeia* 2009:556–562.
- CHARLAND, M. B., AND P. T. GREGORY. 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). *Journal of Zoology* London 236:543–561.
- DODD, C. K., JR. 1993. Strategies for snake conservation. Pp. 363–393. *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York, New York, USA.
- FITCH, H. S. 1987. Collecting and life-history techniques. Pp. 143–164. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. MacMillan Publishing Company, New York, New York, USA.
- GIBBONS, J. W., AND M. E. DORCAS. 2004. *North American Watersnakes: A Natural History*. University of Oklahoma Press, Norman, Oklahoma, USA.
- GIBBONS, J. W., D. E. SCOTT, T. A. RYAN, K. A. BUHLMANN, T. D. TUBERVILLE, B. S. METTS, J. L. GREENE, T. MILLS, Y. LEIDEN, S. POPPY, AND C. T. WINNE. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653–666.
- GIBBONS, J. W., AND R. D. SEMLITSCH. 1987. Activity patterns. Pp. 396–421. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. MacMillan Publishing Company, New York, New York, USA.
- GRAPHPAD SOFTWARE INC. 2009. *GraphPad Prism 4*. GraphPad Software, Inc., LaJolla, California, USA.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. Pp. 366–395. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.), *Snakes: Ecology and Evolutionary Biology*. MacMillan Publishing Company, New York, New York, USA.
- HARMATA, A. R., AND G. J. MONTOPOLI. 2001. Analysis of bald eagle spatial use of linear habitat. *Journal of Raptor Research* 35:207–213.
- HEARD, G. W., D. BLACK, AND P. ROBERTSON. 2004. Habitat use by the inland Carpet Python (*Morelia spilota metcalfei*: Pythonidae): Seasonal relationships with habitat structure and prey distribution in a rural landscape. *Austral Ecology* 29:446–460.
- HEBRARD, J. J., AND H. R. MUSHINSKY. 1978. Habitat use by five sympatric water snakes in a Louisiana swamp. *Herpetologica* 34:306–311.
- HOOGE, P. N., AND B. EICHENLAUB. 1997. *Animal movement extension to arcview*. Ver. 2.0. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage, Alaska, USA.

- KECK, M. B. 1998. Habitat use by semi-aquatic snakes at ponds on a reclaimed strip mine. *The Southwestern Naturalist* 43:13–19.
- KINGSBURY, B. A., AND C. J. COPPOLA. 2000. Hibernacula of the copperbelly water snake (*Nerodia erythrogaster neglecta*) in southern Indiana and Kentucky. *Journal of Herpetology* 34:294–298.
- KOFRON, C. P. 1978. Foods and habitats of aquatic snakes (Reptilia, Serpentes) in a Louisiana swamp. *Journal of Herpetology* 12:543–554.
- MADSEN, T., AND R. SHINE. 1996. Seasonal migration of predators and prey: A study of pythons and rats in tropical Australia. *Ecology* 77:149–156.
- MEBERT, K. 2008. Good species despite massive hybridization: Genetic research on the contact zone between the water snakes *Nerodia sipedon* and *N. fasciata* in the Carolinas, USA. *Molecular Ecology* 17:1918–1929.
- MUSHINSKY, H. R., AND J. J. HEBBARD. 1977. Food partitioning by five species of water snakes in Louisiana. *Herpetologica* 33:162–166.
- MUSHINSKY, H. R., J. J. HEBBARD, AND M. G. WALLEY. 1980. The role of temperature on the behavioral and ecological associations of sympatric water snakes. *Copeia* 1980:744–754.
- PATTISHALL, A., AND D. CUNDALL. 2008. Spatial biology of northern watersnakes (*Nerodia sipedon*) living along an urban stream. *Copeia* 2008:752–762.
- REINERT, H. K. 1992. Radiotelemetric field studies of pitvipers: Data acquisition and analysis. Pp. 185–197. *In* J. A. Campbell and E. D. Brodie, Jr. (Eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas, USA.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- RODRIGUEZ-ROBLES, J. A. 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. *Copeia* 2003:391–396.
- ROE, J. H., AND A. GEORGES. 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. *Biological Conservation* 135:67–76.
- ROE, J. H., B. A. KINGSBURY, AND N. A. HERBERT. 2003. Wetland and upland use patterns in semi-aquatic snakes: Implications for wetland conservation. *Wetlands* 23:1003–1014.
- ROE, J. H., B. A. KINGSBURY, AND N. A. HERBERT. 2004. Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources. *Biological Conservation* 118:79–89.
- ROHDE, F. C., R. G. ARNDT, J. W. FOLTZ, AND J. M. QUATTRO. 2009. *Freshwater Fishes of South Carolina*. University of South Carolina Press, Columbia, South Carolina, USA.
- ROTH, E. D. 2005. Buffer zone applications in snake ecology: A case study using cottonmouths (*Agkistrodon piscivorus*). *Copeia* 2005:399–402.
- ROTH, T. C., AND B. D. GREENE. 2006. Movement patterns and home range use of the northern watersnake (*Nerodia sipedon*). *Copeia* 2006:544–551.
- SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- SEIGEL, R. A. 1993. Summary: Future research on snakes, or how to combat “lizard envy.” Pp. 395–402. *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York, New York, USA.
- SEIGEL, R. A., J. W. GIBBONS, AND T. K. LYNCH. 1995. Temporal changes in reptile populations: Effects of a severe drought on aquatic snakes. *Herpetologica* 51:424–434.
- SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17:1219–1228.
- SEMLITSCH, R. D., AND J. W. GIBBONS. 1982. Body size dimorphism and sexual selection in two species of water snakes. *Copeia* 1982:974–976.
- SHINE, R., AND R. LAMBECK. 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes: Acrochordidae). *Herpetologica* 41:352–361.
- SPSS, INC. 2008. SPSS 15. SPSS, Inc., Chicago, Illinois, USA.
- TIEBOUT, H. M., AND J. R. CARY. 1987. Dynamic spatial ecology of the water snake, *Nerodia sipedon*. *Copeia* 1987:1–18.
- TINKLE, D. W. 1959. Observations of reptiles and amphibians in a Louisiana Swamp. *American Midland Naturalist* 62:189–205.
- WEATHER WAREHOUSE. 2010. Available at: [http://Weather-warehouse.com/WeatherHistory/PastWeatherData\\_Florence8Ne\\_SC\\_January.html](http://Weather-warehouse.com/WeatherHistory/PastWeatherData_Florence8Ne_SC_January.html). Accessed: May 25, 2010.
- WILLSON, J. D., C. T. WINNE, M. E. DORCAS, AND J. W. GIBBONS. 2006. Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: Insights on different strategies for persistence in a dynamic habitat. *Wetlands* 26:1071–1078.
- WORTON, B. J. 1987. A review of models of home range for animal movement. *Ecological Modelling* 38:277–298.
- WRIGHT, A. H., AND A. A. WRIGHT. 1957. *Handbook of Snakes of the United States and Canada*. Comstock Publishing Associates, Ithaca, New York, USA.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, New Jersey, USA.

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