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Core Terrestrial Habitat Around Wetlands: Contributions from the Spatial Ecology of the Redbelly Watersnake (*Nerodia erythrogaster erythrogaster*)

Jeffrey D. Camper[1]

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Terrestrial habitats around wetlands are important in wetland conservation because many vertebrate animals use them during part of their life cycle. There is relatively little information concerning terrestrial habitat use by aquatic snakes adjacent to wetlands. Radiotelemetry was used to study the spatial ecology and terrestrial habitat use of *Nerodia e. erythrogaster* in the upper coastal plain of northern South Carolina. Snakes used terrestrial habitats extensively during the summer and fall. Use of both wetlands and southern mixed hardwood forest were significantly greater than predicted by habitat availability within the snakes' home ranges. Agricultural fields were used significantly less than predicted. A distance of 344 m from wetlands is necessary to encompass 95% of the terrestrial localities documented in this study. Home range estimates based on 95% fixed kernels were significantly larger than those calculated using the 95% minimum convex polygon methods. Home range estimates for this species are comparable to those of large terrestrial colubrids and are greater than home range estimates reported for congeners. Snakes spent an average of about ten days out of wetlands during terrestrial movements with a maximum of 23 consecutive days spent out of a wetland. These results suggest that in excess of 300 m of forest habitat buffering wetlands may be necessary to sustain populations of *N. erythrogaster*.

AN important aspect of wetland conservation is the amount of terrestrial habitat protected around wetlands. Currently there are no federal guidelines in the United States requiring terrestrial habitat protection adjacent to and outside of a federally delineated wetland (Burke and Gibbons, 1995). Land surrounding wetlands has been referred to as buffer zones (Burke and Gibbons, 1995) and more recently as terrestrial core habitat (Semlitsch and Jensen, 2001). Core habitat is used in this paper because the term buffer zone implies that these areas are optional and therefore not necessary (Semlitsch and Jensen, 2001). Because many species that depend upon wetlands also need the surrounding terrestrial habitats during part of their life cycles, accurately estimating the amount of terrestrial core habitat is crucial to preserving intact wetland communities. Estimates for the amount of terrestrial core habitat needed by wildlife species range from just over 30 m for macroinvertebrates in northern California riparian areas (Newbold et al., 1980) to over 600 m for pond breeding amphibians in Florida sandhill habitats (Dodd, 1996). Semlitsch and Bodie (2003) reviewed the topic for amphibians and reptiles. They indicated that the mean core habitat width around wetlands ranged from 168 to 304 m for snakes. They concluded that core habitat should extend out to 142 to 289 m with an additional 50 m buffer zone for all amphibians and reptiles studied so far (Semlitsch and Bodie, 2003). Although few studies have examined this for snakes, Roe et al. (2003) found that 95% of Copperbelly Watersnake (*Nerodia erythrogaster neglecta*) locations were within 125 m of wetland boundaries for a peripherally isolated population at their Michigan/Ohio study site.

The Plainbelly Watersnake (*Nerodia erythrogaster*) is a widespread species common to many wetlands in eastern and central North America (Conant and Collins, 1991). Compared to other *Nerodia*, this species is known to be relatively terrestrial (Diener, 1957; Preston, 1970; Keck, 1998; Roe et al., 2003, 2004). The spatial ecology of federally threatened Copperbelly Watersnakes has been investigated in the northern disjunct part of the species' range by Roe et al. (2003, 2004). Relatively little information is available for eastern populations of *N. erythrogaster*, or from further south in the main portion of the species' geographic range. The objectives of this study were to quantify the amount of terrestrial core habitat needed by *N. e. erythrogaster*, ascertain which terrestrial habitats were used by these snakes, generate spatial use or home range estimates, and estimate movement distances and movement frequencies made by these animals.

MATERIALS AND METHODS

The Pee Dee Research and Education Center (PDREC) is an experimental agricultural facility owned and operated by Clemson University in the upper coastal plain of South Carolina in southeastern Darlington County (Fig. 1). The site is 972 ha with about one-third of PDREC planted in row crops. Non-agricultural habitats include pine forest, southern mixed hardwood forest (SMHF), riparian deciduous forest, pine plantations, old fields, artificial ponds, a swamp, and a lake (Dargan's Pond). Back Swamp is a riparian swamp consisting of beaver ponds, Red Maple (*Acer rubrum*) thickets, and flooded stands of cypress (*Taxodium* sp.) and Water Tupelo (*Nyssa aquatica*). I studied snakes in a series of artificial ponds (Fig. 1A) created from a single stream, the swamp (Fig. 1B), and a barrow pit (Fig. 1C).

I captured snakes in the springs of 2001–2005 using aquatic minnow traps, hardware cloth funnel traps (Fitch, 1987), metal coverboards, or by hand. Radio transmitters were surgically implanted using the method of Reinert and Cundall (1982). Animals were anesthetized using isoflurane gas that was administered in a clear plastic tube. I used radio transmitter model SB-2 (5.1 g; 10 mo battery life; Holohil Systems Ltd., Carp, Ontario, Canada) or AWE-RS (5.5 g; 10 mo battery life; American Wildlife Enterprises, Monticello, FL). Transmitters weighed from 0.6–3.5% of the snake's mass. Passive integrated transponder (PIT) tags (AVID, Norco, CA) were implanted in the snakes for identification in case of transmitter failure. Snakes were released at their capture site one to three days post surgery.

Snakes were located once each day, five days per week from the release date in the spring until late August. From late August until mid-November animals were located two

[1] Department of Biology, Francis Marion University, Florence, South Carolina 29506; E-mail: jcamper@fmarion.edu.
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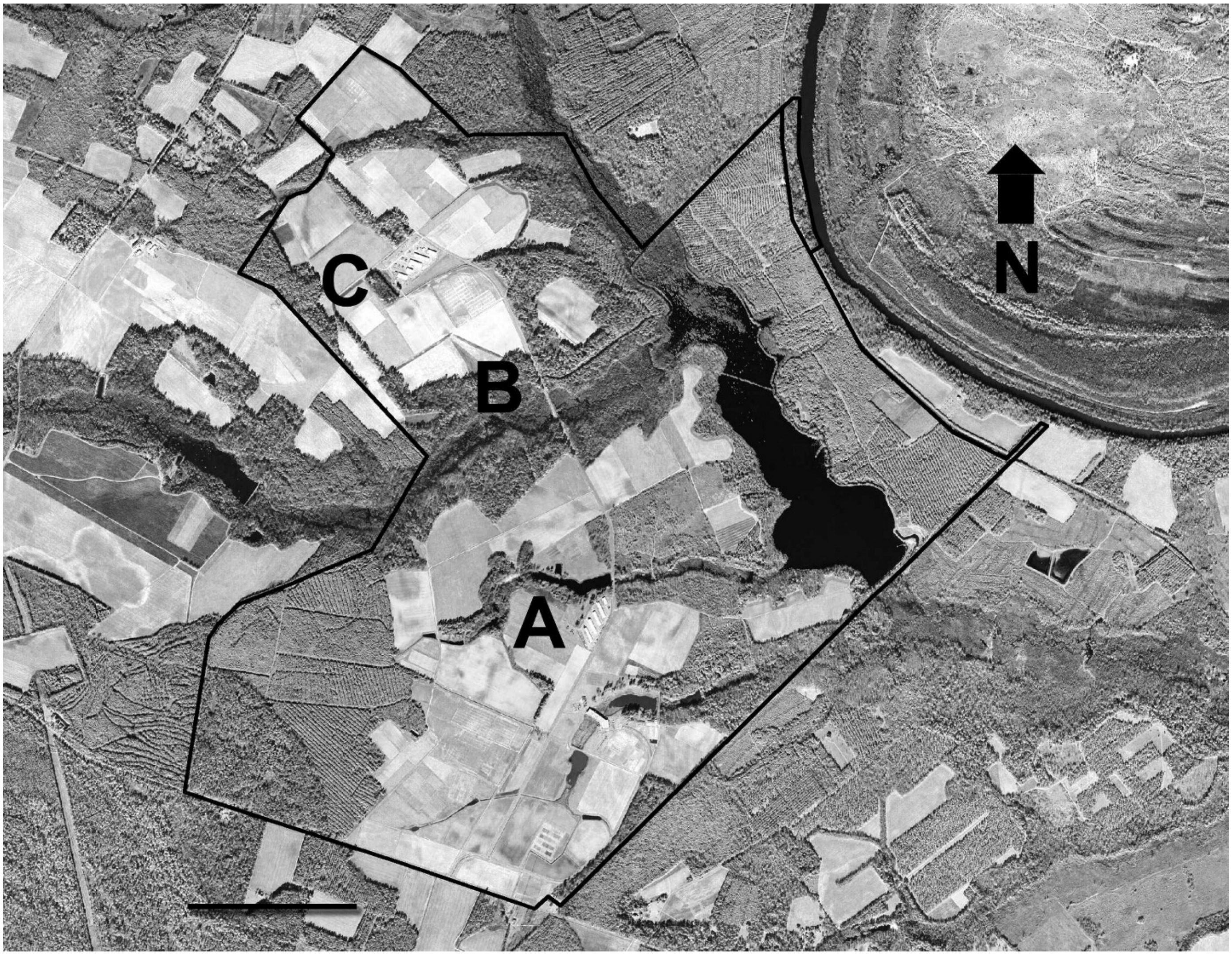

Fig. 1. Pee Dee Research and Education Center, Darlington Co., South Carolina, bordered by the heavy black line. Animals were radio-tracked in three areas. Area A is a sequence of six artificial ponds, area B is the swamp, and area C is a barrow pit. The bar in the lower left-hand corner is 800 m. The lake to the right of A and B is Dargan's Pond, and the Great Pee Dee River borders PDREC on the upper right.

to four times per week as my schedule allowed. Each time a snake was located, its location was marked with flagging tape, and latitude and longitude coordinates (decimal degrees), time, and macrohabitat type were recorded. Snakes were tracked using a Yagi antenna and an R-1000 receiver (Communications Specialists Inc., Orange, CA) during 2001–2003, or a TR-4 receiver (Telonics Inc., Mesa, AZ) during 2004–2005. Global positioning system coordinates were detected with a Garmin GPS III plus (2001–2003) or a Garmin GPS V (2004 and 2005; Garmin International Inc., Olathe, KS). Because visual observations of the snakes were rare, 2.9–26.5% per snake (mean = 8.9; SD = 6.7%, $n = 12$ snakes), few behavioral observations were made.

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, CA). All movement distances and distances from wetlands were measured as straight line distances using ArcView. Movement distances ≤10 m were not included in movement analyses.

Both 95% minimum convex polygon (MCP) and 95% kernel home range analyses were estimated using the animal movement analysis extension of ArcView 3.2 (Hooge and Eichenlaub, 1997). The 5% outliers were removed using the harmonic mean method prior to MCP calculation. Fixed kernel (KHR) estimates, using least squares cross validation as the smoothing parameter, were used because they have been shown to give reliable results (Seaman and Powell, 1996). The 50% KHR estimates were defined as the core area of the home range and were considered areas of intense use (Rodriguez-Robles, 2003). Spatial use estimates based on time series analysis (Reinert, 1992) utilized 95% kernel estimators. Localities were split into approximately monthly intervals for time series analysis.

Six terrestrial macrohabitats were recognized on PDREC and included bottomland deciduous forest that were dominated by Sweetgum (*Liquidamber styraciflua*), oaks (*Quercus* sp.), and Tulip Poplar (*Liriodendron tulipifera*). Five upland macrohabitats included pine forest, SMHF, pine plantations, old fields, and agricultural fields. Pine forest was defined as forest dominated by Loblolly Pine (*Pinus taeda*) that received periodic winter burns, whereas SMHF was not burned and therefore was characterized by a mixture of Loblolly pine, Sweetgum, and several oak species. All aquatic habitats (ponds and the swamp) were lumped together for habitat analyses.

Table 1. Spatial Use Estimates for Redbelly Water Snakes (7 F, 5 M) in the Upper Coastal Plain of South Carolina Studied from 2001–2005. Time series analysis (TSA) was based on 95% fixed kernels. Core areas are 50% kernel home ranges. Ranges appear under mean ± 1 SD. Seasonal analyses used two-sample *t*-test with 16 degrees of freedom for both.

Estimate	95% MCP (ha)	Range length (m)	95% KHR (ha)	Core area (ha)	Percent of total used as core area	Time series analysis (ha)
Total	15.70 ± 13.69 0.78–45.03	585.25 ± 257.39 176–999	32.52 ± 27.14 3.24–102.41	8.38 ± 8.31 1.01–31.18	25.20 ± 5.64 12.75–31.96	11.13 ± 9.82 0.4–34.48
Summer	9.34 ± 9.10 0.90–27.28	462.56 ± 264.21 159–893	—	—	—	—
Fall	6.61 ± 6.10 0.67–18.82 $P = 0.466$	493.78 ± 273.91 161–893 $P = 0.809$	—	—	—	—

Data were tested for normality using the Shapiro and 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. Non-parametric tests were used when transformed data did not conform to the assumptions of normality and homoscedasticity. Statistical testing used SPSS 10 (SPSS Inc., Chicago, IL) and GraphPad Prism 4 (GraphPad Software, Inc., La Jolla, CA).

Tests for seasonal differences compared only summer (June–August) to fall (September–November) because there were too few data for spring and the snakes rarely moved during winter. Seasonal comparisons used paired-sample *t*-test if the variables were correlated, two-sample *t*-test if they were not correlated, or the Wilcoxon paired-sample test (Zar, 1984). No significant differences were found between the sexes in any estimate tested, so they were combined for all analyses. The Spearman ρ statistic was used for correlation analysis. Analyses of habitat use employed the *G* goodness of fit test with Williams correction for a two-cell case (Sokal and Rolf, 1981). Expected habitat locations were calculated as the product of the proportion of a given habitat in the MCP multiplied by the total number of locations for the snake. Observed and expected numbers were summed over all snakes for each habitat.

RESULTS

Eight male and eight female *Nerodia erythrogaster* had transmitters implanted in them during this study. Due to snakes passing transmitters (Pearson and Shine, 2002), predation, and the fact that four animals were tracked for two years each, 16 ''snake years'' worth of data were generated. Data from each year for the snakes that were tracked for two years (two males, two females) were analyzed separately and only one year's data were used in the final analyses. Therefore, sample size was 12 (seven females, five males) for analyses. Snakes were relocated an average 79.1 (SD = 18.7; range 42–109) times per active season.

No significant seasonal differences were found in any home range estimates (Table 1). Only nine snakes were used in seasonal analyses due to transmitter failure during autumn. Kernel home range estimates were significantly larger than 95% MCPs (Wilcoxon paired-sample test, $W = -64$, $n = 12$, $P = 0.009$) and time series analysis estimates (Wilcoxon paired-sample test, $W = 76$, $n = 12$, $P = 0.001$). Time series analysis estimates were not significantly different from either 95% MCPs ($t = 1.129$, df = 11, $P = 0.283$) or core areas (50% kernels; $t = 0.44$, df = 22, $P = 0.664$). Two snakes (1 F 9.49 ha core, 1 M 1.77 ha core) had core areas split into two areas, and one female had her 11.82 ha core area split into three separate parts. Core areas averaged 25.20 (SD = 5.64%; range 12.75–31.96%) of the total home range (Table 1). Minimum convex polygon home range estimates can be influenced by the number of localities (White and Garrott, 1990). The number of locations was not correlated with MCP size (Spearman's $\rho = 0.529$, $P = 0.077$).

Nerodia e. erythrogaster used terrestrial habitat frequently with a mean of 63.66 (SD = 27.67%; range 6.0–100%) of relocations more than 10 m from wetlands. One male was always located in terrestrial habitat because he spent much of his time in a ditch that was usually dry, and ditches were not considered natural wetlands in this study. Seasonal differences in the amount of terrestrial activity were not significant (summer: mean = 65.25; SD = 30.78%; range 0–100%; fall mean = 57.33; SD = 28.97%; range 10.3–100%; paired-sample *t*-test, $t = 1.153$, df = 9, $P = 0.279$, $n = 10$ snakes). Although most terrestrial localities were less than 150 m from wetlands there were 32 observations of snakes farther than 300 m from wetlands (Fig. 2). Snakes were located a mean distance of 97.7 m (SD = 57.6; range 24.3–229.2 m) from wetlands. The mean maximum distance from wetlands was 252.3 m (SD = 120.0 m). Maximum distances that snakes moved from wetlands ranged from 52 to 386 m. A distance of 344 m from the wetland boundary is required to encompass 95% of the terrestrial locations used by snakes during this study. Most terrestrial movements were of a relatively short duration of five days or less (Fig. 3). Snakes spent an average of 10.49 days (SD = 7.81; range 2.67–23.0 days) in terrestrial habitats each time they left a wetland. The mean maximum time spent out of wetlands was 20.33 days (SD = 12.48; 5.0–42.0 days). A positive correlation was found between SVL and the maximum time spent out of wetlands ($r^2 = 0.549$, $P = 0.028$).

Snakes used all seven macrohabitats present at PDREC. Wetlands (ponds and the swamp) were used most frequently. However, only wetlands and SMHF were used more than was expected (Table 2). Agricultural fields were the only habitat used significantly less than expected. Even though *N. erythrogaster* used pine forests more than deciduous forests they had to cross 15–150 m of the latter to get to upland pine habitats. There was a significant positive correlation between MCP size and amount of agricultural field within the MCP ($r^2 = 0.725$, $P = 0.008$). Snakes did not

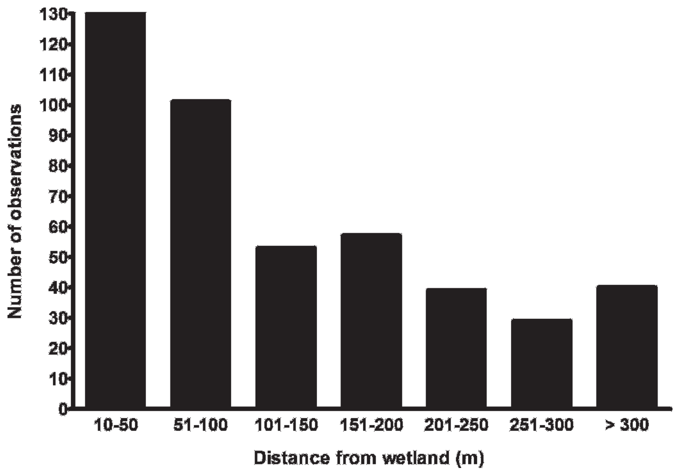

Fig. 2. Frequency distribution of the distances (m) of terrestrial locations for 12 *Nerodia e. erythrogaster* at PDREC in the upper coastal plain of South Carolina. Only distances of 10 m or more from the wetland edge were considered terrestrial ($n = 325$ observations). Drainage ditches were not considered wetlands; therefore, locations in ditches were considered terrestrial and are included in this data set.

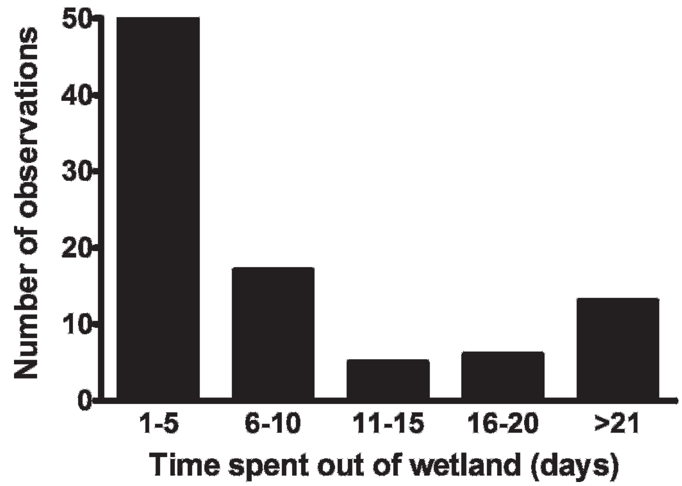

Fig. 3. Frequency distribution of the number of consecutive days spent out of wetlands for 12 *Nerodia e. erythrogaster* at PDREC in the upper coastal plain of South Carolina from 2001–2005 ($n = 70$ observations).

use habitats in different proportions during summer and fall (paired t-test, $t = 0.145$, df = 48, $P = 0.885$).

Total distance moved was significantly greater in summer (Table 3), but no other seasonal differences in movement estimates were found. The number of relocations for each snake was not correlated with the total distance moved by each snake ($r^2 = 0.546$, $P = 0.066$). Most snakes moved frequently with a mean of 57.50% (SD = 14.36; range 35–79%) new locations. Snakes moved on average every 1.62 days (SD = 0.44; range 1.16–2.78 days). Snakes did not move significantly less frequently during fall (mean between moves 1.80; SD = 0.52; range 1.29–2.77) than in summer (mean between moves 1.70; SD = 0.49; range 1.16–2.78; paired t-test, $t = 0.929$, df = 8, $P = 0.380$).

Table 2. Habitat Selection Data for 12 Redbelly Watersnakes (7 F, 5 M) at PDREC in the Upper Coastal Plain of South Carolina. Last column is the G statistic. Expected habitat locations were calculated as the product of the proportion of a given habitat in the 100% MCP multiplied by the total number of locations for a particular snake and summed over all snakes.

Habitat	Observed number of locations	Expected number of locations	G
Wetland	274	146	39.60**
Pine forest	108	128	1.69
Deciduous forest	77	86	0.48
SMHF	115	79	6.61*
Pine plantation	25	13	3.45
Old field	9	16	2.06
Agricultural field	13	153	134.42**

* significant at $P < 0.05$
** significant at $P < 0.01$

DISCUSSION

Like *N. e. neglecta* (Roe et al., 2004), *N. e. erythrogaster* are more similar in their spatial ecology to large terrestrial colubrids than to other *Nerodia*. Home range sizes reported here and in Roe et al. (2004) were larger than spatial use estimates recorded for *Nerodia sipedon* (Roe et al., 2004; Roth and Greene, 2006) and sympatric *Nerodia fasciata* (J. Camper, pers. obs.). Home range sizes found here were similar to the terrestrial colubrids *Coluber constrictor* (Plummer and Congdon, 1994; Fleet et al., 2009), *Elaphe obsoleta* (Weatherhead and Hoysak, 1989; Durner and Gates, 1993), and *Masticophis flagellum* (Dodd and Barichivich, 2007). Although MCP home range estimates from this study are similar to those found by Roe et al. (2004), the core areas found in this study were an order of magnitude larger (Table 1). They made up 25% of the total home range whereas core areas were only 13% for *N. e. neglecta* home ranges (Roe et al., 2004). Plummer and Congdon (1994) and Fleet et al. (2009) argued that home range size in snakes should be affected by the quality of foraging habitat and the size of the animal. I believe that the study site of Roe et al. (2004), with numerous closely spaced ephemeral wetlands, represents better foraging habitat than is present outside of permanent wetlands at PDREC where no ephemeral wetlands exist. Thus, *N. erythrogaster* at PDREC may need to move greater distances to acquire enough resources.

Movement of *N. e. erythrogaster* is also more similar to large terrestrial colubrids than to other natricine snakes. Movement rates reported here are greater than for western populations of *Coluber constrictor* (Fitch, 1963; Brown and Parker, 1976), and comparable to *Elaphe obsoleta* in Maryland (Durner and Gates, 1993). Movement rate and distances reported here for *N. erythrogaster* are higher than for *Nerodia sipedon* (Roe et al., 2004; Roth and Greene, 2006) and *Nerodia fasciata* (J. Camper, pers. obs.). Movement rate and total distance moved were greater for females in this study compared to female *N. e. neglecta* (Roe et al., 2004), but movement parameters were comparable among males. This discrepancy may reflect the fact that male movements are influenced more by mate searching (Madsen et al., 1993; Brown and Weatherhead, 1999), whereas non-reproductive female movements may be more affected by foraging. If the study site of Roe et al. (2004)

Table 3. Movement Statistics for 12 Redbelly Watersnakes (7 F, 5 M) at PDREC in the Upper Coastal Plain of South Carolina. Means ± 1 SD are presented with ranges underneath. Seasonal analysis of mean and maximum distance per move used the paired *t*-test. All others used the two-sample *t*-test.

	Mean distance/move (m)	Movement rate (m/day)	Maximum distance/move (m)	Total distance moved/year (m)
Summer	92.20 ± 43.17 48.54–164.32	53.21 ± 29.51 25.33–103.65	285.11 ± 136.50 128–484	2976 ± 1196* 1090–4854
Fall	103.59 ± 84.31 36.74–318.83 $P = 0.57$	63.32 ± 46.34 19.86–166.35 $P = 0.59$	330.44 ± 220.20 109–844 $P = 0.35$	1677 ± 967 725–3826 $P = 0.02$
Total	95.01 ± 43.52 48.54–205.11	57.42 ± 24.38 21.76–98.19	371.00 ± 186.24 128–844	4636 ± 2450 1893–9230

* Significant at $\alpha = 0.05$, two-sample $t = 2.54$, df = 16.

is more productive, and if population densities are similar between the two sites, then male movement patterns should not differ between the two sites because there should be similar densities of females. However, female movement patterns could differ between the sites if prey is more patchily distributed at PDREC. This assumes that movement patterns of non-gravid and postpartum females are influenced more by foraging than by reproductive activities (King and Duvall, 1990; Charland and Gregory, 1995).

Unlike northern populations of *N. e. neglecta* (Roe et al., 2003), *N. e. erythrogaster* did not appear to use uplands for travel among isolated temporary wetlands. In their extensive use of upland habitats, *N. e. erythrogaster* is more similar to northern populations of *N. e. neglecta* than to southern populations of this taxon (Roe et al., 2003). The differences in upland use patterns between populations of *N. erythrogaster* shows the importance of examining the ecology of more than one population of widespread species before conservation recommendations can by made with any confidence.

The reason for the extensive terrestrial habitat use by *N. e. erythrogaster* is unclear. Many life history attributes could explain extended use of terrestrial habitats by *N. e. erythrogaster*. The extensive nature of terrestrial activity by most of the animals in this study precludes these movements as merely random forays or migrations between wetlands. Movements between wetlands were observed for only two snakes during this study. One male moved 404 m from the swamp (Fig. 1A) south across agricultural fields to the ponds (Fig. 1B), and then back to the swamp again. One female moved 825 m south from the barrow pit (Fig. 1C) across agricultural fields to deciduous forest on the north side of the swamp (Fig. 1B) to overwinter, and returned to the barrow pit the following spring. Therefore, the rather extensive use of terrestrial habitats does not seem to be associated with wetland shifts and must allow the snakes to fulfill some other necessary life history requirements such as resource acquisition, thermoregulation, reproduction, or predator avoidance. *Nerodia erythrogaster* feed mainly upon anurans (Mushinsky and Hebrard, 1977; Kofron, 1978; Roe et al., 2004). Although the terrestrial anuran *Bufo terrestris* seems fairly abundant at PDREC and is eaten by *N. erythrogaster* there (Brown, 1979; J. Camper, pers. obs.;), anuran biomass is higher in deciduous forests (Bennett et al., 1980) and wetlands (Roe et al., 2004; Gibbons et al., 2006) than in drier pine forests. Terrestrial habitat use for reproductive purposes seems unlikely because mating takes place in the spring (Diener, 1957; Preston, 1970; Parker, 2003). Spring mating probably occurs in this population because two males from PDREC contained sperm in their cloacae in May and early June (J. Camper, pers. obs.). Although I never witnessed snakes mating during this study, the limited amount of spring data that I was able to record indicated that females remained in and around wetlands until the onset of warmer temperatures in early June, which indicates that mating probably occurs in or close to the wetlands. Males used terrestrial habitat as much as females and neonates have only been found along wetlands at PDREC (J. Camper, pers. obs.). Therefore, females do not appear to be using terrestrial habitats for parturition. If leaving wetlands was an effective way to escape predation, then other species of sympatric aquatic snakes would probably be more terrestrial as well. However, there is little evidence of extensive terrestrial habitat use by other *Nerodia*, *Regina*, or *Agkistrodon piscivorus* (Tiebout and Cary, 1987; Keck, 1998; Brown and Weatherhead, 1999; Roe et al., 2003). Data on *Nerodia fasciata* at PDREC showed that they rarely left the ponds they inhabited (J. Camper, pers. obs.). Thermoregulation by filtering cover (Slip and Shine, 1988) may be ideal in the relatively sparse canopy of pine forest that these snakes used. Fewer observations were made in more closed canopy deciduous forest. In fact, snakes needed to move through several meters of deciduous forest to get to pine forest when leaving the swamp. Relatively open pine forest was the native vegetation type found in the southeastern coastal plain prior to European invasion (Ware et al., 1993), and may provide good filtering cover for thermoregulation (Slip and Shine, 1988).

The 344 m needed to include 95% of terrestrial locations in this study is greater than the 289 m that Semlitsch and Bodie (2003) suggest for other amphibian and reptile species. However, with the addition of the 50 m buffer zone that they advocate, the distance increases to 339 m, which is very close to what was found here; therefore, the recommendations of Semlitsch and Bodie (2003) are applicable to this population of *N. e. erythrogaster* as well. The main differences between this study and the results of Keck (1998) and Roe et al. (2003, 2004) were that the snakes in this population made few inter-wetland movements and did not use ephemeral wetlands even though they still spent a considerable amount of time in upland forest habitat far from any wetland. *Nerodia e. neglecta* used only 125 m of terrestrial habitat and was found to frequently forage in ephemeral wetlands (Roe et al., 2003, 2004). I believe that this difference reflects the different distribution of wetlands in the two study sites. Their study site included numerous ephemeral wetlands that were relatively close together, whereas PDREC contains almost no ephemeral wetlands (J. Camper, pers. obs.). Some snakes at PDREC used ditches that sometimes contained water and anurans, but many snakes spent long periods in forested habitats away from any water. This study and the work of Roe et al. (2003, 2004) emphasize the need for comparative ecological studies on several populations of widespread species like *N. erythrogaster* before conservation recommendations can be made with any confidence.

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