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Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources

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Abstract

Obtaining information on movement and spatial patterns of animals and understanding the factors that shape their movements about the landscape are critical steps in designing conservation strategies. We conducted a comparative radiotelemetry study of two snake species, the northern water snake, *Nerodia sipedon sipedon*, and the imperiled copperbelly water snake, *Nerodia erythrogaster neglecta*, in northwest Ohio and southern Michigan to assess differences in movement patterns, spatial ecology, and resource use. *N. e. neglecta* moved distances (53.3 ± 7.1 m/day and 4809 ± 603 m/year) over twice as far as *N. s. sipedon* (25.6 ± 2.7 m/day and 2244 ± 228 m/year), and used areas nearly four times larger (15.8 ± 2.7 ha) than *N. s. sipedon* (4.0 ± 0.9 ha). When wetlands were widely dispersed in the landscape, *N. e. neglecta* moved longer distances and used larger areas, whereas spatial and movement patterns in *N. s. sipedon* were unaffected by wetland spatial distribution. *N. e. neglecta*'s long movements and large area use are likely related to its use of variable resources such as ephemeral wetlands and anuran prey. *N. s. sipedon* used more permanent wetlands and preyed more generally on fish and anurans. Habitat alterations that change the spatial distribution of wetlands in the landscape, such as the loss of small isolated wetlands, have likely increased energetic costs and mortality rates for *N. e. neglecta*. Conservation strategies for vagile wetland animals that use spatially and temporally variable resources over broad spatial scales should focus on protecting and restoring large areas with numerous, heterogeneous wetlands.

Keywords: Conservation; Diet; Management; *Nerodia erythrogaster neglecta*; *Nerodia sipedon sipedon*; Radiotelemetry; Spatial ecology

1. Introduction

Determining the ultimate causes of a species' decline is rarely straightforward. For instance, species declines are often generally attributed to habitat modifications, yet seemingly similar species continue to persist or increase in numbers in the same area (Shine and Fitzgerald, 1996). Identifying particular aspects of a species' ecology that make it susceptible to habitat loss and fragmentation is a critical step in designing conservation strategies. However, this basic biological information upon which conservation decisions should be based is lacking for many imperiled species, especially for under-studied taxa such as reptiles (Buhlmann and Gibbons, 2001; Gibbons et al., 2000).

Wetlands have been lost at astounding rates in the United States (Dahl, 1990). Numerous reptiles that use wetlands have declined as well (Gibbons et al., 2000), including the copperbelly water snake, *Nerodia erythrogaster neglecta*, a subspecies of the plainbelly water snake. The northernmost populations of *N. e. neglecta* are listed as endangered by Ohio, Michigan and Indiana and federally threatened by the United States Fish and Wildlife Service (Pruitt and Szymanski, 1997). Despite *N. e. neglecta* declines, the northern water snake, *Nerodia sipedon sipedon*, a sympatric congener, remains common.

Nerodia erythrogaster neglecta and *N. s. sipedon* differ in some aspects wetland use. *N. e. neglecta* from the northernmost populations regularly use numerous, widely dispersed wetlands and move frequently among these wetlands, whereas *N. s. sipedon* move infrequently

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among fewer wetlands (Roe, 2002). If these observed patterns of wetland use by *N. e. neglecta* are requisite for maintaining healthy populations, *N. e. neglecta* may be more sensitive to the loss of wetlands than typically less vagile species such as *N. s. sipedon*. However, why these species use the landscape differently has not been determined.

Numerous factors may influence how animals use the landscape. The spatial and temporal distribution of critical resources in the landscape influence patterns of movement and space use in many animals, including snakes (Gregory et al., 1987). For example, when resources such as hibernacula and foraging sites are widely dispersed, snakes must move long distances between them (King and Duvall, 1990). The distributional patterns of preferred prey also influence movement patterns and spatial ecology (Huey and Pianka, 1981; King and Duvall, 1990; Schoener, 1971). Also, using resources that vary unpredictably may require individuals to be vagile and use large areas, while use of more predictable, permanent resources may allow individuals to be more sedentary and to use smaller areas (Guibé and Saint Girons, 1955; Schoener, 1971; Huey and Pianka, 1981).

We conducted a comparative radiotelemetry study to identify factors responsible for *N. e. neglecta* population declines by examining how it differs from *N. s. sipedon*, which remains abundant despite many changes to the landscape in the midwestern United States. The syntopic occurrence of these closely related, wetland-obligate species allows a unique opportunity to assess ecological differences while limiting potentially confounding phylogenetic and environmental factors. We assess between-species differences in space use and movement patterns, and whether the spatial distribution of wetlands in the landscape influences movement and space use patterns of either species. We also assess differences in resource use (prey, wetland types), as well as spatial and temporal variation in these resources in the landscape to gain additional insight into what factors shape each species' use of the landscape. Knowledge of factors shaping patterns of movement and space use in these species can help us interpret the consequences of past, present, and future land use practices. Understanding the causes of *N. e. neglecta*'s decline may help in the development of conservation strategies for not only *N. e. neglecta*, but for wetland communities in general.

2. Methods

2.1. Study site and mapping

The study site is located in northwesternmost Ohio and southern Michigan in an area harboring one of the last known large populations of *N. e. neglecta* in the northern part of its range (B. Kingsbury, unpublished data). The site consists of a stream and numerous forested, shrub–scrub and open aquatic habitats within an upland matrix of hardwood forest, old field, shrub–scrub, and agricultural habitats (Fig. 1). The dimensions of our study site (723 ha) were determined by drawing a rectangle with east–west and north–south running sides around the outermost relocations of the radiotracked snakes.

Maps describing the distribution of habitats in the study area were digitized from aerial photographs (digital orthophoto quarter-quadrangle images) and ground-truthing. Wetlands were categorized as lacustrine, palustrine, or riverine based on descriptions in Cowardin et al. (1979). We defined the wetland edge as the place demarking a change from a temporarily flooded drying regime to upland habitat (Cowardin et al., 1979). Wetlands that completely dried at any time were classified as ephemeral, and those that held water continually were classified as permanent.

2.2. Capture and implantation

Twenty-eight snakes (15 *N. e. neglecta*, 13 *N. s. sipedon*) were captured in spring of 2001 and 2002. Snakes were captured in pairs (one of each species) from the same wetland. Snakes were implanted with hermetically sealed radiotransmitters (5.1–13.0 g, $0.9 \times 3 - 1 \times 5$ cm, 20 cm whip antenna, Holohil Systems, Ltd.) using a technique modified from Reinert and Cundall (1982) and Weatherhead and Anderka (1984). Snakes were anesthesized with vaporized isoflurane before being surgically implanted with transmitters roughly two-thirds of the way down the body from the head. Transmitters were placed in the intraperitoneal cavity, with the antenna running subcutaneously from the transmitter towards the head. The initial snout–vent length (SVL) and mass of seven female *N. e. neglecta* was 81.1 ± 6.3 cm and 372.6 ± 77.1 g, and for eight males it was 75.5 ± 2.4 cm and 261.3 ± 21.7 g. For *N. s. sipedon*, initial SVL and mass of nine females was 66.7 ± 2.8 cm and 232.8 ± 29.9 g, and for four males it was 53.3 ± 1.7 cm and 95.5 ± 2.9 g. Transmitters ranged from 1.3% to 5.8% (3.7 ± 0.2%) of the snake's body mass. Snakes were held for 5–7 days for recovery before being released at their point of capture.

2.3. Radiotracking data collection and handling

During 2001 and 2002, snakes were located 6–7 days a week from late April to August 15, and 1–2 times per week following this period until they entered hibernacula in September–November. At each location, the coordinate position was determined using hand-held GPS units (GPS III Plus, Garmin Corp., Olathe, Kansas) or by calculation based on distance and bearing measurements from known location points. Coordinate positions collected by GPS units had an error of 1–7 m. The coordinates of each snake's location were plotted on the habitat maps using ArcView GIS (ESRI Inc., 1992).

Movement distances were estimated as the minimum straight-line distance between sequential locations. During the period of frequent radiotracking (late April–August 15), we report distance moved per day and the total (cumulative) distance moved for each snake. Minimum convex polygon (MCP) and kernel density techniques were used to estimate the size of total and activity center area use for each snake over a defined time period of one year. This began with emergence from hibernation or initial capture in the spring, and ended when the snake entered a hibernaculum in the fall, or upon the final location for a snake that could not be tracked to a hibernaculum (e.g., mortality, transmitter failure). We included all recorded locations for each individual, including one location each for initial capture and hibernation sites in the analysis. Because both species tend to hibernate in close proximity to one another and within the area used during the active season (i.e., they do not migrate to distant hibernacula; Roe, 2002), including hibernation sites in area use estimates would not influence potential between-species differences in area use. For kernel density analysis, we employed the fixed kernel method and the least squares cross validation method to select a bandwidth for the smoothing parameter, *h*. We used the 95% and 50% isopleths to estimate size of total and activity center area use, respectively (e.g., Secor, 1994; Tiebout and Cary, 1987). Estimations of area usage and movement distances were performed with the Animal Movements extension for ArcView GIS.

For each snake, the number of movements to ephemeral wetlands was determined. A movement to an ephemeral wetland was defined as any between-wetland movement where the destination was an ephemeral wetland. The spatial distribution of wetlands used by each snake was calculated as the mean minimum straight-line distance between the edge of each wetland and the nearest edge of all other wetlands used by the snake. Between-wetland distances were calculated using the Nearest Neighbor extension for Arc View GIS.

2.4. Diet and prey availability and abundance

Non-radiotagged snakes were captured opportunistically, and prey items were identified after regurgitation. Observations of radiotagged snakes during foraging encounters were also recorded. Prey items were identified to the species level when possible, and prey recovered from palpated snakes were frozen and stored at The Center for Reptile and Amphibian Conservation at Indiana-Purdue University at Fort Wayne.

To assess prey abundance in wetlands, 12 wetlands were sampled from May–August using minnow traps (2.5 cm openings, 0.3 cm mesh). Between six and nine traps were placed near structures (e.g., logs, herbaceous and woody emergent vegetation) in shallow water (10–20 cm). The number of traps used in each wetland depended on the size of the wetland (e.g., more traps were placed in larger wetlands). Traps were set for 48 hours and checked at 24-hour intervals. We report the number of individuals captured per trap per day as an index of each prey type's relative abundance.

2.5. Statistical analyses

Statistical analyses were performed with SPSS Version 10.0 (SPSS, 1999). In all cases, we examined the assumptions of homogeneity of variances and normality; when data failed to meet these assumptions, transformations were performed to better approximate normal distributions or equal variances. Nonparametric tests were used when transformed data deviated significantly from normality or equality of variances. Statistical significance was accepted at the $\alpha = 0.05$ level except where stated otherwise, and means presented ± one standard error (SE).

Six of each species (2 female and 4 male *N. e. neglecta*, 6 female *N. s. sipedon*) were radiotracked for both years. Because spatial and movement variables were calculated based on one-year monitoring periods, two sets of variables were calculated for these 12 snakes. Two repeated measures MANOVAs were used to assess whether snakes exhibited differences in spatial or movement patterns between years, and a Wilcoxon matched-pairs signed-rank test was used to examine yearly differences in movements to ephemeral wetlands. Daily and total movement distances were defined as dependent variables in the first MANOVA, and all four area use estimates were the dependent variables in the second MANOVA. Both MANOVAs used year and year × species as within-subjects factors, and species as the between-subjects factor. If no differences between years were detected, one year's data for those snakes tracked for both years was randomly chosen to include in further analyses investigating between-sex and between-species differences to avoid complications associated with the pseudoreplication (non-independence) of data.

Daily and total movement distances and all area use estimates were logarithmically transformed prior to analyses. Differences between species and sex (independent variables) in daily and total distance moved (dependent variables) were examined using MANOVA. To examine differences in the frequency with which individuals moved 0–20, 21–40, 41–60, 61–80, 81–100, and 101 m or more, we used MANOVA on arcsin-transformed proportions, with species and sex as independent variables, and the proportions of movements within distance categories as dependent variables. Differences between species and sex in the number of shifts to ephemeral wetlands were examined using a Kruskal–Wallis test. All area use estimates (dependent variables) were tested for differences between sex and species (independent variables) using a MANOVA. Because variation among individuals in the number of locations obtained may potentially contribute to variability in estimates of space use and movement, we regressed the number of locations on the daily distance moved, the total distance moved, and all estimates of area usage to assess possible correlations.

To investigate factors influencing within-species variation in area use and movement patterns, we used regression analysis. We assessed how three independent variables (mean between-wetland distance of wetlands used by an individual, number of locations, and length [SVL]) influenced estimates of space use and movement (dependent variables) for individuals of both species. Multiple linear and quadratic regression models that included all independent variables were initially used to determine which factors significantly contributed to variation in the spatial and movement patterns. We dropped all terms with a P value above 0.10, then used multiple or simple regression models to re-assess relationships between the dependent and the remaining independent variables at the $\alpha = 0.05$ level. When multiple models explained a significant amount of the variance, we report the statistics for the model that explained the greatest portion of the variance. We used GraphPad Prism software, version 3.03 (2002), for non-linear regression, and SPSS (1999) for linear regression.

3. Results

3.1. Between-year differences

Based on the 12 individuals tracked during both years, neither species exhibited different patterns of movement or area use between years (MANOVA, movement, year: Wilk's $\Lambda = 0.58$, $F_{2,9} = 3.32$, $P = 0.083$; year × species: Wilk's $\Lambda = 0.95$, $F_{2,9} = 0.25$, $P = 0.785$, species: Wilk's $\Lambda = 0.25$, $F_{2,9} = 13.49$, $P = 0.002$; area use, year: Wilk's $\Lambda = 0.42$, $F_{3,8} = 3.75$, $P = 0.060$; year × species: Wilk's $\Lambda = 0.717$, $F_{3,8} = 1.06$, $P = 0.420$, species: Wilk's $\Lambda = 0.38$, $F_{3,8} = 4.29$, $P = 0.044$). The number of movements to ephemeral wetlands was similar in both years for each species (*N. e. neglecta*: Wilcoxon $Z = -0.37$, $P = 0.715$, *N. s. sipedon*: Wilcoxon $Z = -0.46$, $P = 0.655$). Pooling of data resulted in relatively equal representation from both years, including 15 snakes (7 *N. e. neglecta*, 8 *N. s. sipedon*) from 2001 and 13 snakes (8 *N. e. neglecta*, 5 *N. s. sipedon*) from 2002.

3.2. Movement patterns and spatial ecology

Nerodia erythrogaster neglecta were located 85.4 ± 3.5 times (range 62–98) over the one year period, and *N. s. sipedon* were located 78.7 ± 4.2 times (range 53–99). No spatial or movement variables were correlated with the number of locations obtained (movement variables: $r^2 < 0.29$, $P > 0.06$; space use variables: $r^2 < 0.21$, $P > 0.29$). Because the number of locations was not correlated with any variable, we included all 28 snakes in analyses.

Nerodia erythrogaster neglecta differed from *N. s. sipedon* in daily and total movement distances. Between-species differences were independent of sex, and no between-sex differences were detected (MANOVA, species: Wilk's $\Lambda = 0.64$, $F_{2,23} = 6.58$, $P = 0.006$; sex: Wilk's $\Lambda = 0.89$, $F_{2,23} = 1.35$, $P = 0.278$; species × sex: Wilk's $\Lambda = 0.98$, $F_{2,23} = 0.22$, $P = 0.808$; Table 1). Individual univariate analyses for both movement variables indicate *N. e. neglecta* moved distances over twice as far as *N. s. sipedon* (ANOVA, daily movement, species: $F_{1,24} = 12.84$, $P = 0.001$, sex: $F_{1,24} = 2.76$, $P = 0.110$, species × sex: $F_{1,24} = 0.03$, $P = 0.862$; total movement, species: $F_{1,24} = 13.44$, $P = 0.001$, sex: $F_{1,24} = 2.04$, $P = 0.167$,

Table 1
Movement and space use patterns in *Nerodia erythrogaster neglecta* and *Nerodia sipedon sipedon*

Species	Movement		Total area usage		Activity center area usage	
	Daily movement (m/day)	Total movement (m)	MCP (ha)	95% Kernel density (ha)	50% Kernel density (ha)	Proportion of total area used as activity center
N. e. neglecta	*	*	*	*		*
F	44.8 (7.1)	4105.8 (773.2)	12.1 (3.3)	9.7 (2.9)	1.1 (0.3)	11.8 (1.0)
M	60.7 (11.7)	5424.3 (897.4)	18.9 (3.9)	16.0 (3.7)	2.2 (0.6)	14.3 (1.7)
All	53.3 (7.1)	4809.0 (604.3)	15.8 (2.7)	13.1 (2.5)	1.7 (0.4)	13.1 (1.0)
N. s. sipedon						
F	22.9 (7.7)	2067.2 (315.5)	3.3 (0.6)	3.1 (0.9)	0.4 (0.1)	15.3 (2.3)
M	31.5 (6.2)	2640.8 (638.0)	5.6 (2.9)	6.9 (3.6)	1.6 (1.0)	20.8 (1.8)
All	25.6 (2.7)	2243.7 (228.3)	4.0 (0.9)	4.3 (1.3)	0.8 (0.3)	17.0 (1.8)

Values are means and (1 SE). Column variables with an asterisk indicate differences between species determined by MANOVA, followed by separate univariate ANOVAs. There were no significant differences between sex or species × sex subgroups. See text for explanation of movement and space use estimation methods.

species × sex: $F_{1,24} = 0.01$, $P = 0.928$; Table 1). The largest differences between species occurred for the shortest and longest movements regardless of sex, with *N. s. sipedon* moving distances less than 20 m more frequently than *N. e. neglecta*, and *N. e. neglecta* moving distances exceeding 100 m more frequently than *N. s. sipedon*, but these differences were only marginally significant (MANOVA, Wilk's $\Lambda = 0.55$, $F_{6,19} = 2.60$, $P = 0.052$; Fig. 2). *N. e. neglecta* moved to ephemeral wetlands 2.1 ± 0.5 times, which was seven times more often than *N. s. sipedon* (0.3 ± 0.2 times; Kruskal–Wallis, $X^2 = 8.80$, df = 1, $P = 0.003$). Moreover, 73% of *N. e. neglecta* and 27% of *N. s. sipedon* used ephemeral wetlands.

Patterns of area use differed between species, but not between sexes (MANOVA, species: Wilk's $\Lambda = 0.54$, $F_{3,22} = 6.29$, $P = 0.003$, sex: Wilk's $\Lambda = 0.76$, $F_{3,22} = 2.37$, $P = 0.098$, species × sex: Wilk's $\Lambda = 0.95$, $F_{3,22} = 0.36$, $P = 0.783$). *N. e. neglecta* used total areas (mean MCP = 15.8 ha, range = 1.1 to 34.4 ha) 3–4 times larger than *N. s. sipedon* (mean = MCP 4.0 ha, range = 1.0 to 14.9 ha; Table 1). *N. s. sipedon* used 3.9% more of their total area as activity centers compared to *N. e. neglecta*, but the size of activity centers did not differ between species (ANOVA, MCP, species: $F_{1,24} = 15.06$, $P = 0.001$, sex: $F_{1,24} = 2.04$, $P = 0.166$, species × sex: $F_{1,24} = 0.23$, $P = 0.637$; 95% kernel density, species: $F_{1,24} = 6.80$, $P = 0.015$, sex: $F_{1,24} = 2.70$, $P = 0.113$, species × sex: $F_{1,24} = 0.02$, $P = 0.899$; 50% kernel density, species: $F_{1,24} = 3.48$, $P = 0.074$, sex: $F_{1,24} = 4.90$, $P = 0.036$, species × sex: $F_{1,24} = 0.02$, $P = 0.896$; proportion of area used as activity center, species: $F_{1,24} = 5.90$, $P = 0.023$, sex: $F_{1,24} = 4.06$, $P = 0.055$, species × sex: $F_{1,24} = 0.77$, $P = 0.389$; Table 1; Fig. 1).

The initial SVL and the spatial distribution of wetlands were significant predictors of space use and movements for *N. e. neglecta*. However, SVL and the spatial distribution of wetlands used were significantly correlated with each other ($r^2 = 0.47$; ANOVA, $F_{2,12} = 5.33$, $P = 0.022$). For snakes between 52 and 83 cm SVL, the larger snakes used more widely dispersed wetlands. However, snakes measuring between 83 and 100 cm showed the opposite trend, with the larger individuals using wetlands that were slightly closer together. The mean distance between wetlands used by *N. e. neglecta* changes with SVL according to the following equation: mean distance between wetlands = $-2613.8 + 71.7 \times \mathrm{SVL} - 0.4(\mathrm{SVL})^2$. Consequently, we ran two separate multiple regression analyses (one using initial SVL, one using wetland distribution) to avoid complications of collinearity of independent variables.

As the mean distance between wetlands in an area increases, *N. e. neglecta* move longer distances and traverse larger areas. Among *N. e. neglecta*, variation in the structure of the surrounding wetland landscape accounted for 32% and 54% of the variance in daily and total movement distances (ANOVA, daily movement:

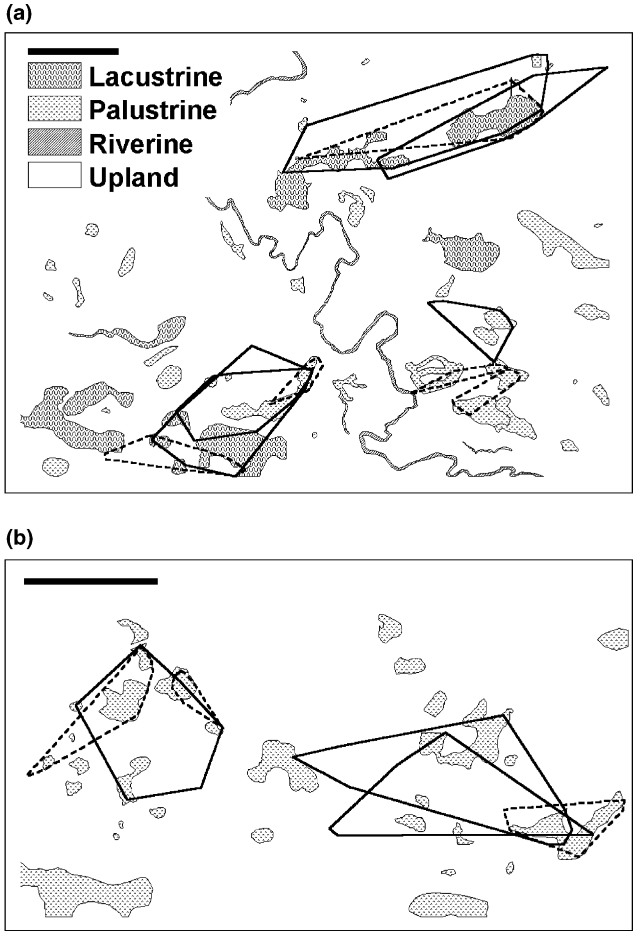

Fig. 1. Habitat composition and area use estimates (minimum convex polygons) for 8 *Nerodia erythrogaster neglecta* (solid lines) and 8 *Nerodia sipedon sipedon* (dashed lines) at the western (a) and eastern (b) study sites. The legend is for both sites, and the scale bar for each site in the upper left corner represents 400 m. See text for descriptions of habitat types.

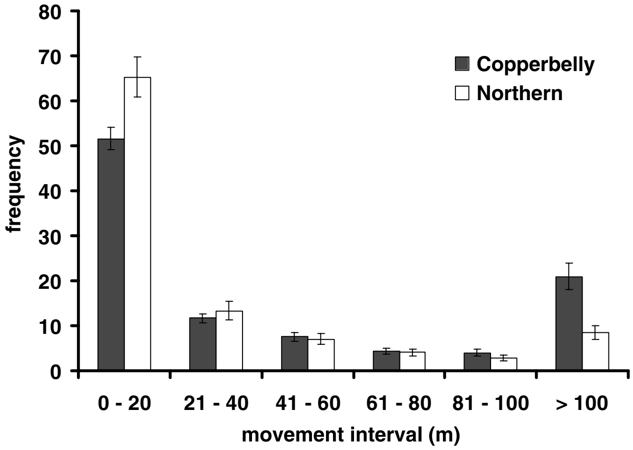

Fig. 2. Frequency distribution of movement distance intervals for copperbelly (*Nerodia erythrogaster neglecta*) and northern (*Nerodia sipedon sipedon*) water snakes. Between species differences in the frequency of movements within intervals were detected only for 0–20 m and >100 m intervals. Differences between species were tested using MANOVA, followed by univariate ANOVAs. Error bars are ±1SE.

$F_{1,13} = 5.98$, $P = 0.029$; total movement: $F_{2,12} = 7.04$, $P = 0.010$; Fig. 3). Variation in between-wetland distances accounted for and 81% and 82% of total area use (ANOVA, MCP: $F_{1,13} = 58.21$, $P < 0.001$; 95% kernel density: $F_{1,13} = 56.57$, $P < 0.001$; Fig. 4). As wetlands become more widely dispersed, *N. e. neglecta* move longer distances and use larger areas according to the following equations: $\log_{10}$ daily movement = 1.509 + 8.1×10^{-4}(wetland distribution); $\log_{10}$ total movement = 3.3 + 2.56×10^{-3}(wetland distribution) − 3.18×10^{-6}(wetland distribution)^2; $\log_{10}$ MCP = 1.389 × (1 − exp(−0.01091 × wetland distribution)); $\log_{10}$ 95% Kernel density = 1.423 × (1 − exp(−0.007632 × wetland distribution)).

Variation in *N. e. neglecta* SVL accounted for 51% and 56% of the variance in daily and total movement distances (ANOVA, daily movement: $F_{2,12} = 6.15$, $P = 0.014$; total movement: $F_{2,12} = 7.77$, $P = 0.007$). Variation in SVL accounted for 84% and 88% of the variance in total area use (ANOVA, MCP area use: $F_{2,12} = 45.50$, $P < 0.001$; 95% kernel density: $F_{2,12} = 30.56$, $P < 0.001$). As initial SVL of *N. e. neglecta* increases from 52 to 83 cm, *N. e. neglecta* increase movement distances and size of area used, but from 83 to 100 cm, movement distances and area use decrease slightly. Movement distances and area use change with initial SVL according to the following equations: $\log_{10}$ daily movement = −1.87 + 8.58×10^{-2}(SVL) − 5.05×10^{-4}(SVL)^2; $\log_{10}$ total movement = −0.76 + 0.11(SVL) − 6.8×10^{-4}(SVL)^2; $\log_{10}$ MCP = −8.52 + 0.24(SVL) − 1.41×10^{-3}(SVL)^2; $\log_{10}$ 95% Kernel density = −10.01 + 0.27(SVL) − 1.63×10^{-3} (SVL)^2. None of the factors were identified as being significant predictors of space use or movement patterns in *N. s. sipedon* ($r^2 < 0.33$, $P > 0.206$ in all cases).

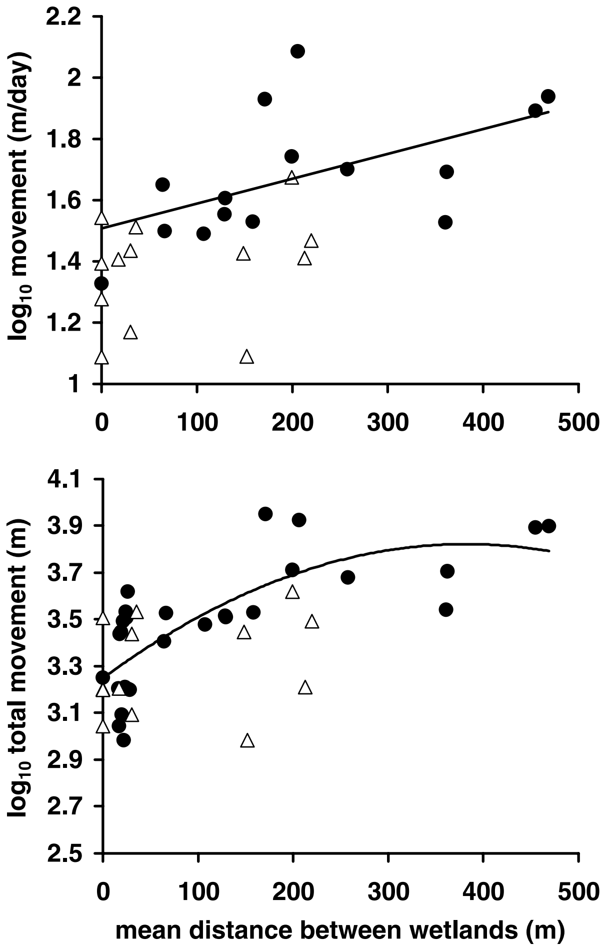

Fig. 3. Relationships between movement variables and the spatial distribution of wetlands for *Nerodia erythrogaster neglecta* (circles and solid lines). Movements for *Nerodia sipedon sipedon* (triangles) were not significantly related to wetland distribution. See text for regression equations and statistics.

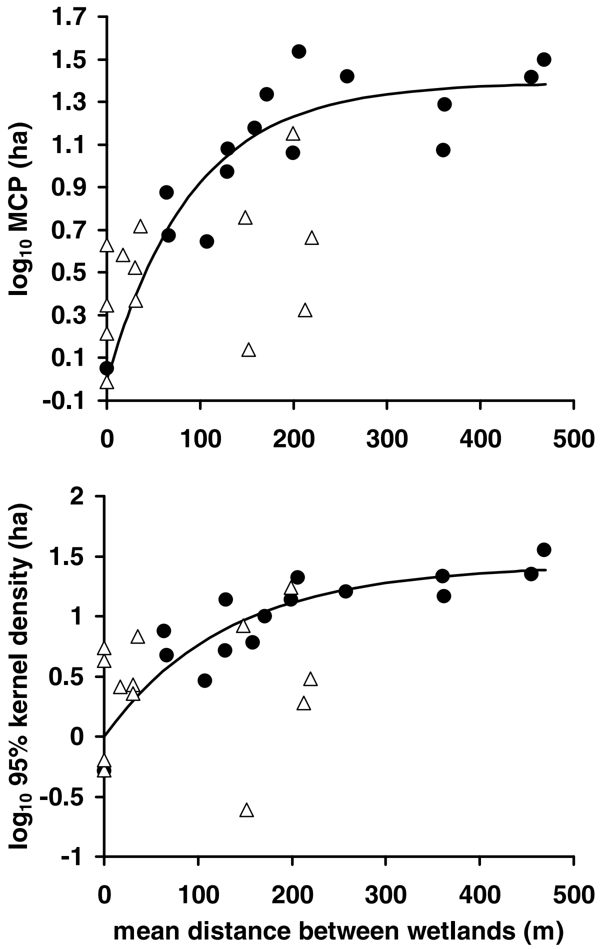

Fig. 4. Relationships between estimates of area use and the spatial distribution of wetlands for *Nerodia erythrogaster neglecta* (circles and solid lines). Area use estimates in *Nerodia sipedon sipedon* (triangles) were not significantly correlated with the spatial distribution of wetlands. See text for regression equations and statistics.

3.3. Diet and prey availability and abundance

Sixty-one prey items were recovered from snakes after regurgitation, and 12 observations of foraging encoun-

Table 2
Prey items for *Nerodia erythrogaster neglecta* and *Nerodia sipedon sipedon*

Prey category	*N. e. neglecta*	*N. s. sipedon*
Anurans		
Bufo americanus	2 (2)	0
Rana catesbeiana	4 (1)	0 (1)
Rana clamitans	5	7
Rana pipiens	0 (1)	1
Rana sylvatica	2 (2)	0
Ranid (species unknown)	10 (3)	11 (1)
Total	23 (9)	19 (2)
Fish		
Cyprinidae	0	5
Ictalurus spp.	0	3 (1)
Lepomis spp.	0	2
Notemigonus crysoleucas	0	1
Umbra limi	0	3
Unidentified	0	4
Total	0	18 (1)
Crayfish	1	0

Number of prey items regurgitated from palpated snakes and (observed foraging encounters). Sizes of snakes ranged from 37.5 to 101.5 snout–vent length (SVL) for *N. e. neglecta*, and 29.5–82.5 SVL for *N. s. sipedon.*

ters were made. Prey species composition of snake diets differed between species (Table 2). Among the 33 prey items for *N. e. neglecta*, 97% were anurans (tadpoles, transformed frogs) and 3% (1 item) were crayfish. Among the 40 prey items for *N. s. sipedon*, 52% were anurans and 48% were fish.

Of the 12 wetlands sampled, we chose to show three ephemeral and three permanent wetlands that exhibited the typical patterns of prey abundance characteristic of these two wetland types on our study site (Fig. 5). Anuran (tadpoles, transformed frogs) relative abundance varied widely between months, fluctuating from periodic high abundance to near or complete absence in all wetlands. The timing of peak anuran abundance varied between wetlands within years, and also within wetlands between years. Anuran abundance was especially variable in ephemeral wetlands, with abundance periodically dropping to zero in each wetland. Fish were usually absent or not abundant in ephemeral wetlands, but fish were present in all permanent wetlands during all months of both years at relatively consistent abundance (1.5–4 fish per trap day).

4. Discussion

4.1. General movement, spatial and resource use patterns

Nerodia erythrogaster neglecta differed distinctly from *N. s. sipedon* in patterns of movement and space use (Table 1, Figs. 1 and 2). Use of relatively large areas and frequent long distance movements for *N. e. neglecta* were consistent with findings from other, more southerly *N. e. neglecta* populations (Coppola, 1999; Hyslop, 2001). Also, the use of relatively small areas and shorter movements observed in *N. s. sipedon* was similar to studies of this species in other parts of its range (Brown and Weatherhead, 2000; Fitch and Shirer, 1971; Tiebout and Cary, 1987), as well as for other species of *Nerodia* (Macartney et al., 1988; Mills et al., 1995; Whiting et al., 1997). *N. e. neglecta* appear to be more vagile and tend to use larger areas than other *Nerodia*.

The divergent diets between sympatric *N. e. neglecta* and *N. s. sipedon* in this study support the contention that prey are one of the most commonly partitioned resources in snake communities (Mushinsky and Hebrard, 1977; Toft, 1985). Diet compositions for *N. e. neglecta* and *N. s. sipedon* in this investigation are similar to those reported for these species in other parts of their wide geographic ranges. Diet for *N. e. neglecta* was similar to more southern populations of *N. erythrogaster*, indicating that this species relies predominantly on anuran prey throughout its range (Deiner, 1957; Brown, 1979; Mushinsky and Hebrard, 1977; Mushinsky, 1987). Diet consisting of both fish and anurans is commonly reported for *N. sipedon* throughout its range, with the relative proportions of fish and anurans included in diet as the primary difference between populations (Brown, 1958, 1979; King, 1986, 1993). In fact, evidence from a population of *Nerodia sipedon insularum* suggests a degree of dietary plasticity as the availability of anurans and fish changes over time (King, 1993). Throughout their respective ranges, as well as at our study site, *N. s. sipedon* appears to be a more opportunistic forager, perhaps eating fish and anurans according to availability, whereas *N. e. neglecta* is a more specialized anuran feeder.

Although ephemeral wetlands were not exclusively used by *N. e. neglecta*, these habitats appear to be an important resource for this species, as well as for other reptiles (Gibbs, 1993; Kennett and Christian, 1994). In fact, other populations of *N. erythrogaster* use ephemeral wetlands more frequently than sympartic species of water snakes, including *N. sipedon* (Conant, 1934; Keck, 1998; Coppola, 1999; Laurent, 2000; Hyslop, 2001). A higher degree of ephemeral wetland use by *N. e. neglecta* may be related to their reliance on anuran prey. Anuran prey are often more abundant in ephemeral wetlands than in permanent wetlands because wetlands that dry often lack fish predators, or only support low numbers of fish (Werner and McPeek, 1994; Snodgrass et al., 2000). Consequently, these wetlands typically have periodic high densities of anurans and may be favorable foraging habitats for anuran feeders at these times.

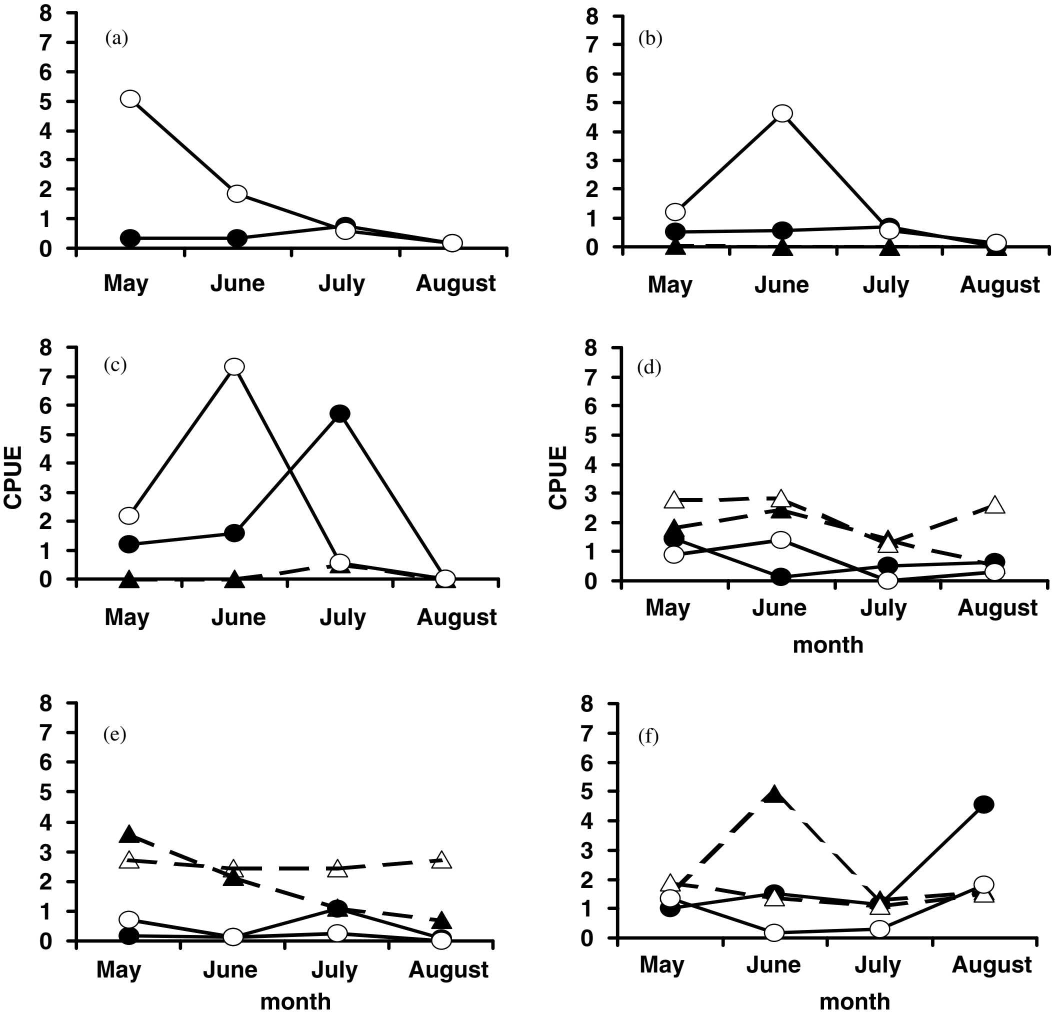

Fig. 5. Relative abundances (CPUE; number of individuals per trap day) of anurans (circles and solid lines) and fish (triangles and dashed lines) in 2001 (open symbols) and 2002 (closed symbols) for six wetlands at the study site. Graphs A, B and C are ephemeral wetlands, and graphs D, E and F are permanent wetlands. Note that anuran abundances fluctuate from temporary high abundance to zero or near-zero in both wetland types and that patterns of abundance are not consistent between years, especially in ephemeral wetlands. Also, while fish relative abundance is low in ephemeral wetlands, fish populations appear to maintain more stable numbers that do not drop to zero in permanent wetlands.

4.2. Factors influencing between-species differences in movement and area use

The use of large areas and frequent long distance movements observed in *N. e. neglecta* are likely a consequence of their frequent movements among numerous, often widely dispersed wetlands (Roe, 2002), but this explanation introduces additional questions concerning why *N. e. neglecta* must move between multiple wetlands. Mate searching is one factor that may cause long movements between numerous wetlands (Morreale et al., 1984; King and Duvall, 1990; Secor, 1994). If different mate seeking strategies influence the divergent movement patterns between *N. e. neglecta* and *N. s. sipedon*, the most pronounced differences in movements among wetlands are expected to coincide with periods of mating behavior. Mating was observed on site from late April through early June, peaking in May for both species, but *N. e. neglecta* continue to move between wetlands equally from May to July, and considerably more often than *N. s. sipedon* during these months (Roe, 2002). Thus, different mate searching strategies between *N. e. neglecta* and *N. s. sipedon* are likely not responsible for their different patterns of movement, space use, and wetland use.

Another factor that may contribute to movement and space use differences between species is *N. e. neglecta*'s more frequent use of ephemeral wetlands. Drying wetlands are challenging environments for wetland-associated species due to declining prey availability, heat or water stress, and exposure to predators (Gibbons et al., 1983; Seigel et al., 1995; Buhlmann and Gibbons, 2001). Consequently, use of ephemeral wetlands may be a proximate cause for long movements and extensions of area use as individuals seek more favorable habitats following wetland flooding and drying.

Evolutionary explanations of divergent spatial and movement patterns between species have been offered for animals that rely on using patchily distributed resources that vary unpredictably in space and time versus those that use more permanent, predictable resources. Using resources that vary unpredictably may require animals to regularly traverse large areas, to intensively use only a small portion of this area as multiple, widely dispersed activity centers, and to frequently travel long distances between numerous resources (Guibé and Saint Girons, 1955; Schoener, 1971; Huey and Pianka, 1981). Because the filling and drying of ephemeral wetlands are dependent on precipitation patterns, which vary between seasons and years, the availability or quality of these habitats often fluctuates unpredictably over time and across spatial landscapes (Semlitsch et al., 1996; Naugle et al., 2001). Similarly, anuran abundance often varies over time and space, resulting in wide between- and within-year fluctuations in amphibian abundances in wetlands (this study, Pechmann and Wilbur, 1994; Semlitsch et al., 1996). Also, most anurans typically exhibit seasonal habitat shifts, associating with wetlands in the spring and early summer (as breeding adults and larvae), then moving into adjacent terrestrial habitats following breeding or metamorphosis (Wilbur, 1980).

For *N. e. neglecta*, foraging for anurans in one wetland can be periodically productive, especially in ephemeral wetlands, but unpredictable fluctuations in anuran abundances may not allow *N. e. neglecta* to meet short-term energy demands without searching for alternative foraging sites. Successful use of such a resource would require familiarity with numerous potential foraging sites over a large area and the capability to frequently move long distances between sites (Schoener, 1971). In contrast, because *N. s. sipedon* has a more general diet, it may not encounter the same selective pressures that have likely shaped *N. e. neglecta*'s movement and spatial patterns. For instance, the temporary unavailability of one prey type (e.g., anurans) would only require *N. s. sipedon* to shift foraging to other prey (e.g., fish) in the same wetland, instead of seeking alternative foraging sites, such as in another wetland. As a result, *N. s. sipedon* may not need to use numerous wetlands or frequently travel long distances and traverse large areas.

4.3. Factors influencing within-species differences in movement and area use

The spatial distribution of wetlands in the landscape appears to be an important factor in shaping *N. e. neglecta's* movement and space use patterns, but not for *N. s. sipedon*. *Nerodia e. neglecta* inhabiting areas are wetlands were more dispersed move longer distances and traverse larger areas (Figs. 3 and 4). This finding has implications for understanding the consequences to *N. e. neglecta* populations in altered landscapes. For instance, as wetlands become more widely dispersed due to the loss of other nearby wetlands, *N. e. neglecta* would likely be forced to move longer distances and traverse larger areas, increasing their exposure to and rate of encounters with predators (Huey and Pianka, 1981; Madsen and Shine, 1993; Secor, 1995), and potentially requiring them to travel through unsuitable habitat (e.g., agriculture, roads) which may further increase mortality rates (Dodd et al., 1989; Shine and Fitzgerald, 1996). *Nerodia e. neglecta* would also use more energy by moving longer distances and traversing larger areas (Huey and Pianka, 1981; Walton et al., 1990), likely resulting in less energy allocated to growth, reproduction and storage, all of which may have population-level ramifications (Congdon et al., 1982).

Continuing frequent travel between multiple wetlands seems to be a critical aspect of *N. e. neglecta*'s ecology even if long distances must be traveled, whereas such behavior seems less critical for *N. s. sipedon*. *Nerodia s. sipedon*'s use of more permanent resources and its broader diet may allow it to continue to traverse small areas and move short distances even when wetlands are widely dispersed, enabling them to avoid the high costs likely incurred by *N. e. neglecta* inhabiting the same area. Consequently, while *N. e. neglecta* has declined, *N. s. sipedon* may continue to persist despite the drastic changes to the landscape in the Midwest.

Movements and space use in *N. e. neglecta* were also positively correlated with body size, a finding consistent with larger individuals using more widely dispersed wetlands than smaller individuals. Differences between large and small snakes may relate to physiology. For instance, larger individuals in the genus *Nerodia* can sustain maximal locomotor activity considerably longer than small snakes due to ontogenetic changes in blood oxygen capacity and affinity (Pough, 1978). If small *N. e. neglecta* are less capable of traveling long distances, they may face different challenges than large snakes in areas where wetlands are widely dispersed, for small snakes may be effectively isolated from essential resources that can only be acquired in other wetlands. Alternatively, larger *N. e. neglecta* may require use of different resources, such as prey, that necessitate use of larger areas. However, there is no indication that small and large *N. e. neglecta* differ in diet in the population we studied, despite evidence of ontogenetic dietary shifts in southern populations of *N. erythrogaster* (Mushinsky et al., 1982). A broader range of snake sizes for dietary analyses and radiotelemetry may be necessary to detect size-related dietary shifts, habitat use, movements, and spatial ecology in *N. e. neglecta*, but current limitations of transmitter size, and the difficulty of finding neonate snakes, precluded the inclusion of small snakes in this study. Future directions of research should include examining the resource needs and spatial ecology of neonate and juvenile *N. e. neglecta* in order to identify whether these individuals face a different set of risks than adults.

4.4. Conservation implications

Our comparative approach using closely related species allowed us to identify ecological characteristics that might make a species more vulnerable to landscape fragmentation. *Nerodia e. neglecta* frequently moves long distances and uses large areas, likely due its use of spatially and temporally variable resources, whereas *N. s. sipedon*'s more general diet and use of more permanent wetlands allow it to be relatively sedentary. The movement and spatial patterns of animals that rely on temporally dynamic resources may not permit their long-term persistence in small, isolated fragments. Consequently, habitat fragmentation coupled with wetland losses may have caused (and continue to cause) individuals from the northernmost *N. e. neglecta* populations to incur high energetic costs and mortality rates as they continue to attempt frequent movements among multiple, widely dispersed wetlands.

The conservation of animals that use temporally dynamic resources would likely require a landscape level approach to habitat conservation. For *N. e. neglecta*, such a plan should include protection of wetland complexes over broad spatial scales that encompass numerous ephemeral and permanent wetlands and intact upland habitats adjacent to and between wetlands that offer safe travel corridors. Similar suggestions have been offered as conservation plans for many other wetland-associated species, including birds (Haig et al., 1997; Naugle et al., 2000, 2001), amphibians (Dodd and Cade, 1998; Semlitsch, 1998; Semlitsch and Bodie, 1998; Snodgrass et al., 1999), and turtles (Buhlmann and Gibbons, 2001; Burke and Gibbons, 1995; Joyal et al., 2001), underscoring the importance of broad scale conservation efforts that focus on maintenance of the connectivity of wetland landscapes for maintaining intact wetland communities.

While the vagile nature of *N. e. neglecta* has left it vulnerable to habitat fragmentation, it may also help promote its recovery. Given the proclivity of the snakes to move substantial distance across the landscape, they may efficiently move into restored habitat. The most important aspect of rescuing this species may thus not be a matter of delivering some rare or unique environmental or dietary attribute, but simply enough landscape for them to sustain viable populations.

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