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HABITAT USE BY SYNURBIC WATERSNAKES (*NERODIA SIPEDON*)

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ABSTRACT: We examined habitat use in a population of synurbic watersnakes with equal access to urban and natural habitats to test the hypotheses that species occupy urban environments either by (1) restricting their activities to any remaining natural areas, or (2) capitalizing on, instead of avoiding, artificial features. For three years we radio-tracked 50 northern watersnakes (*Nerodia sipedon*) living in a 40-ha area along 2 km of a city stream in Pennsylvania (USA). Half the study site is urbanized (municipal park and an active industrial area), and half is a relatively natural conservation area. Habitats selected by snakes in the two areas were significantly different: in the natural half, snakes occupied areas with a wide riparian zone and dense canopy cover; in the urban half, they frequently used artificial substrates and were in close proximity to people. Snakes were relocated 2520 times, yet were found at only 113 sites. Frequently reused sites were mostly artificial, including piles of scrap metal or concrete, holes in a railroad bed adjacent to the stream, and dead evergreen trees secured into the stream bank to combat erosion. Urban and natural areas were approximately equal in area and stream length, and had similar numbers of snake-selected sites (64 urban, 49 natural), but urban sites were used by more snakes. Of sites used by more than five different snakes, 22 of 26 were in the urban area. Snakes were found within 5 m of a tagged conspecific at 38% of urban area relocations compared to 15% of natural area relocations. These data suggest that anthropogenic structures in urban environments provide conditions (concealment, thermal) that offset dangers posed by closer proximity to people.

Key words: *Nerodia sipedon*; Radio-telemetry; Riparian; Site reuse; Urban

THE DELETERIOUS impacts of urbanization are wide-ranging and well-documented, but urbanization can also create favorable conditions for some species (Adams, 2005; DeStefano and DeGraaf, 2003; Luniak, 2004). Synurbanization, the adjustment of animal populations to urban habitats (Andrzejewski et al., 1978; Babiñska-Werka et al., 1979), may require modification of resource use and behavior by organisms living in urban environments. Here we examine some of those modifications in the common North American watersnake, *Nerodia sipedon*.

In general, animals that persist in urban environments exhibit wide ecological amplitudes, flexibility in their behavior and habitat use, and tolerance to disturbance (Adams, 2005; Luniak, 2004). Documented biological differences between urban and natural populations include changes in dietary composition (Eeva et al., 2005; Lavin et al., 2003), activity range (Riley et al., 2003; Rodewald and Shustack, 2008; Rubin et al., 2002), migratory patterns (Partecke and Gwinner, 2007), circadian activity (George and Crooks, 2006; Grinder and Krausman, 2001), timing of reproduction (Partecke et al., 2005; Yeh and Price, 2004), use of artificial habitat features (Duchamp et al., 2004; Traweger et al., 2006), and increased tolerance to humans (Herrero et al., 2005; Walker et al., 2005). Synurbanization is relatively well-documented among endotherms (birds: Marzluff, 2001; mammals: Gloor et al., 2001; Prange et al., 2003), but the effects of urbanization on ectotherms are less well-understood (Germain and Wakeling, 2001).

As urbanization increases, species that do not adapt to urbanized environments may face population reductions or extinctions. Explicit studies of urbanization and its effects on species distribution and behavior are rare. However, given the rapid geographic spread of urbanization (Gilbert, 1991; McDonnell, 1997; Miller and Hobbs, 2002), such studies are increasingly important. Finding explanations for these effects and predicting changes as urbanization proceeds are major challenges for ecological research (Alberti et al., 2003; Grimm et al., 2000; Niemelä, 1999).

Appropriate habitat is vital to every life-history activity, and numerous considerations (including those related to reproduction, foraging, and thermoregulation) are likely to be involved in the selection of habitat (reviewed for snakes by Reinert, 1993). Many

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widely-distributed organisms, like northern watersnakes (*Nerodia sipedon*), have been shown to utilize a variety of habitat types throughout their geographic ranges, and habitat generalists are more likely to respond successfully to environmental change than habitat specialists (Adams, 2005; Luniak, 2004). *Nerodia sipedon* inhabits virtually every waterbody throughout its large geographic range, which extends essentially throughout the eastern half of the United States (Gibbons and Dorcas, 2004), and has been studied in a wide range of environments, including a stream in Kansas (Beatson, 1976), an undisturbed lake in Wisconsin (Tiebout and Cary, 1987), an isolated marsh in Ontario (Brown and Weatherhead, 2000; Robertson and Weatherhead, 1992), the islands of Lake Erie (King, 1986; King et al., 2006), an urbanized canal in New Jersey (Burger, 2001; Burger et al., 2004), a wetland area in Ohio/Michigan (Roe et al., 2004), and a lake conservation area in Missouri (Roth and Greene, 2006). *Nerodia sipedon* is commonly found on floating aquatic vegetation (Tiebout and Cary, 1987) and tree and shrub branches along waterways (Burger et al., 2004; Robertson and Weatherhead, 1992). It has the greatest documented prey diversity of any watersnake (Gibbons and Dorcas, 2004) and will feed readily on nonnative prey (King et al., 2006).

We radio-tracked members of a population of watersnakes that had approximately equal access to urban and natural habitats to test the hypotheses that watersnakes occupy urban environments either by (1) restricting their activities to any remaining natural features or (2) capitalizing on, instead of avoiding, artificial features. Because previous studies of watersnake habitat identified only relatively natural features as suitable habitat (Burger et al., 2004; Robertson and Weatherhead, 1992; Tiebout and Cary, 1987), and because the use of natural resources does not require deviation from probable ancestral habitat use characteristics, the first hypothesis would appear to be the most parsimonious prediction. If snakes predominantly use natural features, there should be relatively few snake-selected sites in the urban areas either by fewer snakes being present in the urban area relative to the natural area, or by few urban sites being selected by more individuals. Alternatively, watersnakes may exploit urban environments by selecting artificial features, thereby adding to the range of suitable habitats utilized. Other studies of snakes in habitats altered by humans (Burger and Zappalorti, 1986; Neill, 1950; Shine and Fitzgerald, 1996; Slip and Shine, 1988) lend support to this second hypothesis. In this case the number of snake-selected sites in urban areas should be similar to, or may even exceed, the number in the natural area.

MATERIALS AND METHODS

Study Area

This study was conducted in eastern Pennsylvania (USA) on snakes living along Monocacy Creek, a 32-km long, 4th order, low-gradient, spring-fed stream with water temperatures ranging from 10 to 19 C during the snake activity season. Though watersnakes can be found along much of the stream's length, our study site surrounds a 2-km stretch that flows through downtown Bethlehem (population estimate 72,000). The first 0.3 km of the stream flows through a manicured municipal park, where it is channelized and heavily used by fishermen. The next 1.0 km of stream flows through a conservation corridor with a wide riparian zone and a small footpath lightly traveled by a regular group of fishermen and hikers. The last 0.7 km flows between two active industrial properties with numerous large piles of sheet metal, plastic, wood pallets, and concrete. A railroad track that is used between one and three times daily parallels the stream through the entire study site. We consider the upstream park and the downstream industrial area urban and the middle conservation corridor natural. This approach was taken with the understanding that there are a few urban habitat features (railroad bed and walking path) in the natural area and some remaining natural features (trees and shrubs) in the urban areas (Fig. 1).

Subjects and Tracking Dates

Between May 2004 and October 2006 we captured adult *N. sipedon* by hand and implanted each with a radio-transmitter (Reinert and Cundall, 1982). See Pattishall and

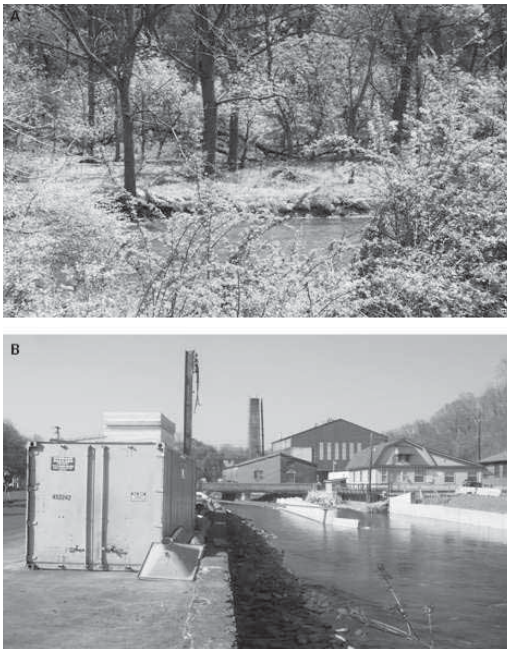

FIG. 1.—Photographs representative of (A) the natural area and (B) the urban area.

Cundall (2008) for additional methods related to transmitter implantation and tracking. Fifty snakes (36 females, 14 males) were tracked by walking the study area and were relocated (meaning their locations were found and recorded, usually once per day) for as long as their transmitters continued to function. Because male *N. sipedon* are considerably smaller than females, only the largest could be implanted, resulting in disproportionately more data for females. The mean number of relocations per snake was 50 and ranged from 1 to 261. In total, 2520 relocations (984 of gravid females, 1145 of nongravid females, 391 of males) were made.

Variables Measured

Each time a snake was relocated, its precise location was recorded along with as many of the 29 habitat and behavior variables (Table 1) as possible. Detailed descriptions of locations were recorded and were then plotted on high-resolution aerial photographs. Habitat variables included distances of snakes from urban features (people, roads, buildings, man-made clearings, etc.), width of the nearest riparian buffer, and extent of canopy and vegetative cover. Behavioral variables included the snake's activity (basking, mating, foraging, etc.), the number of snakes known to be within 5 m of the focal snake, and whether a snake was within a 1-m radius of a spot that was at some time used by another tagged snake. It should be noted that regarding the number of snakes known to be near the focal snake, "known" means either easily seen or located with telemetry. We did not actively search for conspecifics because we did not want to disturb the focal snake or the habitat. Therefore we could have, and certainly sometimes did, underestimate the extent to which snakes were in close proximity to one another.

Most or all variables were usually obtainable when snakes were in a more naturalistic environment, but when snakes were in a more urbanized area, variables periodically had to be recorded as unknown in part because not all of the land owners in the study site allowed access to their property at all times and also because snakes often used large, immobile piles of metal, wood, concrete, and garbage and were not visible. Because some parts of the site were heavily used by people, and because several snakes were intentionally killed during the study, it was at times necessary to record only those variables that could be determined at a distance so that we did not draw attention to the presence of the snakes.

Random Site Selection

Habitat variables measured at snake-selected locations were compared with those measured at 250 randomly selected locations within the study site (Fig. 2). To determine the locations of random sites, the study area boundary was drawn on an aerial photograph of the area. The upstream and downstream boundaries were defined by the most upstream and most downstream points occupied by an implanted snake; the boundaries on either side of the stream were determined by the maximum distance (100 m) an implanted snake was found away from the stream. The size of the study area was approximately 40 ha (2.0 × 0.2 km). A 1 × 1 m grid was overlain on a map of the study area and a computer was used to generate 250 random XY coordi-

TABLE 1.—Variables that were collected on habitat and behavior.

Variable	Explanation
Natural/urban	urban versus natural part of the study area
Substrate	type of structure beneath snake
Substrate type	natural versus artificial substrate
Substrate temperature	surface temperature of substrate was measured, when possible, with a laser thermometer (Raytek® MT4, Santa Cruz, CA)
Ambient temperature	air temperature near the snake (within 3 m)
Canopy	type of canopy directly above snake (1 = none, 2 = understory (<5 m), 3 = tall trees (>5 m))
Vegetative cover	type of vegetation covering snake (1 = none, 2 = leaf litter/twigs, 3 = ivy/groundcover, 4 = perennials, 5 = small shrubs, 6 = large shrubs)
Sun	amount of sun exposure of snake (1 = none, 2 = partial, 3 = full)
Buffer	width (m) of riparian buffer at snake location
Bank cover	type of stream bank cover closest to snake (1 = man-made, 2 = naturally occurring rock, 3 = grass, 4 = perennials, 5 = shrubs, 6 = trees)
Perch height	distance (m) between snake and ground
Water	distance (m) to nearest water body
Water temperature	temperature (C) of closest water
Road	distance (m) to nearest road
Building	distance (m) to nearest building
Path	distance (m) to nearest footpath
Human	estimated distance to nearest human (1 = <1 m, 2= 1–5 m, 3 = 6–10 m, 4 = 11–20 m, 5 = >20 m), not recorded for random sites. A calibrated Coleman ranging optimeter® was used for estimates <10 m.
Clearing	distance (m) to nearest human-induced clearing
Activity	type of activity performed by snake (basking, mating, swimming, etc.)
Proximity to snake	approximate distance to another snake (1 = touching, 2 = <1 m, 3 = 1–5 m, 4 = 6–10 m, 5 = 11–20 m, 6 = >20 m)
Snakes within 5 m	number of snakes observed within a 5 m radius (only snakes that were immediately visible or tagged snakes known to be within 5 m)
% exposed	approximate % of snake's body that was not under cover (1 = none, 2 = <25%, 3 = 25–50%, 4 = 51–75%, 5 = 76–100%)
Visibility	estimate of how easy it was for investigator to see the snake (1 = impossible, 2 = difficult, 3 = fairly easy, 4 = obvious)
Snake temperature	surface body temperature measured with a laser thermometer (when possible to obtain without significant disturbance)
Moved from previous	whether the snake moved more than 3 m from its previously-recorded position
Former location	whether the snake was in a formerly used location (within 1 m radius)
Another's location	whether the snake was in a location that another tagged snake has used (within 1 m radius)
Prey item	identity of prey item (when large and easily visible)

nates. The random points were plotted on the map and then in the field habitat information was collected at each location.

Data Analyses

Analyses were conducted to examine habitat differences between urban and natural males, gravid females, nongravid females and random sites (eight-group comparison). No individual snake contributed more than 10% of the total number of relocations used for analysis. First, ANOVA and the post-hoc Games-Howell tests were used to determine if there were significant differences between the groups based on individual habitat variables. Then MANOVA and follow-up pairwise comparison tests were used to evaluate differences between groups. Finally discriminant function analysis was used to determine which habitat variables, or combinations of variables, best differentiated the groups.

Prior to conducting multivariate tests, the assumptions of multivariate normality and homogeneity of covariance matrices were tested. Box's test indicated the assumption of homogeneity of covariance matrices was violated; however, this is common for ecological data, and despite this violation, the value of the following analysis has been defended (McGarigal et al., 2000; Sokal and Rohlf,

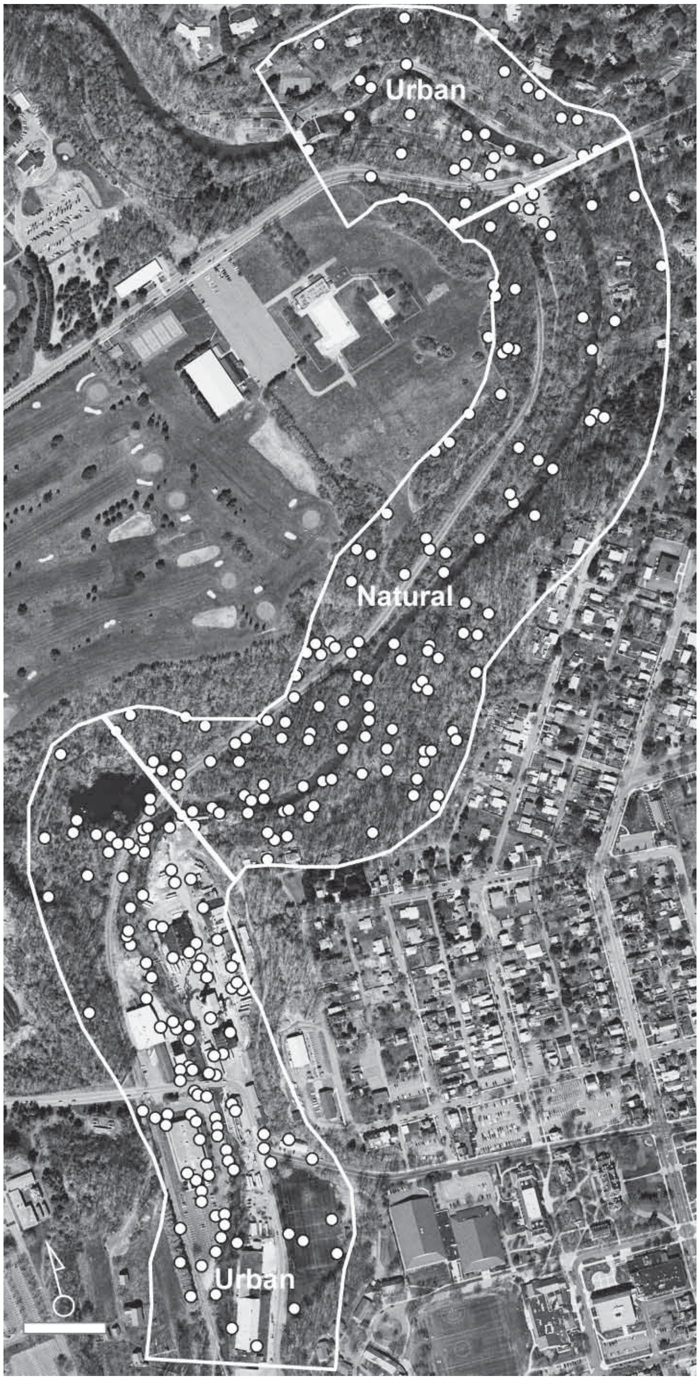

FIG. 2.—An aerial photograph of the study area with locations of randomly selected points and the study site boundary. White lines delineate urban and natural portions of the study area. White scale bar = 100 m.

1995). Skewness and kurtosis of individual variables were examined and variables that were not normally distributed were log-transformed. Analyses were conducted both by using only the original variables and also by substituting the log-transformed values for raw data (for variables that were not normally distributed).

The statistical tests employed here also assume observations were independent, but we made repeated observations on a limited number of individuals that occupied a limited number of locations. To address this issue, we conducted multivariate tests on a sub-sample of the original data in which each site for each snake was only used once. To do this, scores on those variables that could change from one relocation to the next for that site were averaged and the mean value for each site was used. Variables describing distances to permanent features did not change. For example, if a snake was relocated 50 times but at only 10 different sites, analyses were conducted first using all 50 relocations and then using only the means for varying features or the values for nonvarying features for the ten sites. If another individual used five of the same sites as the first snake and also used another ten sites, that snake's sub-sample size would be 15. This sub-sampling reduced the sample size from 2520 (relocations) to 323 (locations or sites). Analyses yielded very similar results and interpretations regardless of variable transformation or sample size.

Chi-square tests were used to compare relative frequencies of the use of common sites between urban and natural areas and between reproductive groups. Expected frequencies for the urban areas were derived from the observed frequencies in the natural areas (if urban snakes did not behave differently from natural snakes, we would expect them to have the same frequency of common site use as those in the natural area). Expected frequencies for gravid females were derived from the observed frequencies for both males and nongravid females. MANOVA was used to compare the habitat features of sites selected by only one snake with sites selected by multiple snakes.

A chi-square test was also employed to compare relative frequencies of relocations in which snakes were found to be within 5 m of another snake between urban and natural areas. Expected frequencies for the urban areas were derived from the observed frequencies in the natural areas.

Results

Habitat Use

Snakes were found more often in the urban half of the study site (75% of relocations) than in the natural half. Of the 50 snakes, 21 were found only in the urban area, 21 in both areas, and 8 only in the natural area. Snakes frequently used artificial habitat features (41% of relocations) and were often in or under large piles of scrap metal and garbage or buildings. Snakes also were found in or under branches (28%), rocks (13%), and leaf litter (12%) and were only found in the water at 2% of relocations. Snakes were less conspicuous in the urban area. Snakes were scored as easy to see or fairly easy to see at only 17% of urban relocations but at 30% of natural relocations.

When in urban areas, snakes were found near people and artificial features more often than when in the natural area (Table 2, Fig. 3A). Gravid females tended to be closer to clearings and people and used artificial substrates more often than nongravid females and males. Gravid females were on average twice as far away from water as nongravid females and males (Table 2, Fig. 3B).

A MANOVA indicated significant habitat differences among the eight groups (urban area and natural area males, gravid females, nongravid females, and random sites, Box's M = 2939, $F_{315,\ 38902} = 8.49$, $P < 0.01$; Wilks' $\Lambda = 0.34$, $F_{63,\ 3199} = 10.9$, $P < 0.01$), and pairwise MANOVAs indicated each group is significantly different from the others. Discriminant function analysis generated four functions that together accounted for 96% of the variance between the groups (Table 3). The first function accounted for 61% of the variance and was most highly correlated with riparian buffer width ($r = 0.79$) and distance to nearest human-induced clearing ($r = 0.65$). The second function accounted for 26% of the variance and was most highly correlated with distance to roads ($r = 0.71$)

TABLE 2.—Original variables (mean ± SE) and ANOVA/post-hoc results, * indicates $P < 0.01$.

	Urban				Natural					
	Gravid (UG)	Nongravid (UN)	Male (UM)	Random (UR)	Gravid (NG)	Nongravid (NN)	Male (NM)	Random (NR)	ANOVA *F*	Games-Howell
Number of cases	91	90	60	142	35	31	16	118		
Canopy cover (index)	1.32 ± 0.06	1.53 ± 0.08	1.25 ± 0.06	1.50 ± 0.05	2.03 ± 0.16	2.23 ± 0.17	1.81 ± 0.25	2.12 ± 0.09	14.64*	(UG, UN, UM, UR, NM) < (NG, NN, NR)
Vegetative cover (index)	2.37 ± 0.21	2.27 ± 0.20	2.33 ± 0.24	1.50 ± 0.11	2.91 ± 0.35	2.48 ± 0.32	2.81 ± 0.51	2.23 ± 0.17	4.44*	(UG, UN, UM, UR) < (NG, NN, NM, NR)
Bank cover (index)	4.81 ± 0.21	3.80 ± 0.21	3.33 ± 0.24	16.89 ± 2.40	4.20 ± 0.16	4.26 ± 0.24	4.56 ± 0.38	60.51 ± 4.84	4.27*	(UN, UM) < (NG, NN, NM) < UG < UR < NR
Riparian buffer width (m)	5.51 ± 0.96	5.26 ± 0.84	2.04 ± 0.36	2.04 ± 0.23	42.01 ± 1.65	40.16 ± 3.09	30.95 ± 5.74	2.04 ± 0.25	48.18*	(UM, UR, NR) < (UN, UG) < NM < (NN, NG)
Distance (m) to water	8.20 ± 1.42	6.83 ± 1.80	3.42 ± 0.64	27.62 ± 2.39	19.31 ± 3.44	8.34 ± 2.88	1.93 ± 1.03	26.01 ± 2.63	17.53*	(NM, UM) < (NN, UN, UG) < NG < (UR, NR)
Distance (m) to road	92.99 ± 8.21	118.39 ± 6.83	41.51 ± 6.95	56.96 ± 5.76	124.94 ± 6.75	127.85 ± 6.88	109.56 ± 16.50	112.25 ± 5.98	17.63*	(UM, UR) < (UG, UN, NM, NR) < (NN, NG)
Distance (m) to building	60.38 ± 4.86	71.65 ± 4.16	36.58 ± 4.36	47.72 ± 4.86	95.67 ± 6.88	93.10 ± 6.33	70.41 ± 10.12	101.82 ± 4.91	18.94*	UM < UR < (UG, UN, NM) < (NN, NG) < NR
Distance (m) to path	2.83 ± 0.52	5.09 ± 0.92	2.60 ± 0.44	7.96 ± 1.06	6.49 ± 1.73	12.10 ± 3.07	2.16 ± 0.54	17.68 ± 1.65	17.26*	UM < (NM, UN, UM, UG) < NG < UR < NR
Distance (m) to clearing	1.57 ± 0.43	4.60 ± 1.05	1.55 ± 0.42	6.37 ± 1.19	16.49 ± 2.78	22.29 ± 3.24	22.69 ± 4.40	31.9 ± 2.85	36.13*	(UG, UM, UN) < UR < (NG, NN, NM) < NR
Estimated distance (m) to human (index)	3.75 ± 0.14	4.28 ± 0.12	3.42 ± 0.12	NA	4.37 ± 0.21	3.87 ± 0.29	3.63 ± 0.44	NA	4.67*	UM < (NG, NM, NN, UN, NG)

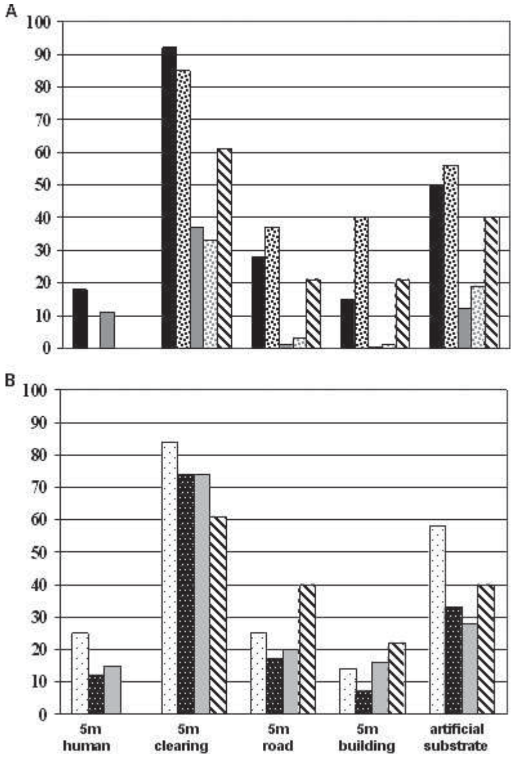

FIG. 3.—Percentage of sites associated with artificial habitat features. (A) Comparison of snake-selected sites and randomly selected sites in the urban and natural areas. Solid black bars represent urban snake locations, speckled black bars represent urban random sites, solid gray bars represent natural snake locations, speckled gray bars represent natural random sites, striped bars represent all random sites. (B) Comparison of random sites to sites selected by the three reproductive groups. White bars with black dots represent gravid female locations, black bars with white dots represent nongravid female locations, light gray bars represent male locations, striped bars represent all random sites.

and buildings ($r = 0.58$). The third function accounted for 6% of the variance and was most highly correlated with distance to water ($r = 0.56$). The first axis indicates that urban area snakes occupied more open, less vegetated areas than natural area snakes. The second axis indicates that males were usually found closer to roads and buildings than females, and the third axis indicates that gravid females tended to be farther away from water than other snakes (Fig. 4). The dispersion of the random points from urban and natural areas (Fig. 5) shows the extent to which habitat features typical of the urban area were found in the natural area and vice versa. Randomly-selected locations were more widely distributed in multivariate space than snake-selected locations, indicating that snakes were not randomly distributed throughout the study site (Fig. 5).

Aggregation

Snakes were significantly more likely to be in close proximity to conspecifics in the urban areas than in the natural area. Considering only relocations after 1 June (after the mating season ended) and before 1 October (before hibernation), at 38% of relocations in urban areas there was at least one other snake known to be within 5 m of the focal snake, compared to 15% in the natural area ($\chi^2 = 292.2$, df = 1, $P < 0.01$). During this time period, 18% of urban relocations had one other snake known to be within five meters, 11% had two, and 9% had three or more. In the natural area 8% of relocations had one other snake known to be within 5 m, 3% had two, and 4% had three or more. The maximum number of adult snakes observed together was approximately 30 individuals found under a large piece of sheet metal (approximately 2 m × 2 m).

Use of Common Sites

The total area that apparently could have been covered by the implanted snakes was approximately 40 ha (based on the way the boundary of the study site was determined for the random sampling). By simply drawing a polygon around all snake-selected sites, we estimate they covered approximately 3 ha. During the 3 yr of radio-tracking, implanted snakes were found at only 113 sites (sites had a 1-m radius). Snakes were found at a site previously occupied by another implanted snake at 94% of relocations. Individuals frequently used the exact same place as others (in the same hole, under the same rock, on the same branch, etc.). Snakes were more likely to occupy sites used by other implanted snakes in the urban areas (98%) than the natural areas (93%) ($\chi^2 = 242.5$, df = 1, $P < 0.01$). Males and nongravid females were both found in common sites at 97% of relocations, which is significantly more often than were gravid females (90%, $\chi^2 = 179.1$, df = 1, $P < 0.01$). Snakes occupied sites used by other snakes

TABLE 3.—Summary statistics for the eight group DFA: correlations between original variables and discriminant functions, and discriminant scores with standard errors for each group.

	Function 1	Function 2	Function 3	Function 4
Eigen value	0.83	0.35	0.08	0.05
% variance	61	26	6	4
r with:				
Buffer width	0.79	0.42	−0.04	−0.02
Distance to water	0.39	−0.39	0.58	−0.23
Distance to road	0.11	0.71	0.56	−0.03
Distance to building	0.34	0.58	0.30	0.11
Distance to clearing	0.66	0.42	−0.04	−0.02
Distance to path	0.46	0.09	0.28	0.60
Bank cover	0.19	0.13	0.19	−0.07
Vegetative cover	−0.03	0.34	−0.35	−0.16
Canopy	0.38	0.37	0.18	−0.12
Group centroids:				
Urban gravid	−0.86 ± 0.06	0.01 ± 0.10	−0.33 ± 0.11	0.02 ± 0.06
Natural gravid	0.43 ± 0.07	0.59 ± 0.16	−0.12 ± 0.08	−0.65 ± 0.09
Urban nongravid	−1.05 ± 0.08	0.52 ± 0.10	0.33 ± 0.11	0.14 ± 0.08
Natural nongravid	0.24 ± 0.15	0.89 ± 0.16	0.06 ± 0.11	0.03 ± 0.28
Urban male	−0.79 ± 0.07	−0.37 ± 0.10	−0.69 ± 0.10	−0.16 ± 0.08
Natural male	−0.08 ± 0.25	0.92 ± 0.28	−0.34 ± 0.19	−0.61 ± 0.23
Urban random	0.15 ± 0.09	−0.89 ± 0.09	0.19 ± 0.09	−0.10 ± 0.09
Natural random	1.50 ± 0.14	0.25 ± 0.11	−0.04 ± 0.10	0.19 ± 0.12

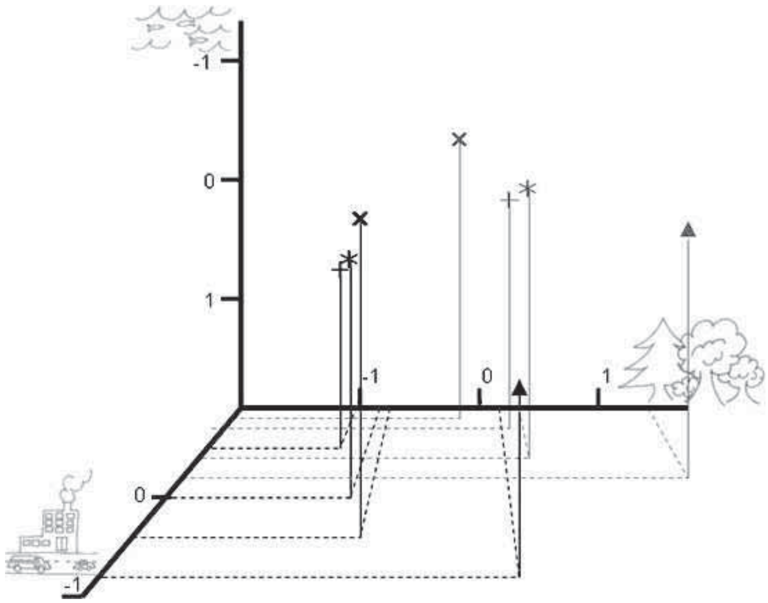

FIG. 4.—Positions of group centroids along the first three discriminant functions are shown. X axis represents the first discriminant function, Z axis represents the second, and Y axis represents the third. Centroids: ▲ = urban random, ▲ = natural random, ✶ = urban gravid, ✶ = natural gravid, + = urban nongravid, + = natural nongravid, × = urban male, × = natural male. Drawings at the end of each axis symbolize the extremes of habitat gradients defined by discriminant function analysis (i.e., moving from left to right along the X axis represents moving from open, unvegetated habitats to those characterized by substantial vegetation and canopy cover).

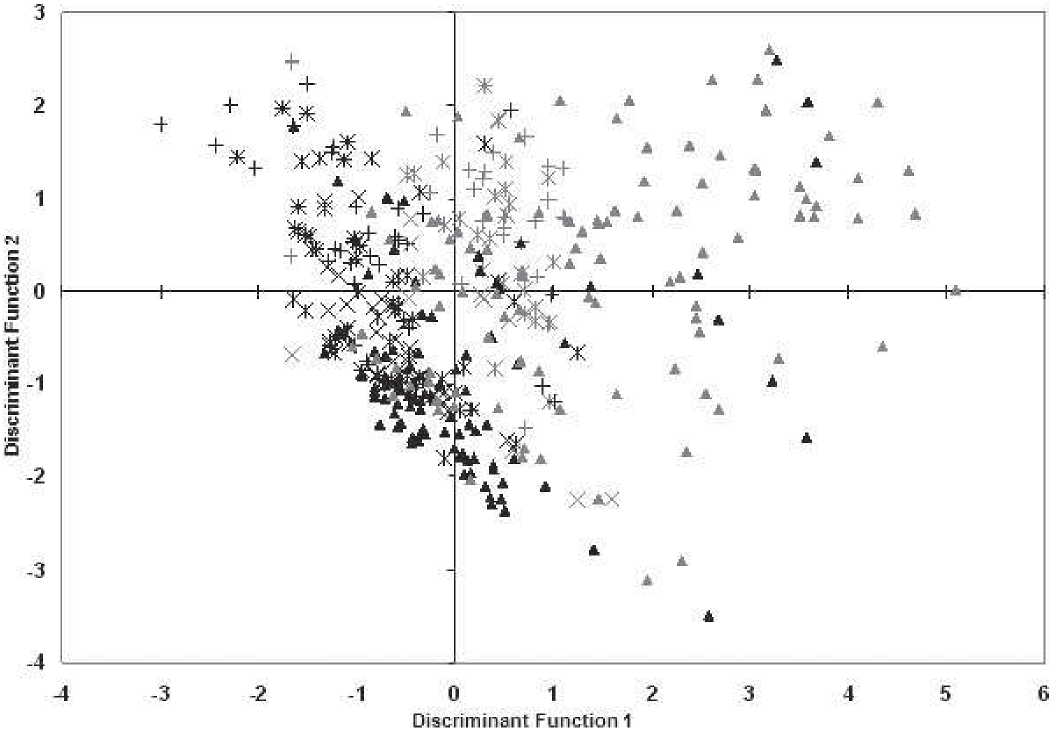

FIG. 5.—Multivariate distribution of 323 snake and 250 random sites on the first two discriminant functions. Symbols are the same as for Fig. 3. The overlap of random sites demonstrates the extent to which habitat features characteristic of the urban area are available in the natural area and vice versa.

with equal frequency throughout the year and appear to have selected these common sites independent of the presence of conspecifics because at 85% of snake relocations there were no other snakes at the site (1-m radius). At 66% of the relocations in which a snake occupied a commonly-used site, there were no other conspecifics known to be within 5 m. The locations of snake-selected sites and the number of tagged snakes are known to have occupied them are shown in Fig. 6. While the numbers of snake-selected locations in the two areas are similar (64 in the urban, 49 in the natural), urban sites tended to be used by more snakes. In the urban half of the study area, there were 22 sites used by more than five individuals, compared to four sites in the natural half. Structural habitat features selected by large numbers of snakes (>10 individuals) were all artificial and all located in the urban area.

Feeding

Although snakes were seldom found foraging (1.4% of relocations were in the water), there were six relocations where snakes obviously contained a prey item, and nine snakes regurgitated fish upon initial capture. These prey items suggest that snakes feed partly on stocked, nonnative brown trout (*Salmo trutta*), most often scavenging remains discarded by fishermen and the dead or dying fish characteristic of the creek in the weeks following a fish stocking event.

Mortality

At this study site humans may kill significant numbers of snakes; several of the people who frequent the area indicated they had either killed a snake there or knew of someone who had. Five radio-tagged snakes (three gravid females, two males) were obviously killed by people, all in the urban half of the

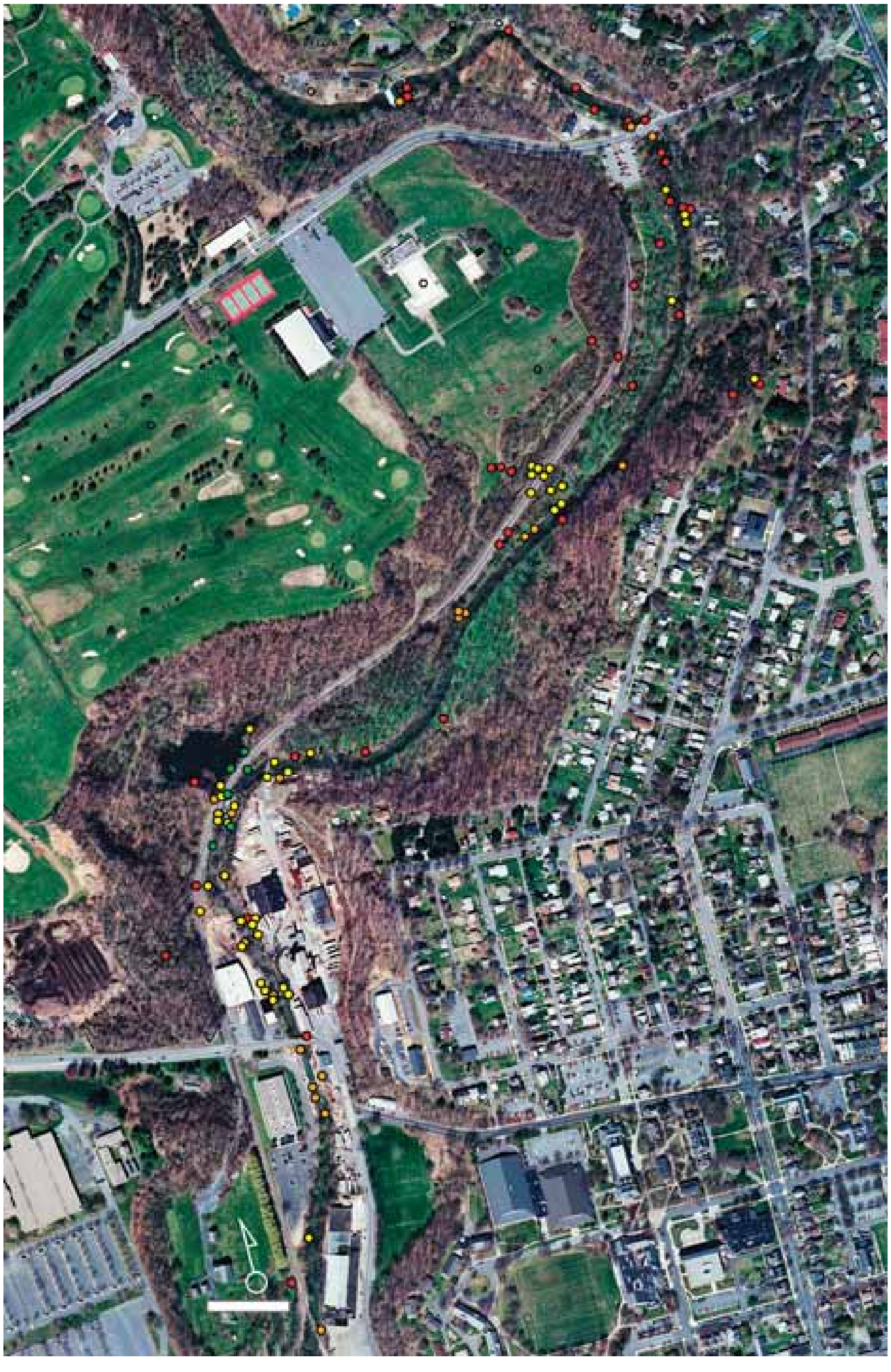

FIG. 6.—Snake-selected sites plotted on an aerial photograph of the study site. Red = sites used by only one tagged snake, orange = 2–5 tagged individuals, yellow = 6–10 tagged individuals, green = 11–16 tagged individuals. White scale bar = 100 m.

site. Snakes are apparently also subject to less direct human-induced mortality: they were occasionally found crushed under pieces of sheet metal and run over by vehicles, and we periodically freed snakes tangled in fishing line and other garbage or removed fishing hooks from their bodies.

Discussion

Previous studies of anthropogenic effects on animal populations have demonstrated the deleterious impacts of increased urbanization on invertebrates (Denys and Schmidt, 1998; Moore and Palmer, 2005; Shochat et al., 2004), fish (Kemp and Spotila, 1997; Wang et al., 2001), amphibians (Rubbo and Kiesecker, 2005), nonavian reptiles (Germaine and Wakeling, 2001; Gibbons et al., 2000), birds (Green and Baker, 2002), and mammals (Kurta and Teramino, 1992; Mahan and O'Connell, 2005). Several features of the urban environment have been implicated in the decline of wildlife, including roads (Fahrig et al., 1995; Gibbs and Shriver, 2002), destruction and removal of key habitat structures (Scott et al., 1989; Webb and Shine, 2000), pollution (Kemp and Spotila, 1997; Limburg and Schmidt, 1990), reduced prey abundance (Miyashita, 1990), and intentional killing (Dodd, 1987; Jennings, 1987).

Considering these hazards, it could be predicted that given a choice between urban and natural areas, organisms would choose the latter. Our snakes had equal opportunities to occupy urban and natural areas and structures. The urban and natural areas were approximately equal in size (area and stream length), random habitat samples indicated that the urban part of the study site contained habitats that were similar to those in the natural area (demonstrated by the substantial overlap of urban and natural random sites shown in Fig. 5), and snakes traveled from one end of the study site to the other, with nearly half of them traveling between the urban and natural parts. Our findings indicate these snakes prefer urban habitats. Snakes were found far more often in the urban areas (75% of relocations), and while the numbers of snake sites were approximately equal in the two areas, urban sites were used by more individuals. Some synurbic species have been shown to achieve higher densities in urban settings than in more natural areas (Rodewald and Shustack, 2008); their success is usually attributed to an increased food supply and/or decreased predation pressure (Faeth et al., 2005; Shochat et al., 2006).

Food availability appears not to be a limiting resource at our study site because the stream is stocked with trout (*Salmo trutta*) by the Pennsylvania Fish and Boat Commission throughout the study site. Even though snakes were radio-tracked nearly every day at all hours of the day and night, snakes were rarely found foraging, suggesting that prey are abundant enough that finding and obtaining food does not require considerable amounts of time. Anthropogenic supplementation of the food supply is common in urban settings and is conducive to the maintenance of urban wildlife (Faeth et al., 2005). Examples for snakes include the watersnakes of Lake Erie, which now predominantly feed on the invasive round goby (*Neogobius melanostomus*, King et al., 2006) and carpet pythons (*Morelia spilota*) in eastern Australia, which primarily prey on commensal taxa, livestock, and pets (Shine and Fitzgerald, 1996).

Snakes in the urban areas could have chosen sites more characteristic of those in the natural area (which typically had a wide riparian buffer and abundant vegetative cover), but instead urban snake-selected sites tended to be less vegetated and closer to people, roads, and buildings. The habitats selected by our snakes in urban areas differ considerably from those previously described on the basis of naturally-occurring features like aquatic vegetation (Tiebout and Cary, 1987), low-hanging tree branches (Robertson and Weatherhead, 1992), and logs and leaf-litter (Burger et al., 2004). These types of features were often used by our snakes, but the structural habitat features selected by large numbers of snakes were all artificial, suggesting that these features provide better conditions than naturally-occurring habitat features. Although there are relatively few studies of habitat use by urban herpetofauna, the use of artificial habitat structures has been reported for a few urban amphibians, lizards, and snakes (Germaine and Wakeling, 2001; Neill, 1950; Shine and Fitzgerald, 1996).

As with many other snake species, gravid *N. sipedon* have been shown to occupy areas that are more open and less densely vegetated than those selected by males and nongravid females, presumably because of the thermal requirements associated with gestation (Brown and Weatherhead, 2000; Greshock, 1998). At our site, gravid females were found in or near clearings and selected artificial substrates more often than other snakes, perhaps because those areas provided better basking conditions. Gravid females also tended to be considerably farther from water than other snakes, probably reflecting the fact that much of the stream was surrounded too densely by riparian vegetation for them to bask effectively, and perhaps indicating that gravid snakes do not feed frequently (but see Aldridge and Bufalino, 2003). Gravid snakes probably use artificial features in part simply because they are more abundant in and around clearings and in part because surfaces like metal and concrete provide desirable thermal conditions. Selecting these types of locations means gravid females are often in close proximity to humans. If this is a common trend, it could potentially be a cause for concern in urban populations.

We were surprised to find that in a 40-ha area, 50 individuals (2520 relocations) would be found at only 113 sites. Snakes used common sites throughout the year, not just during the mating season or hibernation (when snakes typically aggregate) and appear to have selected specific sites used by multiple snakes independent of the presence of conspecifics. Habitat selection occurs at different scales and is considered a hierarchical process (Johnson, 1980; Reinert, 1993; Van Horne, 1983). Preferred habitat is usually described on the basis of physical environmental features (temperature, sunlight, stream flow, vegetative characteristics, etc.), which can fluctuate greatly during an activity season. If animals were selecting locations based predominantly on these factors, their locations should change, to some extent, with changing conditions.

Previous studies in which *N. sipedon* was radio-tracked include estimates of space use but do not provide information about the extent to which individuals overlap in their use of specific sites (Roth and Greene, 2006; Tiebout and Cary, 1987) or indicate only that activity ranges of individuals overlapped (Roe et al., 2004). Much of the existing literature concerning the distribution of individual snakes is focused on aggregation. Snakes are considered largely asocial, but many species can be found in groups during the mating season and often use communal hibernacula. Aggregation outside of these events appears to be common in some snake species, perhaps as a result of individuals attempting to maintain desirable physiological conditions or of poorly understood social behavior (reviewed by Gillingham, 1987; Gregory et al., 1987).

Watersnakes at our site display a number of characteristics typical of synurbic animals, including use of artificial habitat features and exploitation of introduced food resources. These two traits have been implicated in the success of a number of synurbic species (Bender et al., 2004; Germaine and Wakeling, 2001; Marzluff, 2001), including snakes (Shine and Fitzgerald, 1996; Slip and Shine, 1988). Throughout the study site, snakes frequently used sites also selected by conspecifics. Sites used by large numbers of snakes (>10 individuals) were all located in the urban area and were all artificial, suggesting some artificial structural features provide more favorable conditions than do natural features. These structures provided cover for many individuals at the same time and allowed snakes to both bask openly and escape rapidly from danger. Previous investigators may not have observed the use of common sites because they were working in more natural areas where suitable habitat features may be more uniformly distributed. Anthropogenic habitat modifications and fish stocking provide watersnakes at our site with critical resources that may offset the dangers associated with human proximity.

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