Spatial Biology of Northern Watersnakes (*Nerodia sipedon*) Living along an Urban Stream

Abigail Pattishall[1,2] **and David Cundall**[1]

Fifty *Nerodia sipedon* living along two kilometers of an urban stream in northeastern Pennsylvania were radio-tracked over three activity seasons, yielding more than 2520 relocations. Half the stream length is urbanized, flowing through a city park at the head of the study area and an industrial area at the downstream end; the half between is relatively natural, flowing through a conservation corridor. Individual snakes exhibited high site fidelity. For 82% of relocations, snakes were within a one-meter radius of places they had previously occupied, most often using exactly the same hole, rock, branch, or cover object. Snakes were found to have moved to a different site at 27% of relocations. When snakes moved, they returned to previously occupied places 56% of the time. Females exhibited significantly greater site fidelity than males, and snakes occupying the urban half of the study site exhibited significantly greater site fidelity than snakes found in the natural half. Individuals varied greatly in the amount of space they utilized. Snakes had a mean minimum convex polygon (MCP) activity area of 1.13 ha. Snakes appeared to use the stream to travel between locations separated by more than 100 meters. Original MCPs overestimated space use by including large terrestrial areas that were never occupied by and were unsuitable to snakes. Fixed kernel methods underestimated space use by producing multiple small, disjunct contours. Both methods often largely or completely excluded the stream. To address these problems, we provide additional estimates of space use that sum the MCPs encompassing all of a snake's locations within 100 meters of each other and add the area of stream connecting the most upstream and downstream locations.

U RBANIZATION is a threat to many natural habitats and populations. The urban environment presents novel challenges to wildlife, including increased human contact, roads, fragmentation, habitat modification, pollution, and unnatural distribution of food resources. Animals that persist in environments dominated by humans must deal with these problems. Studies of wildlife in urban environments have been limited (Miller and Hobbs, 2002; Morley and Karr, 2002). This is especially true for herpetofauna (but see Slip and Shine, 1988; Garber and Burger, 1995; Husté et al., 2006).

How an animal moves through the environment is one of its most critical life history attributes (Burt, 1943; Andrewartha and Birch, 1954), and understanding spatial biology may be particularly important in assessing the threats of anthropogenic habitat modification (Bonnet et al., 1999; Parent and Weatherhead, 2000; Dodd and Barichivich, 2007). Snakes must move if they are to find food, mates, and hibernacula, but moving snakes may be at greater risk of mortality (Gregory et al., 1987; Bonnet et al., 1999; Andrews and Gibbons, 2005). Reduced movement patterns have been cited as a common feature of urban animals in general (Gilbert, 1991; Luniak, 2004), and a few authors have suggested that snakes may deal with the unique pressures of urban environments by using less space and moving less often than conspecifics living in natural habitats (Bonnet et al., 1999; Parent and Weatherhead, 2000; Moore and Gillingham, 2006).

For three years we radio-tracked Northern Watersnakes (*Nerodia sipedon sipedon*) living along a city stream in eastern Pennsylvania that flows through a mixture of urban and natural landscapes in order to compare home range size, movement frequency, and site fidelity of individuals

inhabiting natural areas with those in urbanized areas. Watersnakes at this site must deal with more than just a physically urbanized landscape. The stream is heavily used by anglers, many of whom are hostile to watersnakes, viewing them as competitors for fish or as ''water moccasins'' (*Agkistrodon piscivorus*, which actually do not occur naturally in Pennsylvania [Conant and Collins, 1998]).

Northern watersnakes inhabit virtually every waterbody throughout their large geographic range, which extends from southern Quebec to North Carolina and from the Atlantic coast to eastern Colorado (Gibbons and Dorcas, 2004). They can be found along pristine wooded rivers, fish hatcheries, the Great Lakes, and urban industrial streams. *Nerodia sipedon* is an aquatic-feeding generalist (Gibbons and Dorcas, 2004) that preys predominantly on fish (Raney and Roecker, 1947) but will also eat amphibians when abundant (King, 1993). Snakes emerge from hibernation in late March or April (Hulse et al., 2001) and soon thereafter can be found in mating aggregations, which often involve one female and several males (Mushinsky, 1979). Females give birth to live young between late summer and early fall, and hibernation is usually between October and March (Hulse et al., 2001). Throughout their activity season watersnakes can often be found basking on logs and branches along stream banks and are occasionally found in forested areas near water (Minton, 1972). Some previous literature suggests *N. sipedon* does not maintain a home range and instead repeatedly shifts from one core activity center to the next (Tiebout and Cary, 1987; Roth and Greene, 2006), but earlier observations suggest they can be found in the same general areas from year to year (Brown, 1940; Stickel and Cope, 1947).

Gregory et al. (1987) and Macartney et al. (1988) reviewed the findings of snake spatial biology studies, and although

these publications are now two decades old, their discussions of the factors that hinder our ability to elucidate general patterns are no less relevant today. Summarizing the findings from previous studies of *N. sipedon* (Tiebout and Cary, 1987; Mills et al., 1995; Roth and Greene, 2006) is difficult, other than to say that movement patterns and home ranges vary considerably among individuals and among populations. One critical limitation is the use of different methods in different studies. In addition, many biological factors have been shown to influence the spatial biology of individual snakes, including sex and reproductive condition (Brown and Weatherhead, 1999), mate distribution (Brown and Weatherhead, 1999), prey availability (Fraker, 1970), habitat structure (Brown and Weatherhead, 1999), temperature (Brown and Weatherhead, 2000), ecdysis (Madsen, 1984), and overall body condition (Roth and Greene, 2006).

In this paper we address some of these confounding issues. We compare home ranges and movements of males to females, both gravid and non-gravid, we compare data collected during the mating season with data collected after, and we quantify site fidelity. To compare our findings with those of other researchers, who employed various methods for estimating watersnake home ranges (Tiebout and Cary, 1987; Brown and Weatherhead, 1999; Roe et al., 2004), we calculated kernel and convex polygon estimates. Because those methods appear not to reflect accurately the spatial patterns we observed, we provide three additional estimates we think better describe the linear nature of our snakes' home ranges, including our own "corridor" home range estimate.

Testing the idea that urban animals exhibit reduced movement patterns compared to their natural counterparts would require conducting identical studies at the same time on the same species in different geographic areas. Any differences found would be difficult to interpret and could be due largely to differences in habitat structure or resource availability (Gregory et al., 1987; Macartney et al., 1988). Our study site allowed us to compare members of a single population, which could potentially use only urbanized areas, only natural areas, or both.

We tested the hypotheses that snakes in urban areas would have smaller home ranges, would move less often, and would exhibit greater site fidelity than snakes in natural areas. Also, we expected that when compared to findings from previous studies of spatial biology of *N. sipedon*, which were all conducted in relatively undisturbed habitats, snakes at our site would exhibit these same reduced movement patterns.

MATERIALS AND METHODS

Study area.—This study was conducted along a two-kilometer stretch of Monocacy Creek that flows through a mixture of urban and natural areas in downtown Bethlehem, Pennsylvania (Fig. 1). The Monocacy is a fourth order, low-gradient, spring-fed stream with water temperatures during the snake activity season ranging from 10 to 19°C. Within the study site, the upper 0.3 km of the stream flows through a manicured municipal park, where it is channelized by gabion baskets and railroad ties and spanned by a series of small rock dams. Here the creek is heavily used by anglers, and the stream banks are grass and are mowed weekly. The creek then flows under a bridge of a heavily

Fig. 1. Aerial photograph of the study site with urban and natural areas labeled. The most frequently used hibernaculum is indicated with a white asterisk. Approximate boundaries of the urban and natural areas are indicated with black lines across the stream. White bar = 100 m.

traveled two-lane road and emerges in a small municipal conservation corridor. Vegetation at the site is largely invasive and includes the shrubs buckthorn (*Rhamnus frangula*), bush honeysuckle (*Lonicera maackii*), red raspberry (*Rubus idaeus*), and Russian olive (*Elaeagnus angustifolia*), and the trees ailanthus (*Ailanthus altissima*), common catalpa (*Catalpa bignonioides*), honey locust (*Gelditsia triacanthos*), and sugar maple (*Acer saccharum*). For the next kilometer the stream has a wide riparian zone, and there is a small footpath that is lightly traveled by a regular group of anglers and hikers. The conservation corridor ends as the riparian zone narrows from between zero to 15 meters in width, and over the next 0.7 km the stream flows between two industrial properties with numerous large piles of sheet metal, plastic, wood pallets, and concrete. The stream then flows under another bridge of a busy two-lane road. 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 (Fig. 1).

Subjects and tracking dates.—From 21 May 2004 through 6 July 2006, we implanted radiotransmitters into 50 (14 male, 36 female) adult *N. sipedon* (Reinert and Cundall, 1982). Unpotted transmitters were purchased from L. L. Electronics (Mahomet, IL), and transmitter packages were assembled in the lab, which allowed us to tailor their size and shape to individual snakes. Thinner packages were implanted in thin snakes (males and smaller females) and shorter, wider packages were implanted in heavier gravid females. Transmitters ranged in weight from 3.15 to 7.58 g and averaged approximately 4.20 g. All transmitters were less than 3.5% of the body weight of the snake in which they were implanted.

Individuals were usually located once per day, and the number of relocations per snake ranged from one to 261. The snout–vent lengths (SVL), dates tracked, and total number of relocations for each snake are listed in Table 1. Six snakes with fewer than five relocations were omitted from any analysis and therefore are not included in Table 1. Male *N. sipedon* are considerably smaller than females, and unfortunately only the largest males could be implanted with transmitters, resulting in disproportionately more data for females than for males.

Hibernation sites are known for 20 snakes, four of which were followed into hibernation in consecutive years. In 2004 we found that some snakes with transmitters replaced late in the activity season (so that the transmitter would still be functioning at the time of spring emergence) did not have sufficient time to heal and in the spring were found with open wounds around the transmitter. In 2005 and 2006 we did not perform any surgeries after 1 September. Consequently we have fewer data for the very beginning and end of the activity seasons due to battery failure.

Individuals were initially captured opportunistically throughout the activity season. All females were considered non-gravid prior to 1 June and after 1 October (Barron and Andraso, 2001). Between these dates the reproductive status of females was determined when they were initially captured for transmitter implantation (for snakes caught after 1 June) or when they were captured opportunistically in mid-summer (for snakes initially caught before 1 June). Most individuals were handled at least once during the season to check for general condition and potential injury.

During the three-year study, 2520 relocations (984 of gravid females, 1145 of non-gravid females, 391 of males; 1883 in the urban areas, 637 in the natural area) were made. Snake locations were recorded along with whether or not the snake was moving at the time and whether or not it had moved from its previous location. At the end of the final field season we reviewed all of the locations for each snake to determine if a site (with a one-meter radius) was ever reused or was only occupied once.

Home range determination.—Using ArcGIS (ver. 9.1, Environmental Systems Research Institute, Inc., Redlands, CA), snake locations were plotted on a digital aerial photograph of the site. Home range estimates were generated using either Hawth's Analysis Tools for ArcGIS (ver. 3.26, Beyer, 2006. http://www.spatialecology.com/htools) or Home Range Extension for ArcGIS (Carr and Rodgers, 1998. http://www.blue.lakeheadu.ca/hre). Home ranges were determined for the 35 (28 female, 7 male) individuals with at least 25 relocations in a year. Ranges were calculated for two of those snakes in all three years and for another six snakes in two successive years. In total, 45 home ranges were calculated, 24 of which are based on 50 or more relocations.

Several techniques are available for estimating home range (reviewed by Powell, 2000; Kernohan et al., 2001). Row and Blouin-Demers (2006) suggest that when attempting to determine maximum home range, minimum convex polygons (MCPs) are preferred for herpetofauna, but that when the goal is to examine habitat preference, kernel estimators are most appropriate. In order to facilitate comparisons between our study and others, we calculated home ranges with two commonly used estimators, MCPs (Hayne, 1949) and the 50 and 95% fixed kernels using least-squares cross validation (LSCV) to choose smoothing parameters (Worton, 1989). Because our data were highly autocorrelated (mean Swihart and Slade index = 2.03 ± 1.01), we also calculated 95% fixed kernels using LSCV after eliminating multiple observations of the same location (Swihart and Slade, 1985; Kernohan et al., 2001).

Kernel and MCP methods were developed for animals that move through the landscape with few restrictions (Blundell et al., 2001), but our snakes were essentially linearly distributed along the creek. We include three additional linear range estimates that we feel more accurately describe the area used by species that are primarily confined to stream-side habitats: the length of stream between a snake's most upstream and downstream locations, the length of stream included within each 95% fixed kernel using reference smoothing parameters (Blundell et al., 2001), and the area described by a method we term "corridor home range." The corridor home range includes the area of the creek between a snake's most upstream and downstream locations plus the non-overlapping areas included in MCPs that were generated from subsets of snake locations isolated from each other by more than 100 meters. Our rationale for developing this estimator is provided in the discussion.

Statistics.—ANOVA was used to test for significant differences in mean home range size estimates among males, gravid females, and non-gravid females, and among snakes using the urban areas only, natural area only, and those that used both. We used chi-square analysis to compare relative frequencies of site reuse and movement between urban and natural areas and between sexes. To determine if snakes

Table 1. Subjects, Tracking Dates, Total Number of Relocations. Snakes 18, 20, 26, 29, 39, and 43 had fewer than five relocations. They were omitted from analyses and are therefore not included in this table.

Snake	Sex	SVL (mm)	Dates tracked (relocations)			Total
			2004	2005	2006	
1	M	663	5/20–7/4 (42)			42
2	F	690	5/23–7/14 (38)			38
3	F	700	5/24–7/24 (44)			44
4	F	775	5/24–10/8 (67)			67
5	F	665	6/2–6/14 (7)			7
6	F	677	6/2–10/10 (68)			68
7	M	651	6/2–8/8 (47)			47
8	F	926	6/2–10/10 (63)			63
9	F	745	6/6–10/10 (72)	6/29–10/19 (69)		141
10	F	662	6/10–8/22 (41)	6/5–6/20 (11)		52
11	F	630	6/17 (1)	5/17–10/21 (57)	4/27–7/7 (35)	93
12	F	751	6/30–10/10 (82)	4/21–10/19 (117)	5/17–10/21 (62)	261
13	F	715	6/23–7/9 (11)			11
14	M	685	6/23–7/19 (12)			12
15	F	755	7/28–10/10 (50)	5/18–10/19 (57)		107
16	F	741	7/22–10/10 (46)	7/10–10/21 (64)	5/5–7/25 (29)	139
17	M	604	8/16–10/10 (28)	4/27–7/28 (50)		78
19	F	714	10/8–10/10 (2)	6/5–10/16 (61)	3/30–10/9 (88)	151
21	F	603		4/26–7/21 (30)	6/19–8/26 (34)	64
22	M	619		5/4–7/11 (19)		19
23	M	657		5/4–8/7 (20)		20
24	F	775		5/4–10/19 (102)	5/18 (1)	103
25	F	695		5/5–10/25 (53)		53
27	M	595		5/14–5/26 (6)		6
28	M	601		5/31–9/4 (54)		54
30	F	625		5/27–10/19 (25)		25
31	F	543		5/27–8/29 (17)	5/9–8/16 (36)	53
32	F	608		6/1–10/18 (51)		51
33	F	994		6/17–10/18 (38)		38
34	F	565		6/17–8/3 (25)		25
35	F	720		6/21–9/26 (13)		13
36	F	645		7/14–8/15 (17)	3/11 (1)	18
37	M	610		9/19–10/19 (8)		8
38	M	564			3/31–6/14 (25)	25
40	F	665			4/11–10/11 (91)	91
41	F	724			4/17–10/21 (28)	28
42	M	624			4/27–7/25 (43)	43
44	F	694			6/5–8/26 (36)	36
45	F	608			6/5–8/31 (35)	35
46	F	616			6/8–10/10 (75)	75
47	M	590			6/20–8/26 (35)	35
48	F	630			6/20–9/4 (44)	44
49	F	625			6/21–10/21 (72)	72
50	F	681			7/6–10/21 (65)	65

in urban areas behaved differently from those in the natural area, expected frequencies for the urban areas were derived from the observed frequencies in the natural area. To determine if snakes showed increased movement in the spring (while males were searching for mates and before females were gravid), we derived expected movement frequencies for spring (prior to 1 June) from observed frequencies in summer and fall (after 1 June). We also tested if females moved less often or exhibited greater site fidelity than males by deriving expected values for female movement frequency and site fidelity from observed male values.

RESULTS

Snakes tended to stay near the stream; 57% of snake relocations were within five meters of water, while only 12% of relocations were more than 20 meters from water, 3% of which were more than 50 meters from water. The farthest a snake was found from the stream was 100 meters (during an extreme flood event). When snakes were not located directly along the stream bank, they tended to occupy relatively distinct centers of terrestrial activity, many of which were separated by considerable distances (100 meters or more).

Table 2. Subjects and Their Reproductive Condition, Number of Relocations, Location, and Seven Home Range Size Estimates. Reproductive condition (cond.): G–gravid, NG–not gravid, M–male; location (loc.): U–only ever found in urban part, N–only ever found in natural part, B–found in urban and natural parts; and number of relocations (reloc.) and the seven estimates of home range size: minimum convex polygon (MCP), corridor method (cor.), meters of stream within MCPs (stm.), 50% and 95% kernels with LSCV, linear method of Blundell et al. (2001), and the 95% LSCV kernel using each novel location only once (sub.).

Snake (yr)	cond.	loc.	reloc.	MCP (ha)	cor. (ha)	strm. (m)	50, 95% (ha)	linear (m)	sub. (ha)
1 (04)	M	U	42	0.53	0.52	380	0.002, 0.018	200	1.84
2 (04)	G	U	38	0.17	0.14	120	0.001, 0.006	175	0.89
3 (04)	G	U	44	1.41	0.56	320	0.006, 0.059	380	4.14
4 (04)	NG	B	67	0.29	0.21	100	0.001, 0.011	120	1.77
6 (04)	G	B	68	0.09	0.14	100	0.001, 0.006	80	1.06
7 (04)	M	U	47	0.11	0.18	140	0.002, 0.010	200	0.26
8 (04)	G	B	63	0.80	0.76	440	0.002, 0.017	125	0.06
9 (04)	G	B	72	0.91	0.52	175	0.008, 0.048	275	0.09
9 (05)	NG	B	69	9.66	1.73	950	0.071, 0.478	1120	10.53
10 (04)	G	N	41	1.43	0.76	530	0.042, 0.240	550	3.12
11 (05)	G	N	57	2.23	1.16	350	0.025, 0.0130	178	1.58
11 (06)	G	N	35	0.12	1.16	37	0.002, 0.012	73	0.58
12 (04)	G	U	82	2.99	1.02	360	0.027, 0.168	575	9.50
12 (05)	G	U	117	1.42	0.58	400	0.008, 0.059	400	6.32
12 (06)	G	U	62	0.32	0.27	170	0.003, 0.018	277	0.68
15 (04)	G	U	50	0.50	0.50	100	0.039, 0.279	228	3.14
15 (05)	G	B	57	0.24	0.31	60	0.003, 0.017	107	0.07
16 (04)	G	U	46	1.11	0.52	330	0.016, 0.087	360	4.28
16 (05)	G	B	64	4.15	2.14	800	0.071, 0.354	300	2.91
16 (06)	G	B	29	0.20	0.20	85	0.004, 0.027	88	1.20
17 (04)	M	U	60	0.25	0.28	290	0.003, 0.018	300	1.47
17 (05)	M	U	50	0.40	0.30	260	0.002, 0.023	240	0.01
19 (05)	NG	U	61	0.29	0.28	80	0.001, 0.001	170	1.51
19 (06)	NG	U	88	0.22	0.22	100	0.002, 0.013	77	0.55
21 (05)	G	U	30	0.08	0.11	50	0.001, 0.005	35	0.27
21 (06)	G	U	34	0.04	0.07	47	0.001, 0.002	94	0.38
24 (05)	G	B	102	6.30	1.73	730	0.028, 0.326	630	1.10
25 (05)	G	B	53	3.05	1.28	510	0.021, 0.213	420	1.71
28 (05)	M	B	54	0.03	0.04	20	0.001, 0.003	31	0.01
30 (05)	G	B	25	0.22	0.28	120	0.005, 0.005	218	01.73
31 (06)	G	B	36	0.02	0.16	65	0.001, 0.006	98	0.01
32 (05)	NG	B	51	0.05	0.05	20	0.001, 0.001	10	0.44
33 (05)	G	B	38	0.01	0.01	10	0.002, 0.002	48	0.02
34 (05)	NG	U	25	0.05	0.09	60	0.001, 0.001	76	0.15
38 (06)	M	U	25	0.91	0.60	400	0.011, 0.085	560	4.62
40 (06)	G	N	91	2.18	0.89	380	0.013, 0.115	445	5.75
41 (06)	G	B	28	0.10	0.15	10	0.001, 0.008	10	0.01
42 (06)	M	N	43	1.51	0.69	490	0.008, 0.065	669	9.40
44 (06)	G	N	36	0.26	0.30	240	0.001, 0.012	291	0.83
45 (06)	G	U	35	0.12	0.12	70	0.001, 0.006	169	0.21
46 (06)	NG	U	75	0.13	0.13	100	0.001, 0.001	63	0.04
47 (06)	M	B	35	2.23	2.23	1425	0.427, 2.220	2369	5.45
48 (06)	G	N	44	1.40	1.04	650	0.037, 0.201	350	0.69
49 (06)	NG	N	72	0.04	0.05	30	0.001, 0.004	12	0.01
50 (06)	G	N	65	0.08	0.08	135	0.001, 0.005	6	0.31

Home ranges.—Home range estimates for each snake are provided in Table 2. Home range sizes did not differ significantly between snakes that occupied only the natural area, occupied only the urban areas, and occupied both, or between males, non-gravid, and gravid females (Table 3). Home range sizes were not significantly different regardless of whether we included every range calculated ($n = 45$) or used the mean range sizes for snakes with ranges calculated in multiple years ($n = 35$). Home range size was not significantly correlated with SVL, the number of relocations, or the number of days a snake was tracked (Table 3).

Movement frequency.—Urban snakes were found actually moving slightly less often (2% of relocations) than natural snakes (4%, $\chi^2 = 18.72$, $P < 0.01$), and females were found moving slightly less often (2%) than males (4%, $\chi^2 = 21.54$, $P < 0.01$). These percentages were not different between spring and summer. Throughout the season snakes were

Table 3. Means, Standard Deviations, and Analysis of Variance of Seven Home Range Estimates for the Three Reproductive Groups and for Snakes in the Urban Area Only, Natural Area Only, and in Both Areas. Correlations with SVL, number of relocations, and number of tracking days are provided for each home range estimator. Abbreviations and units are as for Table 2.

	n	reloc. mean (SD)	MCP mean (SD)	cor. mean (SD)	strm. mean (SD)	50% mean (SD)	95% mean (SD)	linear mean (SD)	sub. mean (SD)
All	45	53.3 ± 21.1	1.1 ± 2.0	0.5 ± 0.6	280.3 ± 288.8	0.013 ± 0.059	0.12 ± 0.341	291.3 ± 386.6	2.0 ± 2.7
G	29	52.9 ± 23.0	1.1 ± 1.4	0.6 ± 0.5	260.8 ± 221.7	0.012 ± 0.017	0.080 ± 0.105	237.6 ± 173.6	1.8 ± 2.3
NG	8	65.1 ± 19.9	1.3 ± 3.4	0.3 ± 0.5	202.9 ± 330.5	0.010 ± 0.026	0.072 ± 0.179	206.0 ± 373.0	1.9 ± 3.5
M	8	44.4 ± 11.3	1.2 ± 2.2	0.5 ± 0.7	425.6 ± 430.5	0.056 ± 0.149	0.305 ± 0.774	571.1 ± 755.2	2.9 ± 3.3
ANOVA		$F_{2,42} = 1.68$, $P = 0.20$	$F_{2,42} = 0.11$, $P = 0.89$	$F_{2,42} = 0.57$, $P = 0.57$	$F_{2,42} = 1.35$, $P = 0.27$	$F_{2,42} = 1.59$, $P = 0.22$	$F_{2,42} = 1.47$, $P = 0.24$	$F_{2,42} = 2.78$, $P = 0.74$	$F_{2,42} = 0.51$, $P = 0.60$
U	19	53.2 ± 23.8	0.6 ± 0.7	0.3 ± 0.3	198.8 ± 133.1	0.006 ± 0.011	0.047 ± 0.071	241.0 ± 157.2	2.1 ± 2.6
N	9	53.8 ± 19.0	1.0 ± 0.9	0.7 ± 0.4	315.8 ± 221.1	0.014 ± 0.016	0.087 ± 0.089	285.3 ± 239.2	2.5 ± 3.2
B	17	53.2 ± 23.7	1.8 ± 3.01	0.7 ± 0.8	367.3 ± 426.0	0.037 ± 0.103	0.214 ± 0.54	250.8 ± 386.7	1.6 ± 2.7
ANOVA		$F_{2,42} = 0.01$, $P = 0.99$	$F_{2,42} = 1.94$, $P = 0.16$	$F_{2,42} = 2.06$, $P = 0.14$	$F_{2,42} = 1.54$, $P = 0.23$	$F_{2,42} = 1.02$, $P = 0.37$	$F_{2,42} = 1.09$, $P = 0.35$	$F_{2,42} = 0.35$, $P = 0.71$	$F_{2,42} = 0.33$, $P = 0.73$
Correlation w/ SVL			$r = 0.13$, $P = 0.38$	$r = 0.99$, $P = 0.11$	$r = -0.04$, $P = 0.81$	$r = -0.11$, $P = 0.49$	$r = -0.09$, $P = 0.57$	$r = -0.05$, $P = 0.74$	$r = -0.05$, $P = 0.64$
Relocations			$r = 0.29$, $P = 0.12$	$r = 0.23$, $P = 0.14$	$r = 0.14$, $P = 0.36$	$r = -0.87$, $P = 0.57$	$r = -0.05$, $P = 0.76$	$r = 0.04$, $P = 0.71$	$r = 0.11$, $P = 0.54$
Days tracked			$r = 0.10$, $P = 0.58$	$r = 0.03$, $P = 0.86$	$r = 0.01$, $P = 0.98$	$r = 0.07$, $P = 0.69$	$r = 0.07$, $P = 0.70$	$r = 0.07$, $P = 0.71$	$r = 0.11$, $P = 0.54$

found to have moved from their previous location at 27% of relocations. Snakes moved slightly more often prior to 1 June (32%, $\chi^2 = 4.22$, $P = 0.04$) than after (27%). Urban snakes moved from their previous location less often (25%) than natural snakes (36%, $\chi^2 = 92.61$, $P < 0.01$). Gravid (25%) and non-gravid (26%) females were not found to have moved at significantly different rates ($\chi^2 = 0.34$, $P = 0.56$), but females (gravid and non-gravid combined, 26%) did relocate less often than males (39%, $\chi^2 = 151.21$, $P < 0.01$). Males relocated more frequently prior to 1 June (48%, $\chi^2 = 15.49$, $P < 0.01$) than after (36%). Gravid females relocated more frequently in June and July (34%, $\chi^2 = 48.91$, $P < 0.01$) than in August and September (18%).

Site fidelity/reuse.—Snakes exhibited considerable site fidelity; 82% of snake relocations were within a one-meter radius of a spot that snake had at some time previously occupied. Most often the reused sites were specific (in the same hole, under the same rock, on the same branch). Snakes were found in former locations significantly more often in the urban environment (86%) than in the natural environment (78%, $\chi^2 = 69.79$, $P < 0.01$). Gravid and non-gravid females did not differ significantly in their site reuse ($\chi^2 = 0.03$, $P = 0.87$), but females (gravid and non-gravid combined) reused sites significantly more often (86%) than males (73%, $\chi^2 = 178.78$, $P < 0.01$). When snakes did move from their previous location, they returned to a formerly occupied site 56% of the time. Urban snakes returned to former sites more often (58%) than natural snakes (52%, $\chi^2 = 8.89$, $P < 0.01$). Gravid (57%) and non-gravid (61%) females relocated to former sites at approximately the same frequency ($\chi^2 = 1.39$, $P = 0.24$) but significantly more often than males (50%, $\chi^2 = 17.89$, $P < 0.01$).

The snakes we tracked in consecutive years used similar areas each year. Snake 12 used the same areas in all three years except that after a major flood event in 2004, she moved 100 meters away from the stream until water levels returned to normal. This one new location doubled the size of her MCP. In 2005 she occupied five new locations in addition to those from 2004, but by 2006 none of her sites were new. Snake 16 completely shifted her home range/activity area between 2004 and 2006; in 2005 she used sites in both the 2004 and 2006 area. Her 2006 MCP was completely contained within her 2005 MCP. Snake 11's MCP from 2006 was completely contained within the MCP of the previous year, and no additional sites were added in 2006. Snake 9 reused many of her 2004 locations again in 2005 but increased the size of her home range ten-fold by traveling to a new site 650 meters upstream of her usual activity center. The remaining snakes tracked for more than one activity season essentially used the same sites and had similar home ranges in successive years.

Of the 20 snakes followed into hibernation, 16 hibernated among large rocks under the railroad bed between the pond and the stream (Fig. 1). Here water from the pond flows under the railroad into the stream and is approximately 10°C in the winter. The remaining snakes hibernated in the middle of the natural area in a section of stream bank within a few meters of each other. Only four snakes were followed into hibernation in consecutive years. Snake 12 used the same hibernaculum in all three years. Snake 19 used the same location in 2004 and 2005 but chose a new hibernation place in 2006. Snake 15 hibernated in the same place both years she was tracked, whereas snake 16 used different hibernacula in the two years she was tracked.

DISCUSSION

Difficulties in comparing home range estimates.—Synthesizing findings from home range studies is difficult because they are conducted in different types of habitats and over various time periods, employ different methods for determining range size, and often do not account for the length of time individuals were followed (Gregory et al., 1987; Macartney et al., 1988). Regarding previous radio-tracking studies of *N. sipedon*, Tiebout and Cary (1987) helpfully provide the numbers of days tracked, the numbers of relocations, the SVLs, and the home range sizes for individual snakes, while Roth and Greene (2006) and Brown and Weatherhead (1999) only provide mean values. In order to facilitate comparisons between studies, it is important to provide the dates and number of tracking days for each snake.

Home range and performance of home range estimators.—Our home range estimates appear smaller than those reported for other *N. sipedon* populations by Roe et al. (2004) and Roth and Greene (2006), but it is difficult to know if our snakes truly used less space than those in other populations. Using the least-squares cross validated (LSCV) fixed kernel method, Roe et al. (2004) report a mean 95% kernel of 3.1 (± 0.27) ha for females and 6.9 (± 7.2) for males, and Roth and Greene (2006) report a mean 95% kernel of 2.72 (± 1.15) ha for females (gravid and non-gravid combined) and 2.92 (± 0.79) ha for males. Using the same methods, we found much smaller values. Our mean 95% kernel size for males was 0.31 (± 0.77) ha, and our mean for females was 0.08 (± 0.12) ha. Although simulations have shown fixed kernel estimators using LSCV to be accurate in most situations, the method may not perform well for situations in which animals reuse locations multiple times (Worton, 1989; Seaman and Powell, 1996; Row and Blouin-Demers, 2006). Seaman and Powell (1996) demonstrate that adding tightly spaced observations to more dispersed locations can lead to a smaller home range estimate than if only the more dispersed locations were used. Our considerably smaller 95% kernel estimates may be due to the fact that snakes at our study site were found in former locations at 82% of relocations. When we conducted the same analysis but only included each snake location once, we arrived at a mean range size estimate of 2.0 (± 2.7) ha, a value much more similar to those reported by Roe et al. (2004) and Roth and Greene (2006). We chose to conduct this sub-sampling method while trying to determine why our 95% kernel estimates were more than an order of magnitude smaller than those found by the authors above. By using each location only once, data sets for most of our animals became far smaller than recommended for this method (Seaman et al., 1999).

In our case, the 95% fixed kernel/LSCV method yielded small disjunct islands and excluded the areas the snakes traveled within and must have been familiar with (Powell, 2000). Also, most of the kernels generated do not include the stream. These problems seem likely to result for relatively sedentary, infrequently feeding species. We rarely found snakes in the water, yet stomach contents collected opportunistically at the time of transmitter implantation indicate they fed exclusively on fish.

Roe et al. (2004) report a mean MCP size of 3.30 (± 0.18) ha for females and 5.60 (± 0.58) for males while we found a mean MCP size of 1.18 (± 1.92) ha for females and 1.32 (± 2.23) for males. A unique feature of our study is that it was conducted along a stream, whereas the previously published studies concerning the spatial biology of *N. sipedon* were conducted around open water. When we generated MCPs, it became obvious that while the method may reasonably portray space use of animals that travel across open areas like a lake or forest floor, it is not well-suited for animals that use winding corridors to travel between distant points. MCPs for snakes that made long-distance movements upstream and downstream often include very little of the creek even though it is almost certainly the route traveled (Fig. 2). Madsen (1984) describes a similar situation in which he thought the MCP method overestimated the area used by *Natrix natrix*, which mostly move along stone fences and hedgerows and periodically travel across unsuitable areas. He chose to calculate MCPs by month and sum them to arrive at a ''combined home range'' that was on average approximately half the size of the original total MCP. As Tiebout and Cary (1987) point out, a problem with that method is the rather arbitrary division of time periods. Also, while Madsen's method did eliminate large areas in which the snakes were never found, what results is a group of polygons that may or may not be connected to each other.

To be biologically meaningful, home range estimates must include the paths snakes used to travel between more intensely used areas, regardless of how quickly the snake moved through them or the apparent unsuitability of the area being traversed. To address this issue, we generated corridor home range estimates. Because snakes were never found farther than 100 meters from the stream and terrestrial activity centers appeared to be smaller than 100 meters in diameter, we think snakes probably used the stream to travel between distant terrestrial locations. The corridor home range includes the MCPs encompassing all of a snake's locations within 100 meters of each other plus the area of stream connecting the most upstream and downstream locations. This estimator outlines the area actually used by the snakes, omits large unused areas, and includes all of the animal's known locations along with the most parsimonious route of travel between distant locations (and in this case the food resource). Based on the corridor method, snakes occupied home ranges averaging 0.51 ha, which is approximately half of the mean MCP value but more than four times greater than the mean 95% kernel value.

Using river otters as a model, Blundell et al. (2001) assessed the effects of kernel methods, smoothing parameters, number of relocations, and autocorrelation on estimates of linear home range. Like us, they found that LSCV smoothing often produced small disjunct contours that frequently excluded important feeding areas and underestimated linear range size. To best estimate linear home range, Blundell et al. (2001) advocate conducting fixed kernel analysis using the reference smoothing parameter and then measuring the length of coastline (stream) within the kernel. By applying their method to our data, we estimated that snakes use an average of 291 meters of stream. By determining the length of stream between a snake's most upstream and downstream locations, we arrived at a very similar average of 280 stream meters.

It is clear that the MCPs include large areas in which the snakes were never found and across which they were unlikely to have traveled. Kernels provide important information about how intensely certain sites were used, but their size depends greatly on the choice of smoothing
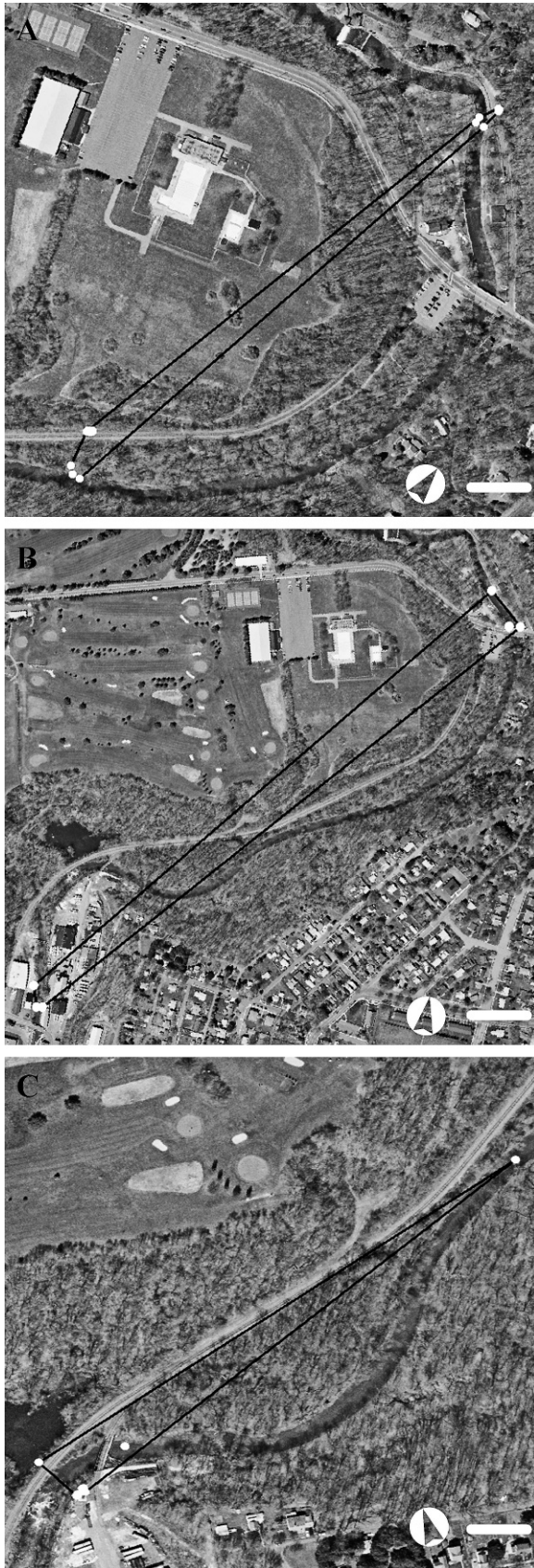
Fig. 2. Location points (white dots) and the minimum convex polygon boundaries (black lines) for snake 48 in A, snake 47 in B, and snake 8 in C. The MCPs that connect distant terrestrial locations almost completely exclude the stream, and in A and B the majority of the MCP is more than twice as far away from water as the furthest observed snake location. White bar = 100 m in A and B and 50 m in C.

parameter. In addition, in instances where data are highly autocorrelated (in this case because animals reuse sites often and move infrequently) kernels can be far too small and are often not connected to each other. Perhaps most importantly, both of these estimators frequently excluded the stream from the home range boundary. Conversely, linear estimates do not account for the areas used by snakes that were not located directly along the stream. At our study site much of the stream corridor is densely shaded, and gravid females spend large amounts of time in more open sunny areas that are 30 to 50 meters away from the stream. Although corridor home range estimates cannot be generated automatically like kernel and MCP estimates, we think they most accurately describe the area used by snakes at our site. To illustrate these points, Figure 3 shows the home range of snake 25 as delineated by the kernel, MCP, and corridor methods.

Movement patterns.—Although home range sizes were not significantly different between urban and natural snakes, urban snakes were found moving less often and were found to have moved from their former location less often than natural snakes. Our findings concerning home range differences between sexes agree with other studies demonstrating that males and females do not differ in the size of their home ranges (Brown and Weatherhead, 1999; Roe et al., 2004; Roth and Greene, 2006). Like Greshock (1998), we found males move more often than females, and gravid females move less often later in the summer. Our estimates of movement frequency are very similar to Tiebout and Cary's (1987) finding that snakes had moved noticeably from their previous location at 27% of relocations, but appear lower than Roth and Greene's (2006) finding that snakes moved on 71% of tracking days.

The maximum linear distance covered by a snake in a year was 1450 meters, which was traveled within one day. Such long-distance movements are rare. We observed only two other movements greater than 300 meters in one day (750 m and 560 m). The snakes that made these long-distance moves all returned to the place they had occupied before the move.

Site fidelity/reuse and maintenance of home range.—Site fidelity in snakes is periodically mentioned in the literature (Shine, 1987; Weatherhead and Hoysak, 1989; Plummer and Mills, 2000) but rarely quantified (but see Whitaker and Shine, 2003; Pearson et al., 2005). Stickel and Cope (1947) reported that a watersnake living along a river was found 380 feet from where it had been captured two years earlier. Carpenter (1952) found that garter snakes recaptured over long periods of time averaged only slightly farther from the point of original capture than those recaptured after a short interval. Not surprisingly, watersnakes living around fish hatcheries do not stray very far (Grant, 1935; Fraker, 1970). Madsen (1984) suggests *Natrix natrix* use the same home range during successive years.

We found the extent to which our snakes reused sites striking, and we are surprised that neither Tiebout and Cary (1987) nor Roth and Greene (2006) mention this phenomenon. Both of their studies describe *N. sipedon* periodically shifting from one core area to another and provide no indication that snakes return to previously occupied areas. Tiebout and Cary (1987) write that snakes "continue to explore new areas and leave old areas behind." Our data
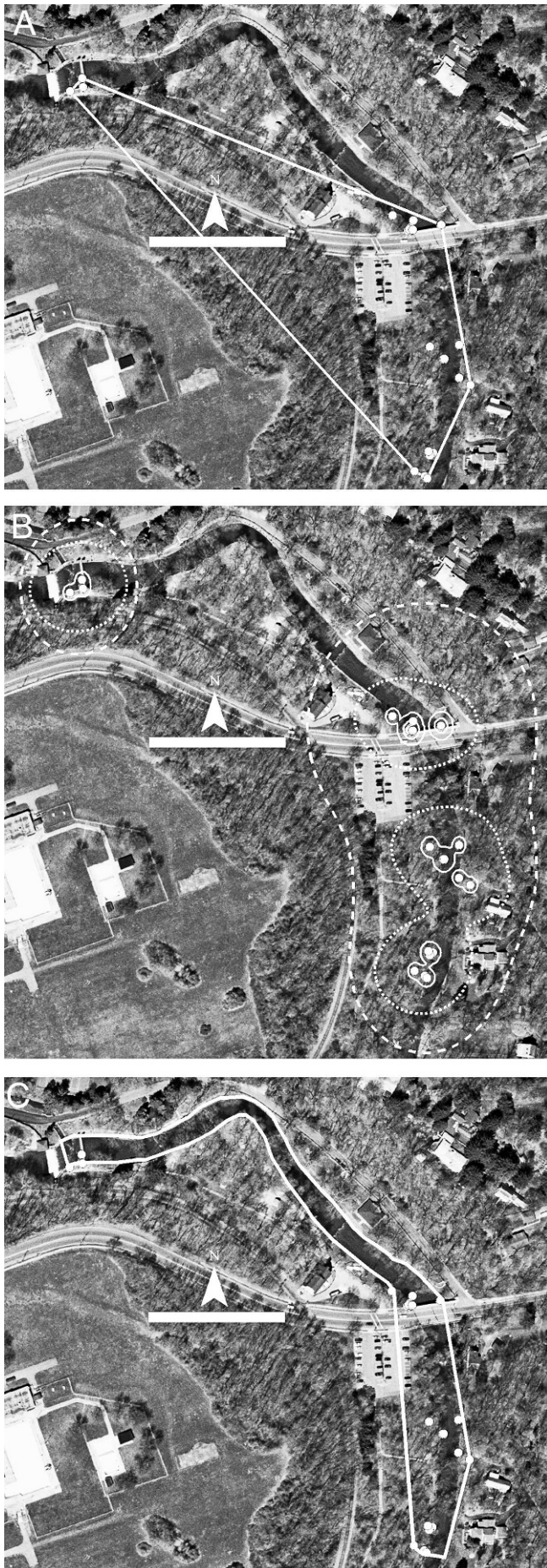
show that some individuals do shift from one core area to another; however, when tracked long enough, they tend to return to previously used sites. We found no evidence that snakes leave old areas behind.

Both of the studies mentioned above found that home range size was positively correlated with the number of days snakes were tracked and therefore conclude that *N. sipedon* does not maintain a home range. Madsen (1984) also found that home range size increases with the number of tracking days but instead interprets the correlation as evidence that snakes should be tracked for longer periods of time. We, like Michot (1981), did not find a significant correlation between home range size and number of tracking days. Both Tiebout and Cary (1987) and Roth and Greene (2006) tracked snakes for only about three months, which may not have been long enough to observe individuals returning to previously occupied locations.

Our data show a trend of increased site fidelity and reduced movements in urbanized areas compared to more natural areas. It may be worth noting that during this study five snakes containing transmitters were obviously killed by people. Each was killed in the urban half of the study site. Several other dead snakes were found in the urban area, and anglers and city workers indicated that snakes were often killed by people. Perhaps the advantages of site fidelity are greater in urban areas where snakes, which are apparently considered dangerous and loathsome by most, must cope with people and various human-made hazards.

ACKNOWLEDGMENTS

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Fig. 3. Location points and home range boundaries determined by various methods for snake 25. The minimum convex polygon is shown in A. In B the 50% and 95% fixed kernels using LSCV are very small and are indicated by solid white lines, the 95% kernel using the reference smoothing parameter is indicated by a small dash line, and the 95% fixed kernel using LSCV but only including each location once is indicated with a large dash line (largest). The home range boundary determined by our corridor method is shown in C. White bar = 100 m.

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