

## Movement Patterns and Home Range Use of the Northern Watersnake (*Nerodia sipedon*)

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The factors that influence spatial use and movement patterns in ectotherms may have important fitness consequences. To examine the effects of sex and condition on spatial use, we used radio telemetry to observe the movement of 18 adult *Nerodia sipedon* in a southwest Missouri lake. Snakes generally remained in close proximity (<5 m) to aquatic habitats throughout the summer. Home range size estimates differed according to calculation method. Monthly total home range sizes peaked in mid-summer, possibly in response to increased amounts of vegetative cover, although core area sizes were consistent across the season. Contrary to previous studies of snakes, mean movement rates and home range sizes of male and gravid female *N. sipedon* were statistically indistinguishable and highly variable. Body size and condition influenced spatial characteristics of females, but only appeared to influence movement frequency of males. When compared to other populations, we found that our population of *N. sipedon* tended to occupy similarly-sized shifting core areas associated with aquatic vegetation. Future studies should focus on the measurement of resource distribution to further understand the factors influencing variation in snake movements and spatial patterns.

THE understanding of movement and the use of space is critical for the understanding of many aspects of an organism's ecology, from behavior to population dynamics and conservation. In particular, the factors that influence spatial use and movement patterns in ectotherms, such as the physiological requirements of thermoregulation and resource acquisition, have important consequences for fitness (Holt, 2003) and as such may be strongly influenced by natural selection. Within a species, differing physiological requirements between sexes may result in differing strategies of spatial use.

Despite the increased effort directed toward the spatial ecology of snakes, many basic questions remain unanswered. Description of spatial patterns is complicated by the variation imposed by age-specific, sex-specific, and environmental factors on seasonal activity and spatial phenomena (Gibbons and Semlitsch, 1987; Gregory et al., 1987), which have seldom been studied (Roth, 2005). Moreover, the identification of such influential factors through comparison has been hindered by incompatibility of methodologies (Macartney et al., 1988). Standardized spatial comparisons are rare for snakes (but see Plummer and Congdon, 1994) but should be valuable for elucidating factors motivating spatial differences (Gregory et al., 1987; Macartney et al., 1988).

Size constraints imposed by transmitter packages have promoted a bias toward the study of relatively large, and often terrestrial, snake species (Reinert, 1992, 1993). We know very little

about the movement patterns of snakes that are restricted to aquatic habitats. For example, despite high relative abundances and a wide geographic distribution, North American watersnakes (*Nerodia* spp.) are under-represented in the snake spatial literature (but see Brown and Weatherhead, 2000; Roe et al., 2004). Early radiotelemetric field studies involving *Nerodia* (e.g., Fitch and Shirer, 1971; Michot, 1981) provided baseline information, but were limited to a few individuals typically monitored over short time periods. Tiebout and Cary (1987) examined a larger sample of female *N. sipedon* and found temporal shifts in activity centers, which may be commonly overlooked by short-term snake studies (Diffendorfer et al., 2005).

Here, we present data on movements and spatial use of both male and female *N. sipedon* in a Missouri lake. We examine the influence of sex, body size, and condition on spatial patterns and provide a comparison of home range data with that of previous studies of *N. sipedon*. We expect that larger individuals will use larger areas, and snakes in better condition will use less area. Variation in spatial use between sexes in snakes prevents the generation of explicit hypotheses on the influence of sex on home range size or movements.

### MATERIALS AND METHODS

*Study area.*—The study was conducted at the Springfield Conservation Nature Center along a 1,300 × 200-m area of Lake Springfield,

a shallow municipal lake on the James River in Springfield, Missouri. Aquatic habitats in our study area were characterized by shallow, vegetated, lentic conditions fed by a medium-sized gravel-bottom stream. An extensive littoral zone along the lake margins was dominated by pondweed (*Potamogeton* spp.), floating primrose (*Ludwigia peploides*), water willow (*Justicia americana*), arrowhead (*Sagittaria* spp.), and cattail (*Typha* spp.). The surrounding terrestrial environment was characterized by oak/hickory forest interspersed with patches of managed grassland. A detailed description of the study site was provided by Roth (1999).

*Telemetry and data collection.*—Eighteen adult *N. sipedon* (nine females, nine males) were captured by hand or with minnow traps from late April to mid-May 1998 and measured for snout-vent length (SVL,  $\pm 1$  mm) and mass ( $\pm 1$  g). Temperature-sensitive radio-transmitters (7.8 grams, Holohil systems SI-2T, operating at 150–152 MHz) were surgically implanted using isoflurane anesthesia following the methods of Reinert and Cundall (1982). All transmitters constituted  $< 5\%$  (except one, which was 6%) of snake body mass. Snakes were released at their site of capture within 48 hours and located once daily using a Telonics TR-2 receiver and a 3-element Yagi antenna. Individual locations were plotted on a map of the study area and later converted to X-Y coordinates for analysis. All female snakes were assumed to be gravid, which is typical of this population (BDG, unpubl. data). Reproductive condition of females was verified when possible by visual observation of distended abdomens or post-partum emaciation.

*Spatial analysis.*—Home range areas were calculated with harmonic mean (HM) and least-square cross validated fixed kernel methods. We did not include the minimum convex polygon method due to its propensity to overestimate spatial use by including areas not used by the subject (White and Garrott, 1990). Harmonic mean estimates of area were calculated using the spatial analysis package Ranges IV (R. E. Kenward, Institute of Terrestrial Ecology). Kernel estimates were derived using the Animal Movement Extension (Hooge and Eichenlaub, 1997) for ArcView (ver. 3.2, Environmental Systems Research Institute, Inc., Redlands, CA, 1996). Total activity areas and core areas were estimated for HM and kernel analyses as 95% and 50% isopleths, respectively (Tiebout and Cary, 1987; Reinert, 1992), using a  $40 \times 40$  grid with unmodified fixes.

We assessed temporal differences in spatial use by separating data for each snake into successive

monthly blocks. A 95% harmonic-mean isopleth was generated for each month of the study to determine the location of monthly activity centers. Areas of overlap among monthly subsets were subtracted and the remaining areas summed for each snake to provide a corrected home range which approximates spatial use more accurately than the total home range estimate (Reinert, 1992). We described the spatial dynamics of each snake by dividing the sum of individual monthly home ranges by their respective seasonal totals. The resulting movement index indicates a shift in activity centers or seasonally static home ranges for values less than and greater than one, respectively (Tiebout and Cary, 1987).

Individual movements were recorded as straight-line distances of  $> 1$  m between successive relocations (i.e., movement steps; Turchin, 1998). Total distance moved was measured as the sum of individual movements over the activity season. Mean distance moved per day was calculated by dividing the total distance moved by the total number of days a snake was monitored. The mean distance per move was calculated as the total distance moved divided by the total number of days in which movement occurred. Activity range length was determined as the linear distance between the two most divergent points within each home range.

To investigate potential causes of individual spatial variation we evaluated the dependence of spatial characteristics on snake body size (SVL) and condition. Body size data from radio-tracked snakes were combined with mark-recapture data from the same population to generate regressions of mass on SVL for each sex. Residuals from these regressions were used as an index of body condition. Since potential inaccuracies exist with this approach (Weatherhead and Brown, 1996; Green, 2001), we also evaluated condition influence using direct estimates of body fat. Fat mass was estimated as the difference between mean fat-free wet mass (FFWM) and measured body mass at a given SVL using the equation  $\ln \text{FFWM} = -7.795 + 3.0656 (\ln \text{SVL})$ , for which fat-free wet mass was determined by lipid extraction by Weatherhead and Brown (1996) for *N. sipedon*.

We make explicit the assumption that size and body condition remain relatively constant among individuals through the course of the season. In an effort not to disturb snake behavior, snakes were not recaptured during the study to measure changes in size or condition. We realize that once females become gravid, condition (i.e., relative fat mass) undoubtedly declines. However, we assume that this decline is a linear function of

TABLE 1. SPATIAL DATA FOR 17 *Nerodia sipedon* MONITORED BY RADIOTELEMETRY. The 95% temporally corrected (TC) harmonic mean (HM) home ranges were calculated as the sum of monthly home ranges excluding overlap (see text for further details). All areas are given in hectares.

	Males ( <i>n</i> = 8)		Females ( <i>n</i> = 9)	
	Mean (SE)	Range	Mean (SE)	Range
SVL (mm)	590.4 (13.5)	547–644	698.4 (25.4)	608–852
Number of fixes	81.4 (10.0)	29–110	98.8 (5.8)	68–116
95% HM	0.51 (0.10)	0.12–1.05	0.58 (0.08)	0.34–0.99
95% TC HM	0.24 (0.04)	0.03–0.37	0.33 (0.06)	0.10–0.77
50% HM	0.08 (0.02)	0.01–0.17	0.10 (0.03)	0.01–0.33
95% Kernel	2.92 (0.79)	1.29–8.20	2.72 (1.15)	0.69–11.64
50% Kernel	0.38 (0.09)	0.11–0.88	0.33 (0.17)	0.11–1.68

the initial measure of condition, and thus occurs at a constant rate for all females.

Nonparametric tests were employed to evaluate differences in movement and home range areas as the data were often non-normally distributed. Mann-Whitney tests and Wilcoxon Matched-Pairs tests were used to assess sexual differences in spatial use and for between-estimator comparisons, respectively. Kruskal-Wallis ANOVA was used to evaluate seasonal differences in home range size for each sex. Statistical tests were conducted using Minitab (Minitab, Inc., State College, PA, 1998), except for Wilcoxon Matched-Pairs tests, which was calculated by hand. All means are reported  $\pm 1$  SE.

As multiple comparisons were made, we employed a measure to reduce the probability of committing a Type I error. Rather than a traditional Bonferroni-type correction, which is overly conservative (Nakagawa, 2004) and increases the risk of a Type II error, we controlled the expected proportion of false positives, or the false discovery rate (FDR; Benjamini and Hochberg, 1995; Storey, 2002; Verhoeven et al., 2005). This procedure reduces the probability of committing a Type I error while maintaining levels of power higher than those typical of traditional Bonferroni adjustments (Storey, 2002). The FDR was estimated using the freely available software package QVALUE Version 1.0 (Dabney and Storey, 2004, <http://faculty.washington.edu/~jstorey/qvalue/>) for R (Ihaka and Gentleman, 1996).

## RESULTS

Overall, we recorded 1540 locations from 17 snakes (eight males, nine females); the ninth male was lost to predation after seven days and thus was omitted from spatial analyses. Monitor-

ing periods for the remaining snakes varied from 29 to 116 d ( $90.6 \pm 5.85$ , mean  $\pm$  SE).

*Home range.*—Home range size estimates varied considerably among individuals and calculation methods (Table 1). Kernel estimates (95%) were significantly larger than the 95% HM temporally corrected estimates of spatial use ( $0.296 \pm 0.038$ , Wilcoxon matched-pairs test,  $W_+ = 153$ ,  $P < 0.001$ ). The 50% HM isopleths ranged from 0.0003–0.3247 ha ( $0.0890 \pm 0.0195$ ; Table 1). Likewise, core areas estimated by the kernel method (mean = 0.36 ha) were significantly larger ( $W_+ = 153$ ,  $P < 0.001$ ) than 50% harmonic mean values (mean = 0.089 ha).

Significant seasonal differences in home range size were observed for the 95% HM areas (Kruskal-Wallis ANOVA;  $H = 12.5$ ,  $P = 0.014$ ,  $df = 4$ ) with peak area use occurring in July and August (Fig. 1). Monthly comparisons were not made for the kernel method as the number of locations was usually insufficient for meaningful monthly estimation. As a rule of thumb, kernel estimates require 30 points for meaningful estimation (Worton, 1989). Harmonic mean estimates do not have the same requirements. Core areas of activity (50% HM isopleths) were not seasonally variable ( $H = 1.68$ ,  $P = 0.793$ ,  $df = 4$ ). Mann-Whitney tests suggested that mean male and female home range sizes were not significantly different for any estimator: 95% HM (female =  $0.56 \pm 0.079$ , male =  $0.51 \pm 0.101$ ;  $U = 85.0$ ,  $P = 0.736$ ,  $Q = 0.244$ ); corrected 95% HM (female =  $0.34 \pm 0.062$ , male =  $0.24 \pm 0.038$ ;  $U = 92.0$ ,  $P = 0.312$ ,  $Q = 0.135$ ); 50% HM (female =  $0.07 \pm 0.011$ ; male =  $0.04 \pm 0.014$ ;  $U = 95.5$ ,  $P = 0.177$ ,  $Q = 0.094$ ); 95% kernel (female =  $2.72 \pm 1.150$ , male =  $2.17 \pm 0.291$ ;  $U = 67$ ,  $P = 0.341$ ,  $Q = 0.143$ ); 50% kernel (female =  $0.34 \pm 0.370$ , male =  $0.31 \pm 0.064$ ;  $U = 66$ ,  $P = 0.289$ ,  $Q = 0.129$ ).

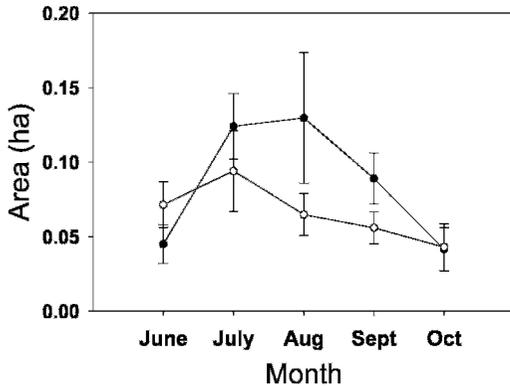


Fig. 1. Seasonal changes in area use of *Nerodia sipedon* described by monthly 95% harmonic mean isopleths. Circles represent mean area with one standard error for each sex by month. Open circles = males; closed circles = females.

**Activity center shifts.**—Core areas of activity were typically located within littoral zone emergent vegetation, which provided dense cover (Roth and Greene, unpubl. data). Temporal analysis indicated that most snakes maintained shifting activity areas throughout the summer. The sums of successive activity range areas minus overlap provided a temporally corrected home range that averaged 55% (SE = 5.21) of the total 95% HM estimates. All snakes demonstrated movement indices of less than one with no statistical effect of sex (female = 0.79 ± 0.109, males = 0.59 ± 0.078; Mann-Whitney, *U* = 91.0, *P* = 0.360, *Q* = 0.147), suggesting that males and females exhibited similar activity center dynamics.

**Movements.**—Overall, watersnakes moved on 71.2 ± 0.026% of days monitored with no significant differences between the sexes (males = 71.6 ± 4.95%, females = 70.8 ± 2.53%; Mann-Whitney *U* = 77.0, *P* = 0.736, *Q* = 0.244; Table 2). Periods of inactivity from 1–5 d (mean = 2.3 ± 0.18) occurred sporadically for all individuals. Such sedentary periods have frequently been attributed to meal digestion or ecdysis in previous studies (Reinert, 1992; Plummer and Congdon,

1994), although the secretive behavior of our snakes during such periods usually prevented observation.

The mean distance/move (range = 36.0–142.2 m, mean = 69.4 ± 6.4) was significantly larger (Mann-Whitney, *U* = 215.0, *P* = 0.0047, *Q* = 0.013) than the mean distance moved/day (range = 25.3–110.8 m, mean = 49.0 ± 4.9), supporting the above analysis that snakes did not move on a daily basis. No overall sexual differences were apparent for mean distance moved/day (males = 48.8 ± 5.34, females = 49.2 ± 8.28; Mann-Whitney, *U* = 75.0, *P* = 0.596, *Q* = 0.224) or mean distance/move (males = 70.5 ± 8.68, females = 68.4 ± 9.89; Mann-Whitney, *U* = 75.0, *P* = 0.596, *Q* = 0.224).

**Body size and condition effects.**—Snake body mass was highly dependent upon SVL for both sexes (females: *r* = 0.919, *n* = 27, *P* < 0.001; males: *r* = 0.919, *n* = 35, *P* < 0.001) and we used the residuals from each regression as an index of body condition. In general, body size and condition were positively associated with female movement features and home range size (Table 3), suggesting that larger females in better condition moved farther and more frequently than smaller females in poorer condition. In general, male body size and condition were not associated with movement distances and home range estimates (Table 3). Body condition indices derived from estimated fat mass demonstrated qualitatively similar but stronger relationships to movement and home range estimates than mass-on-length regression residuals.

DISCUSSION

Our radio-tracked snakes were spatially restricted to aquatic habitats during the summer (see also Roth, 2005). All individuals maintained core areas of activity from which occasional short-term excursions were made to other locations. Consistent with many other studies, we observed high individual variation in movement patterns and home range sizes. The following discussion

TABLE 2. MOVEMENT DATA FOR 17 *Nerodia sipedon* MONITORED BY RADIO TELEMETRY. Movement frequency indicates the percentage of days on which movement occurred of the total days monitored. All distances are given in m.

	Males (n = 8)		Females (n = 9)	
	Mean (SE)	Range	Mean (SE)	Range
Frequency	70.2 (5.3)	41.7–86.2	70.2 (1.9)	59.3–77.5
Distance/move	70.7 (8.7)	36.5–114.3	70.6 (10.5)	42.9–148.3
Distance/day	48.8 (5.3)	25.3–73.9	49.3 (8.3)	29.3–110.8
Maximum move	248 (26)	114–344	352 (55)	176–655
Total distance	3754 (524)	2144–6710	4759 (775)	3024–10526

TABLE 3. REGRESSION ANALYSES OF HOME RANGE SIZE DESCRIPTORS AND MOVEMENT VALUES ON MEASURES OF BODY SIZE AND CONDITION FOR NINE FEMALE AND SEVEN MALE *Nerodia sipedon*. The 95% temporally corrected (TC) harmonic mean (HM) home ranges were calculated as the sum of monthly home ranges excluding overlap. Table values represent coefficients of determination ( $r^2$ ) with associated  $P$ -values in parentheses and  $q$ -values (from FDR analysis) in italics. Significant relationships (as interpreted from  $q$ -values) are in bold.

	SVL		Residual mass		Body fat	
	Female	Male	Female	Male	Female	Male
95% HM	0.110 (0.201) <i>0.109</i>	0.251 (0.143) <i>0.086</i>	0.000 (0.377) <i>0.183</i>	0.347 (0.096) <i>0.078</i>	0.075 (0.240) <i>0.125</i>	0.359 (0.092) <i>0.078</i>
95% HM TC	0.200 (0.127) <i>0.085</i>	0.000 (0.711) <i>0.315</i>	<b>0.630</b> ( <b>0.006</b> ) <i>0.018</i>	0.000 (0.690) <i>0.315</i>	<b>0.815</b> ( <b>0.001</b> ) <i>0.007</i>	0.000 (0.753) <i>0.323</i>
95% Kernel	<b>0.464</b> ( <b>0.026</b> ) <i>0.029</i>	<b>0.874</b> ( <b>0.001</b> ) <i>0.007</i>	<b>0.379</b> ( <b>0.046</b> ) <i>0.048</i>	0.000 (0.938) <i>0.381</i>	<b>0.602</b> ( <b>0.008</b> ) <i>0.019</i>	0.000 (0.940) <i>0.381</i>
Total distance	<b>0.681</b> ( <b>0.004</b> ) <i>0.015</i>	0.171 (0.196) <i>0.109</i>	0.326 (0.063) <i>0.061</i>	0.270 (0.133) <i>0.086</i>	<b>0.691</b> ( <b>0.003</b> ) <i>0.015</i>	0.244 (0.147) <i>0.086</i>
Distance/day	<b>0.532</b> ( <b>0.016</b> ) <i>0.022</i>	0.098 (0.255) <i>0.128</i>	0.264 (0.090) <i>0.078</i>	<b>0.653</b> ( <b>0.017</b> ) <i>0.022</i>	<b>0.532</b> ( <b>0.016</b> ) <i>0.022</i>	<b>0.681</b> ( <b>0.014</b> ) <i>0.022</i>
Distance/move	<b>0.527</b> ( <b>0.016</b> ) <i>0.022</i>	0.000 (0.631) <i>0.297</i>	0.246 (0.146) <i>0.086</i>	0.247 (0.146) <i>0.086</i>	<b>0.515</b> ( <b>0.018</b> ) <i>0.022</i>	0.278 (0.128) <i>0.086</i>

focuses on how body size, body condition, and sex influence spatial use variation in *N. sipedon*. In addition, we compare our data to a previous study of *N. sipedon* and attempt to identify factors promoting spatial differences.

*General spatial use.*—Our mean home range estimate for female *Nerodia sipedon* (mean =  $0.56 \pm 0.079$  ha) was an order of magnitude smaller than that reported for Wisconsin females by Tiebout and Cary (1987; mean =  $5.41 \pm 0.588$  ha; Mann-Whitney,  $U = 125.0$ ,  $P = 0.045$ ). Migration activities did not explain differences in home range size among these populations. Even after removing migratory movements from the Wisconsin, the home range of these snakes ( $n = 10$ ,  $3.4 \pm 1.27$  ha) was still significantly larger than Missouri snakes ( $U = 80$ ,  $P = 0.034$ ), although core area sizes from both localities were not statistically different ( $U = 74.0$ ,  $P = 0.205$ ).

A similar spatial disparity was reported by Plummer and Congdon (1994) who observed large home ranges in a South Carolina population of *Coluber constrictor* compared to western populations evaluated by similar methods.

Variation in home range size and movement rate is often attributed to energetics and prey availability (Duvall et al., 1985; Madsen and Shine, 1996; Whitaker and Shine, 2003). Larger individuals should traverse larger areas than smaller individuals to satisfy their relatively

greater energy requirements (Shine, 1987). In contrast, variation in home range size and movement rate in racers (*Coluber constrictor*) and sidewinders (*Crotalus cerastes*) was explained by prey availability rather than body size (Plummer and Congdon, 1994; Secor, 1994). In our study, body size correlated significantly with home range size for female watersnakes but not males. This pattern was also observed in the elapid *Hoplocephalus bungaroides* (Webb and Shine, 1997), but reversed for the brownsnake, *Pseudonaja textilis* (Whitaker and Shine, 2003), suggesting that spatial consequences of energy constraints vary among species and between sexes.

Home range areas for our *N. sipedon* population tended to peak in July and August for both sexes (Fig. 1), indicating that all snakes occupied larger areas in mid-summer. These results contrast with other studies that have reported decreased feeding rates, activity, and spatial use in gravid females (Keenlyne, 1972; Shine, 1979; Reinert and Zappalorti, 1988), apparently resulting from physiological and mobility constraints during gestation (Seigel et al., 1987; Reinert, 1993; Brown and Weatherhead, 2000). Female *N. sipedon*, however, continue foraging when gravid (King, 1986; Aldridge and Bufalino, 2003) and maintain swimming performance similar to non-gravid individuals through the early stages of gestation (Brown and Weatherhead, 1997), in-

dicating that pregnancy may not appreciably impact activity levels (Tiebout and Cary, 1987). Although reproductive condition was not reported in their study, many individuals presumably were gravid, as female reproductive frequency is high in this species (Aldridge, 1982; Brown and Weatherhead, 1997).

The relative availability of preferred habitat may have also contributed to the summer increase in home range size. Since structural features, including vegetative cover, strongly influence snake habitat use (Reinert, 1993; Roth and Greene, unpubl. data), the distribution and availability of such features should affect spatial patterns. Tiebout and Cary (1987) found that *N. sipedon* strongly associate with emergent herbaceous cover in late spring and summer. At our study site, the height, density, and coverage of emergent vegetation along shoreline habitats increased dramatically from April to June and coincided with greater use of offshore areas by snakes, although not with a shift in overall monthly spatial use. Thus, increased home range sizes in July and August might reflect a facultative response to increased emergent plant cover which reached a vegetative peak during this time (Roth, 1999).

*Effect of condition.*—Male home ranges were largely unrelated to body condition, whereas female body condition explained over 81% of the variance in the 95% corrected HM area (Table 3). A parallel scenario was reported for the elapid *Hoplocephalus bungaroides* in which body size and condition were positively correlated with home range size for females but not males (Webb and Shine, 1997). The tendency for female *N. sipedon* to reproduce annually over a range of body conditions (Aldridge, 1982; Barron, 1997), to demonstrate longer seasonal feeding periods than males (King, 1986), and to experience a survival cost to reproduction (Brown and Weatherhead, 1999) suggests that reproductive investment is an energy allocation priority. Similarly, recent evidence suggests that energy reserves also influence male reproductive success in snakes (Gibbons and Semlitsch, 1987; Bonnet and Nalleau, 1996; Aldridge and Duvall, 2002). Thus, energetic constraints imposed by relatively poor body condition could be reflected in decreased activity levels and spatial use.

*Spatial dynamics.*—Home range areas for *N. sipedon* in this study were spatially dynamic and characterized by repeated temporal shifts in core area use, which is consistent with the Wisconsin population studied by Tiebout and Cary (1987;

see also Reinert and Zappalorti, 1988; Fitzgerald et al., 2002). Rather than occupying a single seasonal home range, most individuals occupied a distinct core area for a period of time and periodically switched to a new location, repeating this pattern several times throughout the season. Individual variation in spatial patterns, however, complicated our attempts to estimate home range size because the movement of some individuals to new core areas sometimes occurred after more than two months of observation. This finding reinforces the need for empirical determination of sample size requirements over complete activity seasons, as short-term investigations may underestimate home range size (Rose, 1982; Reinert, 1992; Diffendorfer et al., 2005) and fail to elucidate temporal patterns of space use (Stone and Baird, 2002).

Telemetric studies of some snakes have revealed seasonal shifts in activity centers in response to habitat changes and fluctuations in resource distribution (e.g., Madsen, 1984; Shine and Lambeck, 1985; Madsen and Shine, 1996). These studies, however, implicated specific resources as proximal factors motivating population-wide responses in snake behavior. We did not observe any obvious changes in physical habitat or prey density that coincided with the shifts in activity centers in *N. sipedon*. Although vegetative biomass increased from spring through mid-summer, shifts in activity centers were not associated with the appearance of new vegetative cover. Moreover, shifts in activity among individuals were independent, rather than synchronous, as might be expected if a single proximate cause was implicated.

*Spatial estimators.*—The description of general spatial patterns in snakes has been inhibited by a lack of methodological standardization among studies (Gregory et al., 1987; Macartney et al., 1988). In addition to differences in tracking regimes and measurement of movement, the choice of home range descriptor has a strong influence on the interpretation of spatial patterns. The harmonic mean and kernel estimates, although different in size, described spatial patterns that were qualitatively similar in shape and location and demonstrated a spatial association of snakes with littoral zone vegetation. Additionally, temporal analyses using the harmonic mean technique facilitated evaluation of spatial dynamics within activity seasons and yielded more precise estimates of spatial use than the total home range. The diversity of assumptions, limitations, benefits, and historical usage of different home range analyses favors the use of multiple descriptors (Reinert, 1992).

Understanding spatial variation in snakes will require thorough standardized descriptions over complete seasons coupled with measurement of the availability and distribution of resources (Whitaker and Shine, 2003).

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