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SPATIAL ECOLOGY AND HABITAT USE OF NORTHERN WATER SNAKES (*NERODIA SIPEDON SIPEDON*) IN A RURAL MICHIGAN, USA, LANDSCAPE

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Abstract.—**We studied habitat use and spatial ecology of Northern Water Snakes (*Nerodia sipedon sipedon*) in a northern wetland and its associated lake ecosystem in central Michigan, USA. We assessed how *N. s. sipedon* responded to a small aquatic ecosystem that was embedded in agricultural land and habitat use in relation to diet and body temperature variation that we published in a companion study. We measured activity areas as Minimum Convex Polygons (MCP) and Utilization Densities based on kernel density and on autocorrelated kernel density estimation. The areas occupied by *N. s. sipedon* at Davis Lake were relatively small when compared to *N. s. sipedon* studied across its range. For example, our mean MCP value of 0.23 ± (standard error) 0.10 ha (range of values 0.02–1.86 ha) was 6–21% of the areas reported for *N. sipedon* in other studies. *Nerodia s. sipedon* were highly aquatic, apparently spending more time in water than has been observed for the species at other localities. The highly aquatic habits of *N. s. sipedon* at Davis Lake were likely related to the distribution of prey items (primarily fish and secondarily anurans), but also to the ability to easily thermoregulate along the edge of the** *Sphagnum* **mat-lake water interface.**

Key Words.—Colubridae; foraging; home range; movements; Natrinae; thermoregulation

INTRODUCTION

The study of habitat-use and movement patterns of animals can lead to an understanding of resource use, antipredator behaviors, social interactions, and thermal ecology. Resources are often unevenly distributed across an environment, and habitat suitability for a species may depend on the availability of suitable foraging areas, thermal patches, cover, mates (Halliday and Blouin-Demers 2016), and on predation risk (Abrahams and Dill 1989; Morris 2003). Thermal quality of a habitat (i.e., the degree of coincidence of environmental temperatures with the preferred body temperature of the animal; Hertz et al. 1993) may be among the most important determinants of habitat suitability for an ectothermic species (Blouin-Demers and Weatherhead 2001; Weatherhead et al. 2012), as it must coincide with the thermal performance breadth of the animal (Huey 1982, 1991). Seasonality in temperature, precipitation, or both can affect prey availability, which in turn can influence the activity and movements of an animal (Ariano-Sánchez et al. 2020). Because habitat and climatic conditions vary among geographic locations, study of habitat use and spatial ecology of animals in populations throughout their range can be useful for detecting trends in local adaptations or plasticity in phenotypic traits such as behavior and physiology (Blouin-Demers et al. 2003; Sperry et al. 2010). Furthermore, favorable habitats within the home range of an animal may be patchy and so the study of movement dynamics can be important not only to understanding the ecology of a species but also to devising conservation measures (Roe et al. 2006).

North American water snakes (*Nerodia* spp.) inhabit lakes, streams, and various aquatic wetlands of the northeast Atlantic and Great Lakes states of the U.S. and in adjacent Canada, west to the eastern

Great Plains states and south to some eastern Gulf states (Gibbons 2017). Common Water Snakes (*Nerodia sipedon*) consume a large variety of fish and amphibians (Mushinsky and Hebrard 1977a; King 1993) using either active or sit-and-wait foraging tactics depending on the ecological context (Gibbons 2017). Semiaquatic reptiles often shuttle among terrestrial, aquatic, and ecotonal zones during foraging, reproductive activities, and movement to overwintering sites (Brown and Weatherhead 1999; Semlitsch and Bodie 2003). Members of various *Nerodia* species move among aquatic and upland terrestrial ecosystems and show spatial shifts among core areas of activity within aquatic systems (Roe et al. 2003, 2004; Pattishall and Cundall 2008). Within their home ranges, highly aquatic water snakes typically occupy the surface of the water and adjacent terrestrial microhabitats (Scribner and Weatherhead 1995). Differences in habitat use and movements among species of *Nerodia* could be related to interspecific differences in diet and foraging requirements (Keck 1998; Roe et al. 2003, 2004). The tendency for semi-aquatic reptiles, such as *Nerodia*, to occupy multiple disjunct wetlands provides opportunities to study movement dynamics across a landscape (Roe et al. 2003, 2004; Semlitsch and Bodie 2003).

Northern Water Snakes (*N. sipedon sipedon*) are a mid-sized *Nerodia* species with well-defined home ranges where individuals show relatively restricted movements within a thermally heterogenous aquatic-terrestrial environment (Roe et al. 2004; Rowe et al. 2022). As a largely piscivorous snake, *N. sipedon* tends to remain close to permanent aquatic ecosystems (Roe et al. 2004) and typically does not make long distance movements among bodies of water (Tiebout and Cary 1987; Brown and Weatherhead 2000). Multiple disjunct activity centers may be established in both lotic (Pattishall and Cundall. 2008) and large lentic (Roe et al. 2003, 2004) ecosystems. Although tightly associated with aquatic ecosystems, *N. s. sipedon* may spend a vast majority of its time in terrestrial habitats (Tiebout and Cary 1987). The fine scale daily activity and movements of *N. s. sipedon* are essentially unknown in relation to different habitats that vary in size and structure and that show different compositions of prey. An array of adjacent terrestrial microhabitats including both living and dead plants and various terrestrial substrates are used by *N. s. sipedon* (Tiebout and Cary 1987; Burger and Jeitner 2004). Body temperatures (T_b) of *N. s. sipedon* in north-temperate latitudes rise rapidly during the late morning hours and attain an early afternoon plateau phase; thereafter, snakes thermoregulate effectively until early evening (Brown and Weatherhead 2000; Rowe et al. 2022). Peak T_b values tend to coincide with peak atmospheric basking activity during late morning (Robertson and Weatherhead 1992). Snake movements are impaired by relatively low environmental temperatures (Scribner and Weatherhead 1995; Finkler and Claussen 1999), which necessitates elevated levels of atmospheric basking when air temperatures are relatively low (Robertson and Weatherhead 1992). Given that thermoregulation in *N. s. sipedon* can be challenging at north-temperate latitudes (Brown and Weatherhead 2000; Rowe et al. 2022), both the distribution of prey items and spatial heterogeneity in thermal quality of the environment would be expected to affect habitat use and movement patterns (Robertson and Weatherhead 1992).

Using radiotelemetry, we studied daily and seasonal habitat and microhabitat use and diet in *N. s. sipedon* in a small northern wetland surrounded by forest and agricultural land in central Michigan, USA. The study area allowed us to evaluate the use of a relatively isolated wetland by *N. s. sipedon* where the use of other major aquatic ecosystems would require individuals to cross several hundred meters of upland forest, agricultural fields, and roads. We therefore expected that individual snakes would remain within the lake basin given the constraints imposed by the surrounding habitat (Roe et al. 2004). Because *N. sipedon* consume both fish and anurans (King 1993; Roe et al. 2004), potential prey items known to occur at Davis Lake were Northern Red-belly Dace (*Chrosomus eos*), Black Bullhead (*Ameiurus melas*), Central Mudminnows (*Umbra limi*), and larval or metamorphosed American Toads (*Anaxyrus americanus*), Green Frogs (*Lithobates clamitans*), Spring Peepers (*Psuedacris crucifer*), and Wood Frogs (*Lithobates sylvaticus*). To gain insights into how variations in habitat structure influence space use in our radio-tagged snakes, we summarized data from the literature on space use in *N. s. sipedon* in various aquatic ecosystem types published to date for comparisons with our data. Operative temperatures (equilibrium body temperatures that could be attained by a non-thermoregulating individual animal; Bakken and Gates 1975) at various locations around the lake indicated that snakes likely regulated their body temperature by occupying the air-water interface or adjacent bog mat (Rowe et al. 2022). Here, we examine the degree to which *N. s. sipedon* used seven microhabitats that we recorded during three daily radiolocations and how they relate to T_b profiles and diet of the species at the site. We were specifically interested in repetitive use of areas that could reveal use of microhabitats that could facilitate thermoregulation and foraging behavior.

MATERIALS AND METHODS

Study site.—We studied *N. s. sipedon* at Davis Lake near Vestaburg in Montcalm County, Michigan, USA (43°23′29″N, 84°53′37″W). Davis Lake is a dystrophic glacial lake that is located at the center of the 94.5-ha Alma College Ecological Station (ACES). Most of the ACES property is a secondary growth Mixed Deciduous-conifer Forest community that is surrounded by agricultural land. Other local bodies of water on the ACES property include an open willow-cattail marsh and a spring-fed stream that courses through a mixed shrub-forest swamp that are located 370 m to the east of, and 100 m southeast of, Davis Lake, respectively. Aquatic habitats that are adjacent to the ACES property, and in reference to Davis Lake, include an artificial lake (8.5 ha surface area) 2 km to the east, a roadside ditch system 445 m to the south, and an extensive cattail marsh (7.4 ha) that is 300 m to the north.

Davis Lake (0.61 ha of open water) has a littoral shelf of variable width (< 5 m) that is vegetated with Bullhead Lily (*Nuphar varigatum*), Watershield (*Brasenia schreberi*), and American White Water-Lily (*Nymphaea odorata*), and that grades down a steep slope into deeper water (11–12 m at the center of the lake). An extensive mat of *Sphagnum* (*Sphagnum angustifolium*; henceforth referred to as the *Sphagnum* mat; 4.6 ha), most of which is densely inundated with Black Spruce (*Picea mariana*), Tamarack (*Larix laricina*), and White Pine (*Pinus strobus*), surrounds the lake. An exposed region of the *Sphagnum* mat (0.35 ha) is immediately adjacent to the edge of the water (2–20 m wide) and is interspersed with young trees, Leatherleaf (*Chamaedaphne calyculata)*, Pitcher Plant (*Sarracenia purpurea*), Marsh Cinquefoil (*Comarum palustre*), and various ferns. A dense band of Pickerelweed (*Pontederia cordata*) or American Water Willow (*Justicia americana*) grows at the *Sphagnum* mat-open water interface. At the transition between the periphery of the *Sphagnum* mat and the surrounding upland forest is a shallow, moat-like ephemeral wetland (< 50 cm deep and 5–20 m wide) that dries during late summer in some years. The Davis Lake basin (5.2 ha) includes the lake and surrounding *Sphagnum* mat wetland.

Collection of snakes and radiotelemetry.—We collected snakes during June and August, 2013–2016, and a subset of those snakes received radio-transmitters during 2014–2016. On 3–7 d each week, we collected snakes by hand from canoes or while we traversed the mat and surrounding areas on foot between the *Sphagnum* mat-lake interface and the adjacent forest. We measured snout-vent length (SVL) to the nearest 1 mm (Astley et al. 2017) and body mass to the nearest 1 g using an electronic balance. We implanted subcutaneous 10 mm passive integrated transponders (Biomark®, Rahway, New Jersey, USA) and sealed the injection site with New-Skin® liquid bandage (Cedar Knolls, New Jersey, USA). From each snake and within 60 min of capture, we attempted to obtain stomach contents by palpation. We preserved stomach contents in 70% ethanol in Whirl-Pak® bags (Madison Industries, Pleasant Prairie, Wisconsin, USA) and maintained them in refrigeration for later prey identification.

We radio-tagged 13 female snakes ($SVL_{females}$: mean ± standard error, 574.6 ± 46.9 mm; range of values 191–720 mm; $mass_{females}$: 179.4 ± 17.8 g; 66.8–240.4 g) of which we caught seven in 2014, three in 2015, and three in 2016. Based on palpation, 10 of the 13 females were pregnant. Because there were a limited number of individuals that were of a size large enough for radio-transmitter implantation (about 50 g body mass such that the transmitter was at most 6% of the snake body mass), the sample size for male snakes was relatively small (n = 5; SVL_{males}: 404.3 ± 72.5 mm; range of values 187–480 mm; $mass_{males}$: 78.1 ± 10.1 g; range of values 49.4–96.7 g) three of which we caught in 2015 and two in 2016. We implanted radio-transmitters with coiled antennae (Model F1100, 3.1 g; Advanced Telemetry Systems, Isanti, Minnesota, USA) into the body cavities of snakes (see Rowe et al. 2022 for details). Snakes recovered in the laboratory for 7–10 d before we released them at their sites of capture.

To record radio-tagged snake locations in the field, we placed a linear array of numbered wire-stemmed (90 cm) flags (10 × 10 cm vinyl) at 5-m increments at the margins of the *Sphagnum* mat-open water interface and a grid of flags 2–5 m apart across the *Sphagnum* mat. We mapped each flag using a Trimble GeoXT GPS unit (Trimble, Westminster, Colorado, USA), and we prepared hardcopy maps to record snake locations. In the field, we made radiolocations using handheld radio receivers (model R410 with H-type antennae; Advanced Telemetry

Table 1. Categories of microhabitats used by Northern Water Snakes (*Nerodia s. sipedon*) at Davis Lake, Michigan, USA, 2014–2016.

Microhabitat category	Abbreviation	Description
Aquatic / Floating-submerged vegetation	AV	Fully aquatic and visible; among stems and leaves of floating or partially submerged emergent vegetation of the littoral zone
Aquatic / Floating-submerged vegetation / Concealed	AV-C	Fully aquatic but not visible; concealed by stems and leaves of floating or partially submerged emergent vegetation of the littoral zone
Basking/Terrestrial vegetation Woody debris	B-TVWD	Outstretched or coiled on terrestrial vegetation (chiefly leatherleaf stems) or on horizontal sticks and trunks of fallen trees immediately adjacent to edge of water; Integument typically dry
Basking / Emergent vegetation	B-EV	Outstretched or coiled on stems of emergent vegetation (Pickerelweed and American Water Willow); Integument usually dry
Sphagnum mat / Concealed	SM-C	On *Sphagnum* mat, typically concealed in *Sphagnum* mound formations; < 5 m from edge of water
Sphagnum mat / Under dense vegetation	SM-DV	Outstretched or coiled on *Sphagnum* mat proper; shaded by dense vegetation (chiefly leatherleaf and black spruce); < 5 m from edge of water; Integument typically dry
Sphagnum mat / Open-Sparce vegetation	SM-OSV	Outstretched or coiled on *Sphagnum* mat either without vegetation cover or among sparse vegetation (chiefly sedges, ferns, or leatherleaf); < 5 m from edge of water; Integument usually dry

Systems, Isanti, Minnesota, USA) from at least three positions so that the location of the snake could be determined by triangulation. We then plotted the relative location of the snake to the nearest flag on the hardcopy map and subsequently on an electronic version of the map in ArcView 3.2. We usually located snakes from watercraft, but sometimes while on foot when snakes moved away from the *Sphagnum* mat-open water interface. During radiolocations, we attempted to maintain distances (> 3 m) from the snake that would minimize the likelihood of disturbing an individual (Tiebout and Cary 1987). At each snake radiolocation, we recorded snake behavior and habitat and microhabitat descriptions at the location of the snake (Table 1). We made three daily radiolocations (0900, 1200, and 1500 ± 30 min) for each radio-tagged snake from June to August using handheld Advanced Telemetry Systems R410 radio receivers 4–6 d per week. Due to occasional logistic constraints, we obtained only a late-morning location for each snake on some days. Because of transmitter failure or movement of snakes to areas where regular daily monitoring was not possible, we monitored radio-tagged snakes for a variable numbers of telemetry days (mean = 32.3 ± 2.6; range of values 10–49 d) and over variable periods of time (mean = 56.8 ± 4.4 d; range of values 14–94 d, n = 18 snakes) for different snakes. Asymptote plots indicated that MCP of snakes residing around the lake largely stabilized in size by 24 telemetry days, so we included only those radio-tagged snakes with at least 24 telemetry days in our activity area size analyses. In the fall of 2014, we monitored activity weekly until snake dormancy but less frequently (2–3-week intervals) in 2015 and 2016. Regular weekly monitoring of snakes was done beginning in April during the spring of 2016 only.

To quantify the degree of nocturnal activity, we radio-located each snake nine times daily at 3-h intervals (± 30 min) between 0000 and 0000 of consecutive days on 10 and 31 July and 5 August 2014. We generally avoided shining lights directly on snakes while they were aquatic such that we could minimize inducing movements by the snakes. We radio-located snakes most intensively between June and August of the active season.

Measurement of daily distances moved and activity areas.—Using ArcView 3.2, we measured distances between successive locations for each snake on each day and summed them to determine a total daily distance moved (TDDM). We determined Minimum Convex Polygons (MCPs) and Utilization Distributions (UDs) based on Kernel Density Estimation (KDE), and Autocorrelated Kernel Density Estimation (AKDE) for data collected between June and August, the period of most intensive and regular radio-telemetric monitoring. An MCP includes the area enclosed by the outermost location points of an individual without consideration of the utilization distribution of points within the MCP. In contrast, UDs of non-parametric KDE allow the determination of relative time spent by individuals at a specific location (Seaman and Powell 1996) such that biologically relevant clusters of repetitive use by an individual can be identified (De Solla et al. 1999; Gitzen et al. 2006). Utilization Distributions as determined by KDE have been commonly used for the spatial ecology of *N. sipedon* (see Appendix Table). We used the Animal Movement Extension in ArcView 3.2 (Hooge and Eichenlaub 1997) to determine MCPs, UD50% and UD95% by KDE using smoothing values that were determined by least squares cross-validation. KDE assumes independence of movement points of an individual, however, whereas animal movements are often highly autocorrelated (Swihart and Slade 1985; Fleming et al. 2015). Also, contour areas are sensitive to bandwidth selection and the smoothing method used (Silverman 1986; Gitzen et al. 2006; Bauder et al. 2015). In general, UDs determined by KDE tend to underestimate space used by individuals (Swihart and Slade 1985; Row and Blouin-Demers 2006; Silva et al. 2021). Because our radio-telemetric sampling varied within and among days, we plotted a single radiolocation per individual per day. Such coarsening of the sampling rate can improve KDE estimates by reducing, but not eliminating, the degree of autocorrelation among animal location points (Swihart and Slade 1985). Autocorrelated Kernel Density Estimators determine UDs without the underlying assumption of independence of data points and therefore improve space use estimates relative to KDE (Fleming et al. 2015). We determined UD95% and UD50% values by AKDE for each snake using the Continuous-Time Movement Modeling (cttm) R package (Calabrese et al. 2016). Because of our irregular radio-telemetric sampling among days, we determined UDs using the optimally weighted area-corrected ADKE model (pHREML-fitted wAKDEc; Silva et al. 2021).

Data analysis.—We analyzed log-transformed MCP and UDs and ln-TDDM (averaged for each snake over the summer, June-August) using a mixed Generalized Linear Mixed Model (GLMM) analysis with sex included as a main effect. Snake identification number was included as a random effect to account for the multiple representations of individuals in the data set between years. To evaluate the proportional use of habitat, we tallied the number of observations within seven possible microhabitat categories (Table 1) for each individual snake for each day, and then expressed each as a percentage of the total daily observations for the individual (n = 3 daily radiolocations). We then determined the average value for each habitat used per snake over the summer months; we combined data for each of the three individual snakes that we monitored over two successive years to maintain statistical independence in the data set. We tested for differences in proportional use of microhabitats using a Kruskal-Wallis test and conducted *post hoc* comparisons using the Dunn test for multiple joint rankings that incorporates Bonferonni adjustment of alpha. We used JMP Software (JMP® version 17.0.0, SAS Institute, Cary, North Carolina, USA) to make statistical tests and we considered significance using an alpha of 0.05.

RESULTS

Activity areas.—During the summer months, snakes remained at the lake margins and on the adjacent *Sphagnum* mat (Fig. 1) with the exception of a single female snake. Utilization Distributions (95% and 50%) using KDE indicated that individual snakes occupied multiple core areas of activity within their larger activity area (Fig. 1). Using AKDE, multiple core areas were detected in UD50% plots of some individuals (Fig. 2). In the three snakes that we monitored across multiple years between 2015–2016, activity areas overlapped between years in all three individuals (see Fig. 1 for a representative male snake) with MCP overlap between approximately 15% and 60%.

We found relatively expansive movements in a single pregnant female that we initially radio-tagged at the margins of Davis Lake (Fig. 3). Following residence along the margins of Davis Lake, the snake moved to the margins of the lake basin (the so-called moat wetland) for 7 d (distances of daily locations from the edge of the lake averaged 106.3 ± 24.5 m; range of values 42–175 m) and then, over the course of a single day, moved to a large cattail marsh to the north where she remained during late summer and into the fall. The maximum distance that the snake was found in the cattail marsh from the margin of Davis Lake was approximately 480 m.

Summer activity areas within the Davis Lake basin were typically < 1 ha regardless of the metric used to calculate area (MCPs or fixed kernels). Average ln-transformed MCP area was 0.24 ha for both sexes combined (Appendix Table) and did not vary between the sexes ($F_{1,16} = 1.780$, $P = 0.208$). Maximum MCP area was about 1.9 ha for a female that moved around both the lake edges and surrounding moat

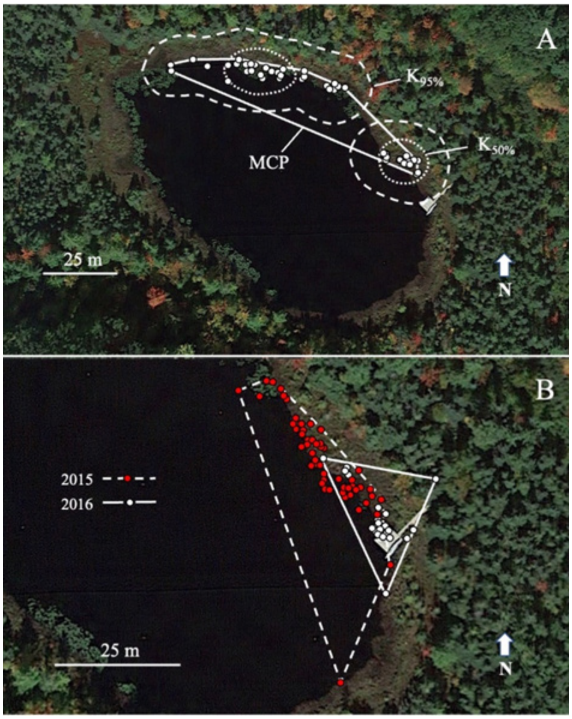

Figure 1. (A) Minimum convex polygon and 95 and 50% kernel estimates of activity areas for a single representative female Northern Water Snakes (*Nerodia s. sipedon*; ID# 151.110) at Davis Lake, Montcalm County, Michigan, USA, June-August 2016, and (B) overlapping minimum convex polygons of a single representative male *N. s. sipedon* (ID# 151.512) monitored over two successive years. Points represent single daily radiolocations. Data projected on an image from Google Earth.

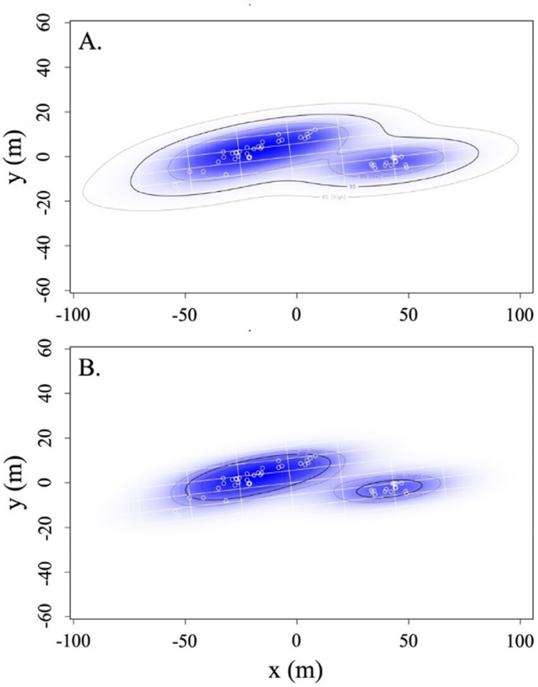

Figure 2. Utilization distributions determined by pHREML-fitted wAKDEc of a single female Northern Water Snake (*Nerodia s. sipedon*; ID# 151.110) at Davis Lake, Montcalm County, Michigan, USA, 2014, (A) UD95% and (B) UD50%. Black lines are UD estimates and inner and outer gray lines are lower and upper 95% confidence intervals.

wetland areas (see Fig. 3, Appendix Table). When we included the movements of the female in the cattail marsh to the north in her MCP estimate, the MCP value was 11.4 ha with an overall mean MCP of 0.75 ± 0.63 ha across all snakes; ln-MCP did not differ between the sexes ($F_{1,17}$ = 1.238, P = 0.289). The UDs based on ln-KDE95% nor ln-KDE50% did not vary between the sexes ($F_{1,17}$ = 0.601, P = 0.454 and $F_{1,17}$ = 0.732, P = 0.408, respectively) for snakes that remained in the Davis Lake basin throughout the summer months. Utilization Densities based on wAKDEs were slightly larger than those based on KDE (Appendix Table) and ln-UD areas did not differ between the sexes (UD95%: $F_{1,17}$ = 1.048, P = 0.325; UD50%: $F_{1,17}$ = 1.064, P = 0.325).

Daily movements and habitat use.—Daily movements by snakes in the Davis Lake basin were very localized as individuals traversed the littoral zone along the edge of the *Sphagnum* mat. Over the summer months, mean TDDM averaged across individuals was 6.52 ± 0.81 m (1.98–15.34 m) and was consistently below 40 m/d (Fig. 4). The maximum daily movement by an individual was 75.30 m but some snakes occasionally did not move over the course of the day. Most TDDM values for snakes along the littoral zone were < 5 m/d (Fig. 4). Mean ln-TDDM did not differ between the sexes ($F_{1,17}$ = 0.089, P = 0.771). The percentage of days where no movement was detected for an individual snake was 27.82 ± 4.01% (range of values 4–60%; n = 627 radiotelemetry days in 17 snakes).

On a 24-h basis, snakes at Davis Lake maintained relatively short-distance movements over time. Daily distances moved based on nine radiolocations made at 3-h intervals over 24 h (for 3 d) averaged 20.63 ± 8.88 m (range of values 0–71.50 m) for five snakes. Snakes moved similar mean distances over the course of the day ($F_{7,83}$ = 1.831, P = 0.092; mean = 2.58 ± 0.88 m, range of values 0–34.23 m) using ln-transformed distances moved between successive radiolocations at 3-h intervals .

Habitat use.—Snakes at Davis Lake were highly aquatic, spending the majority of their time within

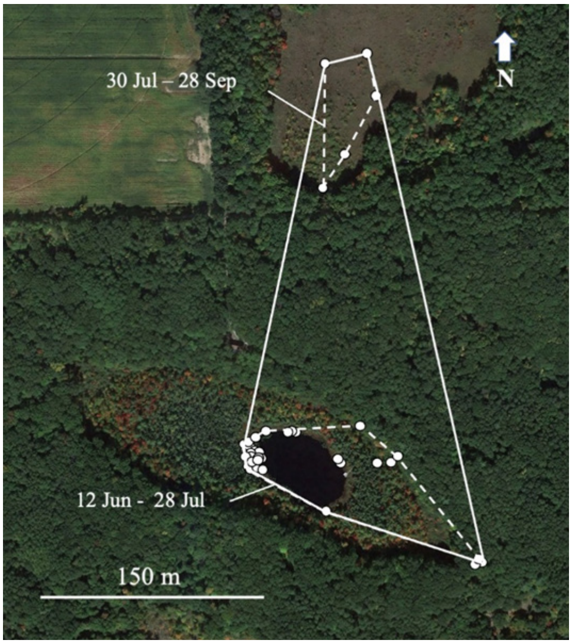

Figure 3. Movements of an individual female Northern Water Snake (*Nerodia s. sipedon*; ID# 151.651) at Davis Lake and adjacent cattail (*Typha* sp.) marsh, Montcalm County, Michigan, USA, 2014. Solid line is MCP for the season, and dashed lines are for two discrete activity areas. Points represent single daily radiolocations. Data projected on an image from Google Earth.

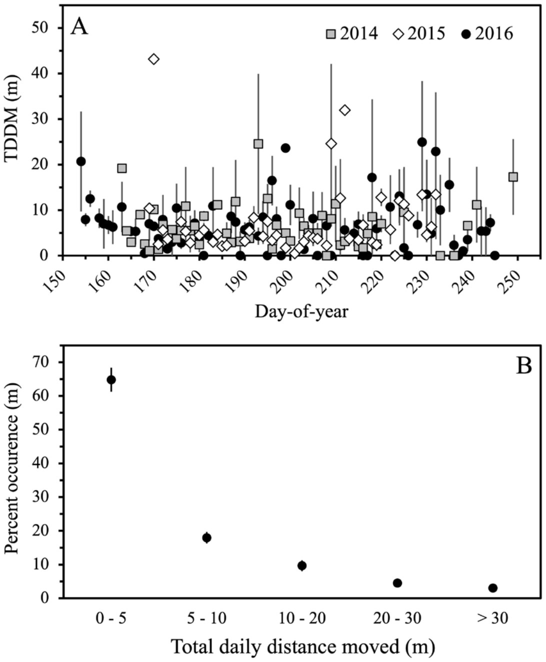

Figure 4. (A) Mean (± standard error) total daily distance moved (TDDM) based on three daily radiolocations for 18 Northern Water Snakes (*Nerodia s. sipedon*) at Davis Lake, Montcalm County, Michigan, USA. In 2014 the mean = 23 ± 4.55 d (range of values 6–37 d per snake) for six snakes; in 2015, the mean = 25.2 ± 4.17 (range of values 10–39 d per snake) for six snakes; and in 2016, the mean = 42.1 ± 3.26 (range of values 25–55 d per snake) for eight snakes. (B) Frequency distributions (percentage occurrence) for mean TDDM values averaged per snake.

aquatic vegetation while apparently foraging along the littoral shelf for fish and anurans (Fig. 5). Across all snakes, 67.2% of all radiolocations (n = 1,578 total radiolocations) were made while snakes were in water, the remaining 32.8% of radiolocations occurred when snakes were on the surrounding *Sphagnum* mat or fully emerged while basking. The proportional microhabitat use (both sexes combined) of *N. s. sipedon* differed significantly in the daily use of microhabitats ($H = 60.96$, df = 6, $P < 0.001$). Snakes were more frequently observed while they were aquatic and concealed in emergent or floating vegetation than they were in other microhabitats ($Z = 3.29$–6.03, dfs = 1, $P < 0.001$–0.0214 across all five comparisons) except for aquatic while visible in emergent or floating vegetation ($Z = 1.67$, df = 1, $P = 1.00$). Snakes were more frequently observed while visible in emergent or floating vegetation than they were while basking on debris ($Z = 4.66$, df = 1, $P < 0.001$) or on the *Sphagnum* mat in dense vegetation ($Z = 4.37$, df = 1, $P < 0.001$). Based on our 24-h sampling regimen, snakes appeared to show dynamic use of microhabitats (Fig. 5). During the early morning hours (0000–0600), some snakes remained immobile and sequestered in *Sphagnum* mounds. Other snakes were aquatic and immobile (either concealed or suspended within view) or active within the littoral zone vegetation.

The diet of *N. s. sipedon* at Davis Lake was composed entirely of anurans and fish. Over the course of the study, we obtained 23 stomach samples from 21 individuals. Green Frogs (*Lithobates clamitans*; tadpoles, a size range of juveniles to adults, and transitional metamorphic forms) comprised 39.1% and Central Mudminnows (*Umbra limi*) comprised 60.9 % of the samples.

In 2014, five of six snakes with functioning transmitters entered hibernation between 25 September and 10 October. One individual was observed active on the *Sphagnum* mat on 17 October before entering hibernation within a week. Mean distance between the edge of the lake and individual hibernation sites for six snakes was 135.6 ± 64.8 m, three of which overwintered in *Sphagnum* mounds between 5 and 75 m from the edge of the lake. Terrestrial hibernation sites of three snakes, apparently within tree root systems, were 60 and 370 m from the edge of the lake and two of these snakes

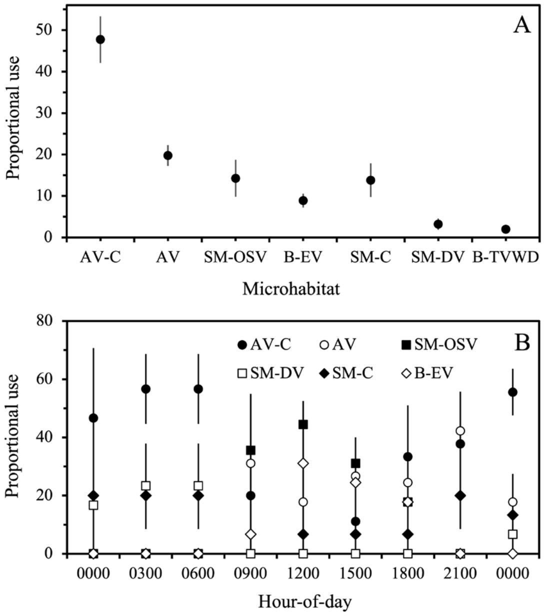

Figure 5. Mean proportional microhabitat use (± standard error) of Northern Water Snakes (*Nerodia s. sipedon*) in seven microhabitats during (A) the daily sampling period throughout the summer months (n = 13 females, n = 5 males), and (B) snakes that used six microhabitats at Davis Lake, Montcalm County, Michigan, USA, June-July 2014–2016, across three days (10 and 31 July and 5 August 2014). We radio-located each snake nine times daily at 3-h intervals between 0000 and 0000 of two consecutive days. See Table 1 for microhabitat abbreviations.

included an upland hillside adjacent to the lake basin and one a lowland area adjacent to a stream. We did not determine the depths at which snakes hibernated.

Discussion

Activity area.—During the summer months, *N. s. sipedon* largely restricted their movements to the Davis Lake basin and along the interface between the *Sphagnum* mat and open water. Activity area size of snakes at Davis Lake, as measured by MCPs and UDs, are small when compared to *N. s. sipedon* in larger lake or riverine ecosystems (see Appendix Table). Although methods used to calculate activity areas of *N. s. sipedon* vary as do the durations of radiotelemetric monitoring (Tiebout and Cary 1987; Pattishall and Cundall 2008), movements of *N. s. sipedon* across a majority of the activity season were monitored in each study that we reviewed and so reasonable comparisons among populations should be possible. Our overall mean MCP estimate is about 6% and 21% of the activity areas reported for *N. s. sipedon* residing in a large complex of marshes, lakes, and streams (Roe et al. 2004) and in a riverine system (Pattishall and Cundall 2008), respectively. Similarly, 95% harmonic mean isopleths for *N. s. sipedon* in large lake-wetland systems exceeded any of our activity area size estimates (Tiebout and Cary 1987; Roth and Greene 2006). We suspect that the amount of available habitat partly determines the activity area size of *N. s. sipedon*.

The degree to which multiple, disjunct activity centers are established by *N. s. sipedon* varies among populations and was uncommon in our study. Multiple disjunct activity centers, and core areas within activity areas, have been well-documented in *N. s. sipedon* (Tiebout and Cary 1987; Roe et al. 2004; Pattishall and Cundall 2008), and some such movements are associated with seasonality (Tiebout and Cary 1987). Although cattail marshes can be the preferred habitat of *N. s. sipedon* (Tiebout and Cary 1987), only a single individual used a cattail marsh in our study. We did not observe radio-tagged snakes using a nearby open willow-cattail marsh that is < 400 m east of Davis Lake, a distance that is within annual movements of *N. s. sipedon* (Roe et al. 2004). Roe et al. (2004) reported that *N. s. sipedon* tend to avoid ephemeral wetlands and therefore show less wide-ranging movements than their congener, the Copperbelly Water Snake (*N. erythrogaster neglecta*). Furthermore, overland movements and the use of uplands is relatively uncommon in *N. s. sipedon* (Tiebout and Cary 1987; Brown and Weatherhead 2000). Largely piscivorous snakes of *Nerodia*, such *N. s. sipedon*, tend to be more closely associated with aquatic ecosystems than are species that consume primarily anurans (Keck 1998). Although the willow-cattail marsh at our site harbored anurans, it occasionally dried completely (pers. obs.), which could limit anuran population size and preclude the establishment of fish populations.

Minimum Convex Polygons and UDs often include terrestrial or open water areas that are rarely, if ever, used by semi-aquatic reptiles such as *N. s. sipedon* (Pattishall and Cundall 2008). Multiple disjunct activity centers and repetitive use of core areas within them can lead to the overestimation of UDs of individual snakes. For instance, Pattishall and Cundall (2008) found that UDs based on KDE for *N. s. sipedon* along a stream system included discontinuous terrestrial areas and excluded critical aquatic foraging habitats. During our study, we observed other non-radio-tagged snakes at various locations across the *Sphagnum* mat, in the immediate surrounding forest, and while they were swimming in open water. We therefore feel confident that our

MCPs and UDs included areas that could be used by snakes at Davis Lake. At the same time, UDs based on KDE may underestimate the areas used by snakes when core area use occurs (Swihart and Slade 1985). We found that our UD95% and UD50% based on wAKDE were larger, about twice as large, as UDs determined by KDE. Although likely to be less biased UD estimates than those determined by KDE (Fleming et al. 2015), our UDs determined by wAKDE were still relatively small when compared to any space use metric for *N. s. sipedon* in other studies (Appendix Table).

The use of relatively small areas (usually determined by UD50%) by snakes within a larger ecosystem could be a common phenomenon in *N. s. sipedon*. For instance, Pattishall and Cundall (2008) found repetitive use of microhabitat features and core areas by individual *N. s. sipedon* along a stream. Interestingly, no such patterns of repetitive space use were observed in *N. s. sipedon* at other localities (Tiebout and Cary 1987; Roth and Greene 2006). Even at the relatively small magnitudes of movement made by our *N. s. sipedon* at Davis Lake, we detected repetitive use of core areas. Repetitive use of microhabitats within core areas by aquatic or semi-aquatic reptiles would be driven by a three-dimensional familiarity of cover, resting sites, foraging locations, and basking sites (Rowe 2003; Rowe and Dalgarn 2010). We cannot, however, discount aggressive interactions and territoriality that might be associated with the use of different core areas by individuals (Edgehouse et al. 2014; Webb et al. 2015), although, to our knowledge, no such territoriality has been documented in *N. s. sipedon*.

Daily movements and microhabitat use.—Like variations in activity area sizes across localities, average daily distances moved by *N. s. sipedon* depended on the ecosystem of residence. Radio-tagged snakes moved relatively short distances along the littoral zone of Davis Lake when compared to *N. s. sipedon* movements along a lake shore or within relatively large wetland complex (Appendix Table). The degree of aquatic versus terrestrial habitat use varies among *Nerodia s. sipedon* in different aquatic ecosystems and may be related, at least in part, to opportunities for foraging. We found that *N. s. sipedon* at Davis Lake was highly aquatic, with over 50% of the daily radiolocations for individual snakes recorded in water along the littoral zone. Roe et al. (2003, 2004) found that *N. s. sipedon* used marshes of variable sizes, hydroperiods, and vegetation cover implying that aquatic activity was common in snakes that consumed fish and anurans with about equal frequency. In contrast, Cundall and Pattishall (2011) reported that only 1.43–2.38% of radiolocations involved snakes in water with 32.7% occurring in mostly inactive snakes on land that were located within 1 m of water. The very limited observed aquatic activity and exclusive diet of native fish and non-native fish stocks indicated that the consumption of relatively large fish prey by *N. s. sipedon* may obviate extensive aquatic foraging activity (Pattishall and Cundall 2009). Tiebout and Cary (1987) described *N. s. sipedon* as an edge species because radiolocations of snakes in open water of the wetland complex were infrequent (10.5%) with snakes typically found on land within 6 m of water. *Nerodia s. sipedon* consumed exclusively small prey relative to snake body size (*U. limi* and *L. clamitans*) at Davis Lake. The most frequently consumed prey, *U. limi*, is a largely sit-and-wait predator and habitat generalist that occupies microhabitats between the benthos to the surface of the water (Paszkowski 1985), where it feeds on small invertebrates, including those attached to aquatic plants (Martin-Bergmann and Gee 1985). *Lithobates clamitans*, while able to move among aquatic habitats as adults, are tied to aquatic habitats for a vast majority of the life cycle (Pitt et al. 2017). Individual *L. clamitans* of variable developmental stages of their highly aquatic life cycle phase would likely inhabit the highly vegetated littoral zones where periphyton food sources would be abundant (Jenssen 1967). Detection and consumption of relatively small *U. limi* and *L. clamitans* in the littoral zone would presumably require snakes to invest substantial amounts of time foraging aquatically but not necessarily over long distances.

The tendency for the *N. s. sipedon* of our study to spend a large percentage of their time aquatic within the dense vegetation of the littoral zone is likely influenced by opportunities to thermoregulate. Although diet may be a significant driver of habitat and microhabitat selection in *N. s. sipedon*, thermal conditions probably interact with diet to determine microhabitat selection (Robertson and Weatherhead 1992). The high thermal conductivity and the short-term thermal stability of water combined with the proximity of surface water to the atmosphere (Manning and Grigg 1997) render the air-water interface to be a high thermal quality microhabitat for aquatic reptiles (Rowe et al. 2014). Indeed, use of the shallow water and basking on emergent vegetation is apparently common across aquatic snake species

(Hebrard and Mushinsky 1978b). Water and body temperatures have been shown to be highly correlated in several *Nerodia* species (Mushinsky et al. 1980) indicating that thermoconforming in favorable aquatic conditions could allow maintenance of T_b within the T_{set} range, a preferred laboratory-determined T_b that is free of environmental constraints (Hertz et al., 1993; Christian and Weavers, 1996). During the activity season, *N. s. sipedon* at Davis Lake maintained body temperatures within their thermoregulatory setpoint range (28°–33° C; Rowe et al. 2022) about 70% of the daylight hours, which is relatively high for *N. s. sipedon* and for north-temperate aquatic or semiaquatic reptiles in general (Edwards and Blouin-Demers 2007; Rowe et al. 2014, 2017, 2020). Data collected during our 24-h diurnal sampling (at 3-h intervals) revealed that *Nerodia s. sipedon* used the *Sphagnum* mat and emergent vegetation for atmospheric basking during late morning, which would be consistent with the rapid body warming phase observed in snakes during late morning (Brown and Weatherhead 2000; Rowe et al. 2022). Our observation that snakes maintained some nocturnal activity, presumably foraging under low illumination, is not unique to members of *Nerodia* (Mushinsky and Hebrard 1977b). Interestingly, environmental temperatures after dark at Davis Lake are typically below the T_{set} range of *Nerodia* (Brown and Weatherhead 2000; Rowe et al. 2022), indicating that snakes can forage at relatively low body temperature.

Questions remain about the spatial ecology of *N. s. sipedon* at Davis Lake in terms of the influences of season, diet, sex, and age of snakes. We know very little about early activity season movements of individual *N. s. sipedon* at Davis Lake that would likely be influenced by overwintering location and dispersion of anurans across the landscape during their breeding seasons. Overall differences in areas occupied by members of each sex does not seem to vary in *N. s. sipedon* (Roe et al. 2004; Roth and Greene 2006; Pattishall and Cundall 2008), and that seems to be the case at Davis Lake. Nonetheless, dispersion of females can affect space use and distribution of male *N. s. sipedon* (Brown and Weatherhead 1999), and gravid females may select different habitats relative to non-gravid females and males (Pattishall and Cundall 2009). Male *N. s. sipedon* show relatively large-scale daily movements during spring when mating occurs (Tiebout and Cary 1987). Where and when snakes mate at Davis Lake could have significant consequences for the spatial ecology of members of each sex over time. Finally, potential ontogenetic shifts in habitat and microhabitat use could occur but are poorly understood for *N. s. sipedon* in general. Pregnant females did not leave the *Sphagnum* mat at Davis Lake, and we presume that parturition occurs locally. Still, we have observed young *N. s. sipedon* not only on the *Sphagnum* mat but also in the surrounding lowland and upland forest areas indicating dynamic habitat use by snakes early in life. Relatively long-term, multiyear study of individual *N. s. sipedon* of each sex and as juveniles would lead to an in-depth understanding of their spatial ecology at Davis Lake.

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Appendix Table. Space use metrics as determined using radiotelemetry for Northern Water Snakes (*Nerodia sipedon*) at different localities throughout its distribution. Values are mean ± standard error or standard deviation*, range of values (if reported in study).

Ecosystem type *Study	Sex Sample size	MCP (ha)	95, 75†, or 50%†† 75 and 95% Harmonic Mean (ha)	KDE $UD_{95\%}$ (ha)	KDE $UD_{50\%}$ (ha)	wAKDE $UD_{95\%}$ (ha)	wAKDE $UD_{50\%}$ (ha)	Linear daily distances moved (m / d or h†) *Method of calculation
Lake-Northern wetland complex, Central Michigan *This study	F	0.29 ± 0.16	--	0.18 ± 0.06	0.04 ± 0.01	0.44 ± 0.17	0.09 ± 0.04	6.42 ± 0.97
	n = 11	0.02–1.86		0.03–0.65	0.005–0.14	0.05–1.66	0.009–0.39	1.98–15.33
	M	0.07 ± 0.03	--	0.07 ± 0.03	0.012 ± 0.006	0.15 ± 0.07	0.03 ± 0.01	6.80 ± 1.55
	n = 4	0.02–0.17		0.02–0.13	0.003–0.03	0.06–0.37	0.009–0.07	3.58–10.88
	Both sexes	0.23 ± 0.10		0.15 ± 0.05	0.03 ± 0.01	0.36 ± 0.13	0.08 ± 0.03	6.52 ± 0.80
	n=15	0.02–1.86		0.02–0.65	0.003–0.14	0.05–1.66	0.009–0.39	1.98–15.33
Shallow wetland complex, Northwestern Ohio-southern Michigan, USA *Roe et al. 2004	F	3.3 ± 0.6	--	3.1 ± 0.9	0.4 ± 0.1			22.9 ± 7.7 *Straight-line distances moved between successive radiolocations / days monitored
	M	5.6 ± 2.9	--	6.9 ± 3.6	1.6 ± 1.0			31.5 ± 6.2
	n = 4			--	--			
	Both sexes	4.0 ± 0.9	--	4.3 ±1.3	0.8 ± 0.3			25.6 ± 2.7
	n = 13			--	--			
Urban stream, Southwest Missouri, USA *Pattishall and Cundall (2008)	Gravid F	1.1 ± 1.4*	--	0.01 ± 0.06	0.01 ± 0.02			--
	n = 28			--	--			
	Non-gravid F	1.3 ± 3.4*	--	0.01 ± 0.02	0.01 ± 0.03			--
	n = 8			--	--			

Appendix Table, cont.

Ecosystem type *Study	Sex Sample size	MCP (ha)	95, 75†, or 50%†† 75 and 95% Harmonic Mean (ha)	KDE $UD_{95\%}$ (ha)	KDE $UD_{50\%}$ (ha)	wAKDE $UD_{95\%}$ (ha)	wAKDE $UD_{50\%}$ (ha)	Linear daily distances moved (m d or h†) *Method of calculation
	M	1.2 ± 2.2*	--	0.01 ± 0.03 --	0.06 ± 0.15 --			--
	Both sexes n = 14	1.1 ± 2.0*	--	0.06 ± 0.15 --	0.01 ± 0.06 --			--
Lake and associated wetlands, Missouri, USA *Roth and Green (2006)	F n = 9	--	0.58 ± 0.08 0.34–0.99 0.10 ± 0.03 0.01–0.33††	2.72 ± 1.15 0.69–11.64	0.33 ± 0.17 0.11–1.68			49.3 ± 8.3 29.3–110.8
	M n = 8	--	0.51 ± 0.10 0.12–1.05	2.92 ± 0.79 0.11–0.88	0.38 ± 0.09 0.11–0.88			*48.8 ± 5.3 25.3–73.9