Articles

Summer and Winter Spatial Habitat Use by the Lake Erie Watersnake

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Abstract

In an effort to provide information to guide habitat management for the Lake Erie watersnake *Nerodia sipedon insularum*, a federally threatened and Ohio state endangered species, we used radiotelemetry to obtain spatial habitat data for adult snakes during the summer active season and during winter hibernation. During the summer active season, terrestrial habitat use was limited to a narrow band of shoreline. Among individuals, maximum distance inland from shore ranged from 1 to 50 m (mean = 8 m) and linear extent of shoreline ranged from 30 to 1,360 m (mean = 261 m). Winter hibernation occurred at varying distances inland with individual hibernation sites ranging from 1 to 580 m (mean = 29 m) from shore. Habitat use did not differ between males and females. Existing U.S. Fish and Wildlife Service habitat management guidelines suggest that ground-disturbing activities within potential hibernation areas (defined as terrestrial habitat within 161 m of shore) should be avoided in winter to prevent harm to hibernating snakes. They suggest further that excavation and removal of shrubs, standing or downed trees, root masses, animal burrows, piled rocks, cliffs, or bedrock within 21 m of shore should be avoided in summer to prevent harm to active snakes. Given that Lake Erie watersnakes have recovered to the point where delisting is being proposed, these habitat guidelines appear to be sufficient. However, maintaining voluntary compliance with habitat guidelines and meeting the need for continued public outreach will be vital to ensure long-term persistence.

Keywords: conservation; habitat use; hibernation; management; snake

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Introduction

Recovery of threatened and endangered species often involves habitat management strategies designed to provide for stable or increasing populations. Ideally, such strategies provide accommodations for key activities (foraging, predator avoidance, reproduction) and are inclusive of all life-stages. In reality, knowledge of habitat use for some species falls short of that needed for effective management and fundamental questions regarding the size and location of key habitat elements may be unanswered.

The Lake Erie watersnake *Nerodia sipedon insularum* is a medium-sized, nonvenomous, live-bearing colubrid snake restricted to a cluster of islands in the Ohio and Ontario waters of Lake Erie. The subspecific status of island populations derives from color pattern differences from mainland populations of the northern watersnake *N. s. sipedon* (Conant and Clay 1937), a difference maintained by a dynamic balance between natural selection favoring a reduction in color pattern on exposed rocky islands shorelines and gene flow from the nearby mainland (King 1993a, 1993b; King and Lawson 1995, 1997). Although the Lake Erie watersnake spends much of its time on land, it forages for fish and amphibians in the near-shore waters of Lake Erie. A dramatic shift in watersnake diet occurred in the 1990s with the arrival of the invasive round goby *Apollonia* *melanostomus*, the abundance of which has contributed to more rapid growth and greater reproductive output among watersnakes (King et al. 2006b, 2008). Legal protection was conferred on this snake when it was declared threatened pursuant to the U.S. Endangered Species Act (ESA) as amended (ESA 1973; Fazio and Szymanski 1999) and endangered under the State of Ohio Administrative Code, Province of Ontario Endangered Species Act, and Committee on the Status of Endangered Wildlife in Canada (summarized in USFWS 2009a). Restricted geographic distribution and declining population size were primary factors contributing to legal protection (Fazio and Szymanski 1999; King et al. 2006a). Recovery efforts involving population monitoring, habitat management, and public outreach, together with beneficial effects of abundant round gobies as food, have resulted in rapid population recovery (R.B. King and K.M. Stanford, Northern Illinois University, personal observation), leading the U.S. Fish and Wildlife Service (USFWS) to initiate actions to delist the Lake Erie watersnake (USFWS 2009a; USFWS 2010). Because delisting will eventually result in reduced legal protection, having appropriate habitat management recommendations in place is vital to the long-term persistence of the snake.

Here we describe spatial habitat use by the Lake Erie watersnake as determined using radiotelemetry. We focus on the location and extent of habitat used during the summer active season and the location of winter hibernation sites because these represent areas necessary for successful reproduction and overwinter survival, respectively. We combine this with published information on Lake Erie watersnake foraging habitat (Jones et al. 2009) to evaluate USFWS habitat management recommendations (USFWS 2003 [appendix D]; USFWS 2009b) and the ''Habitat Protection and Management'' criterion of the Lake Erie Watersnake Recovery Plan (USFWS 2003).

Methods

Radiotransmitters (Holohil, Inc.; model SI-2T) ranging in size from 5.2 to 13.8 g with an expected battery life of 12–36 mo were implanted into adult Lake Erie watersnakes in 2000, 2001, and 2002. We conducted surgery under aseptic conditions using either isofluorane or halothane anesthetic following methods modified from Reinert and Cundall (1982) and Brown and Weatherhead (2000). We positioned transmitters within the body cavity about one-third anterior to the vent and loosely sutured them to the body wall. We inserted transmitter antennas subcutaneously in an anterior direction. We monitored the snakes continuously until they recovered from anesthesia and gave them daily injections of antibiotic (10 mg/kg Baytril) until we released them at their site of capture 2–5 d later. Adult males ($n = 22$) averaged 210 g (range = 118–347 g) and adult females ($n = 32$) averaged 525 g (range = 306–954 g) at the time of surgery. Transmitter mass averaged 2.4% of adult female mass (range = 1.4–3.7%) and 4.1% of adult male mass (range = 2.7–7.1%).

Telemetry occurred on five Lake Erie islands, including Kelleys (2000–2003), South Bass (2001–2003), Middle Bass (2001–2003), North Bass (2001–2002), and Gibraltar (2001–2003; figure 2 in King et al. 2006a). Following release, we located the snakes during daylight hours by searching outward from the release site or previous location using an AVM Instrument Co. LA12-Q receiver and Telonics RA-14K antenna. Depending on transmitter size and snake location, detection distance ranged from about 200 to 1,000 m. Snakes were located on average once every 8 d during the active season (from implantation or emergence from hibernation until death, transmitter failure, or entry into hibernation) and at longer intervals during winter (King RB et al. in review). Intervals between location dates were variable because of weather conditions and the logistics of interisland transportation.

Each time we located a snake, we recorded GPS coordinates using a handheld Garmin eTrex GPS receiver. In addition, we measured distance inland from shore in meters using a tape measure or distance-measuring wheel. We plotted locations onto Digital Orthophoto Quarter Quadrangles using ArcView Geographic Information Systems software. We estimated the amount of terrestrial habitat used during summer active season in two ways. First, following Pattishall and Cundall (2008), we estimated the linear extent of shoreline used as the length of shoreline between the two most distant locations (Figure 1). Second, we estimated the amount of terrestrial habitat by determining the maximum distance inland from shore at which each snake was observed. For snakes monitored during multiple summers, both extent of shoreline and amount of terrestrial habitat were pooled across years because these snakes used approximately the same areas each season.

We measured the distance to shore from hibernation sites (Figure 1) as described above. For those snakes that hibernated inland from shoreline areas not used during the summer, the distance between the shoreline point closest to the hibernation site and the nearest shoreline location used during summer was estimated using ArcView (Figure 1).

Distributions of distance measures (extent of shoreline, maximum distance inland from shore, and distance to shore from hibernation site) were all significantly right-skewed. For analysis, we normalized these variables by adding one and taking natural logarithms. Means and other descriptive statistics were back-transformed for clarity of presentation.

Results

Transitions between summer habitat and hibernation sites were identified based on qualitative changes in watersnake behavior. During the active season, terrestrial habitat use was restricted to a narrow continuous band of shoreline habitat. In autumn, watersnakes typically made longer distance movements to hibernation sites further inland, after which they were found repeatedly within highly localized areas (i.e., within 10 m). In some cases, hibernation sites were directly inland and adjacent to shoreline areas used during summer. However, in other cases, watersnakes moved to hibernation sites that

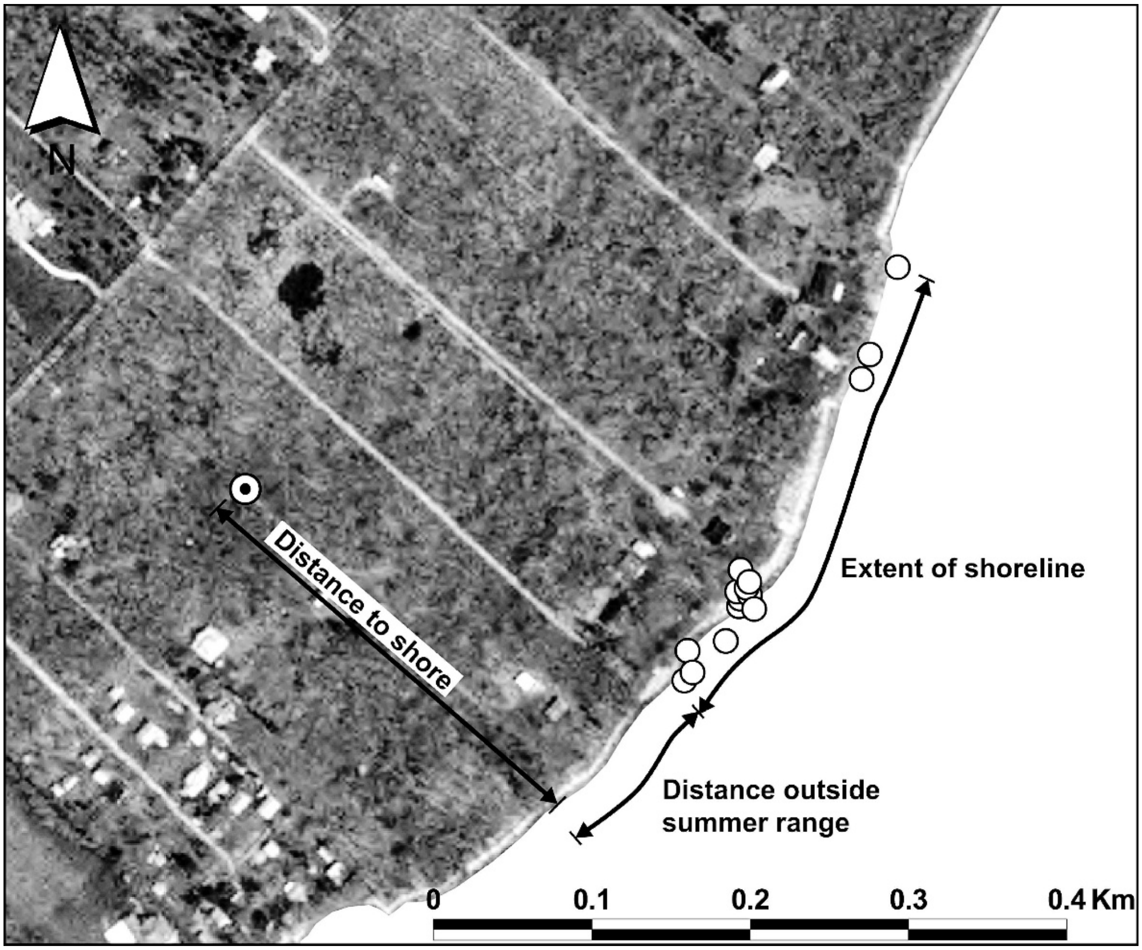

Figure 1. Movements of a representative Lake Erie watersnake, illustrating extent of shoreline used during summer, distance outside summer range to the shoreline point nearest hibernation site, and distance to shore from hibernation site. Open circles are locations at which this snake was found between 19 June 2001 and 12 October 2001 (active-season locations) and span 260 m. The 'bullseye' represents the hibernation site where this snake remained October–April. Before entering hibernation, this snake moved about 135 m along the shore beyond where it spent the active season and 280 m inland to hibernate.

were inland from shoreline areas not used during summer (Figure 1). Entry into hibernation occurred between 8 September and 18 October. Spring emergence was invariably followed by movements back to shoreline areas used the previous summer, and occurred between 20 April and 31 May.

Summer habitat use

Information on habitat use during summer was obtained from 54 watersnakes, 20 that were tracked during a single summer, 27 during two summers, 5 during three summers, and 2 during four summers (Table 1). Locations used by individual watersnakes during summer were recorded 5–41 times throughout the study. For individuals tracked in multiple years, the number of locations in later years was sometimes low because mortality and battery life limited data collection. On average, individual snakes were monitored for a span of 137 active-season days (range = 36–360 d).

Neither extent of shoreline nor maximum distance inland from shore differed significantly between males and females (extent of shoreline: $t = -0.92$, $P = 0.366$; maximum distance inland from shore: $t = 0.60$, $P = 0.55$). Therefore, sexes were pooled to generate a population-wide description of active-season movements. Extent of shoreline ranged from 30 to 1,360 m among individuals and averaged 261 m (Figure 2). Features of summer habitat were not quantified but watersnakes made frequent use of on-shore retreat sites consisting of crevices within exposed bedrock, among loose rocks overlaying bedrock, and within human-made structures (e.g., crib docks, shoreline protection).

Given that snakes were not monitored continuously and some individuals were monitored for only a portion of the active season, distances reported above may be underestimates of the true extent of shoreline used during the active season. In fact, estimated extent of shoreline increased as the number of times snakes were located increased (Pearson correlation, $P = 0.005$). However, the amount of variation explained by number of locations was small ($r^2 = 0.14$), and distributional characteristics of extent of shoreline (i.e., mean, median, SD, data not shown) changed little when analyses were repeated using only the 40 snakes located ≥10 times

Table 1. Characteristics of adult Lake Erie watersnakes ($n = 54$) monitored on five Lake Erie islands in 2000–2003 using radiotelemetry, including island, sex, initial snout–vent length (SVL) and Mass, Dates tracked with number of relocations in parentheses, total relocations (Total), extent of shoreline used (Extent) and Maximum inland distance during summer, and distance from Hibernation to shore.

ID	Island[a]	Sex	SVL (mm)	Mass (g)	Dates tracked (relocations) 2000	2001	2002	2003	Total	Extent (m)	Maximum inland (m)	Hibernation to shore (m)
123	KI	m	753	289	8/9–9/18 (9)	5/9–6/18 (7)			16	155	13.7	20
128	KI	f	928	819	7/24–9/21 (15)				15	85	10.0	
129	KI	f	1,000	954	7/24–9/21 (17)	5/9–11/9 (16)			33	180	10.0	190
157	KI	f	1,079	652	7/24–9/16 (11)	5/10–8/15 (11)	6/4–9/6 (8)		30	725	9.1	580
159	KI	f	977	778	7/24–9/8 (12)				12	110	22.9	
165	KI	m	752	275	7/24–9/25 (14)				14	1,360	20.0	35
168	KI	f	910	651	7/24–9/22 (17)	5/13–9/25 (16)	6/2–10/1 (5)	5/1–6/4 (3)	41	1,180	20.0	24
173	KI	f	794	408	7/24–9/18 (13)	5/22–9/24 (14)	6/2–9/24 (9)	6/4 (1)	37	1,090	20.0	24
184	KI	m	647	221	7/24–1014 (17)	5/10–9/3 (14)	5/17–6/22 (4)		35	140	50.0	15
186	KI	m	723	234	7/24–9/19 (14)				14	665	7.6	10
193	KI	f	864	577	7/29–9/24 (16)				16	160	4.6	
196	KI	m	640	158	7/24–9/24 (13)	5/9–7/9 (9)			22	360	1.2	20
213	KI	m	745	268	7/20–8/22 (8)	5/13–5/16 (2)			10	160	30.0	40
215	KI	f	946	829	7/29–9/18 (11)	5/9–9/24 (16)			27	155	15.2	6
216	KI	m	647	203	7/30–9/25 (12)	5/10–9/25 (13)			25	580	15.2	100
218	KI	f	933	607	7/30–9/16 (12)	5/22–7/19 (7)			19	230	18.3	50
221	KI	m	754	347	7/29–9/25 (15)	5/9–9/3 (15)	6/2–8/12 (7)		37	755	7.6	12
047	MBI	m	700	191		7/12–9/11 (8)	5/23–8/27 (13)		21	420	1.5	20
111	NBI	f	795	461		7/11–11/13 (11)	5/1–8/27 (15)		25	250	7.6	47
139	MBI	f	830	418		7/12–9/11 (7)			7	180	6.1	
16A	KI	f	910	553		7/6–10/9 (9)			9	180	9.1	21
22E	NBI	f	865	565		7/11–9/18 (9)			9	260	9.1	
255	MBI	f	890	653		7/12–9/11 (8)	5/1–7/31 (10)		18	490	7.0	6
26C	NBI	m	645	150		7/11–9/11 (8)	5/1–8/17 (9)		17	440	9.1	141
301	KI	m	770	252		7/9–9/24 (6)			6	725	9.1	18
309	MBI	m	605	131		7/12–9/11 (8)			8	70	4.6	45
35C	SBI	m	590	118		6/21–9/17 (11)			11	720	4.6	17
477	MBI	m	725	237		7/12–9/11 (8)	5/23–9/27 (16)		24	500	3.0	1
507	SBI	f	790	384		6/21–9/17 (11)	6/10–9/6 (12)		23	250	15.0	280
551	MBI	m	645	137		7/12–9/11 (8)			8	120	0.9	180
628	SBI	f	850	397		6/21–9/17 (11)			11	490	6.1	12
67D	KI	f	920	564		7/9–8/20 (6)			6	260	10.7	40
708	KI	m	760	246		7/9–9/25 (8)	4/27–10/1 (14)		22	480	12.2	21
730	MBI	m	675	164		7/12–9/11 (8)			8	485	12.2	395
80A	NBI	f	850	485		7/11–9/11 (8)			8	190	4.6	6
83E	Gib	f	930	606		7/12–9/18 (8)	5/21–10/3 (15)	4/15–5/13 (2)	25	360	5.0	11
A54	MBI	f	740	330		7/12–9/11 (8)	5/1–10/1 (18)	5/26 (1)	27	150	2.0	30
A77	SBI	m	730	214		6/21–9/6 (9)	6/28–9/19 (11)		20	85	10.0	220
B15	SBI	m	680	169		6/21–9/24 (8)			8	105	3.0	162
B1E	KI	f	970	478		7/9–9/24 (8)			8	140	7.6	15
B35	KI	f	695	519		6/23–9/25 (2)	6/2–6/27 (3)		5	230	9.1	40
B69	SBI	f	895	322		7/11–10/21 (11)	4/29–5/31 (5)		16	290	7.6	12
D1C	SBI	m	735	192		7/11–10/12 (10)	4/29–7/23 (12)		22	340	9.1	15
D60	Gib	m	655	170		7/12–9/5 (6)			6	30	3.0	6
D64	SBI	f	820	360		6/21–10/12 (12)	6/10–6/28 (4)		12	100	6.1	9
E66	MBI	f	690	328		7/12–9/11 (7)	5/23–9/5 (14)		21	250	12.2	180

Table 1. Continued.

ID	Island[a]	Sex	SVL (mm)	Mass (g)	Dates tracked (relocations) 2000	2001	2002	2003	Total	Extent (m)	Maximum inland (m)	Hibernation to shore (m)
E71	MBI	f	725	351		7/12–9/7 (8)	5/1–7/19 (8)		16	90	6.0	7
F0F	NBI	f	965	550		7/11–9/18 (9)			9	350	4.6	105
F7D	SBI	f	805	431		6/21–10/12 (12)	4/30–5/2 (2)		14	260	12.2	280
467	MBI	f	825	345			6/12–10/11 (15)	5/13–7/12 (3)	18	380	6.0	20
50C	SBI	m	745	248			6/18–9/19 (13)	5/13–8/21 (5)	18	210	6.0	11
629	SBI	f	785	306			6/10–9/19 (14)	6/24–8/21 (3)	17	315	5.0	6
712	MBI	f	960	591			6/10–9/23 (13)	5/13–10/16 (3)	16	105	12.0	3
D76	SBI	f	965	580			6/10–9/19 (14)	4/15–5/13 (2)	16	490	30.0	9

[a] Island abbreviations: KI = Kelleys Island, SBI = South Bass Island, MBI = Middle Bass Island, NBI = North Bass Island, Gib = Gibraltar Island.

(mean = 296 m) or the 33 snakes located ≥15 times (mean = 279 m). Maximum distance inland from shore ranged from 1 to 50 m among individuals and averaged 8 m (Figure 3).

Hibernation sites

Information on hibernation sites was based on 49 individual Lake Erie water snakes (27 females, 22 males; Table 1). Hibernation sites were located in a single year for 36 snakes, in two successive years for 10 snakes and in three successive years for 2 snakes. Because snakes observed to hibernate, more than once used the same hibernation location (within 10 m), information on hibernation sites was pooled across years.

Of the 49 hibernation sites, 31 were located directly inland from shoreline areas used during the summer by those individuals. The other 18 hibernation sites were located inland from shoreline areas outside of that used during summer (Figure 1). Whether snakes hibernated directly inland from summer habitat was independent of sex ($\chi^2 = 0.002$, $P = 0.961$). To reach hibernation sites located inland from shoreline areas not used in summer, snakes were estimated to have moved between 35 and 1,410 m (mean = 216) along the shore prior to moving inland. Snakes moved through unused shoreline areas quickly (e.g., in ca. 4–14 d between two successive tracking dates), suggesting that they were not an undetected part of summer habitat.

Distance to shore from hibernation sites did not differ significantly between males and females ($t = 0.30$, $P = 0.762$). Therefore, sexes were pooled to generate a population-wide description of this variable. Distance to shore from hibernation sites ranged from 1 to 580 m among individuals and averaged 29 m (Figure 4). The elevation above lake level of the ground surface over hibernating snakes ranged from 1 to 10 m.

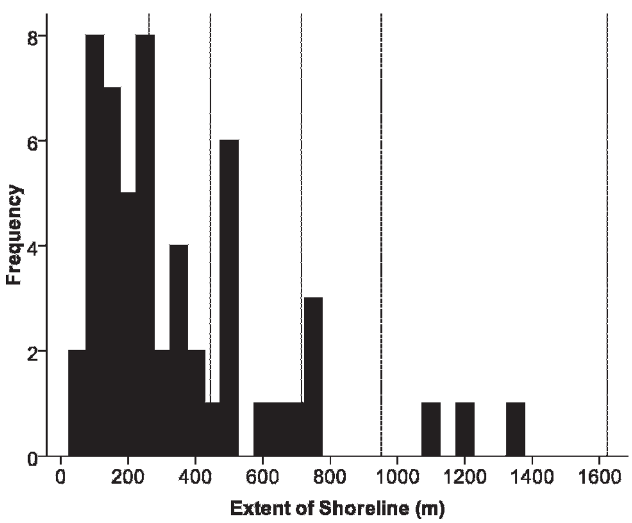

Figure 2. Extent of shoreline used during summer active seasons by adult Lake Erie watersnakes (n = 54). Vertical dashed lines show the estimated extent of shoreline used by, from left to right, 50% (≤261 m), 75% (≤444 m), 90% (≤715 m), 95% (≤952 m), and 99% (≤1,622 m) of the population (based on mean and variance of log-transformed values).

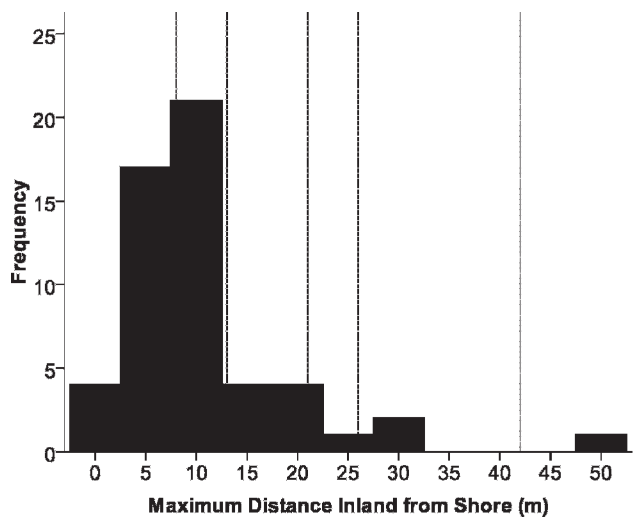

Figure 3. Maximum distance inland from shore during summer active seasons by adult Lake Erie watersnakes (n = 54). Vertical dashed lines show the estimated maximum distance inland for, from left to right, 50% (≤8 m), 75% (≤13 m), 90% (≤21 m), 95% (≤26 m), and 99% (≤42 m) of the population (based on mean and variance of log-transformed values).

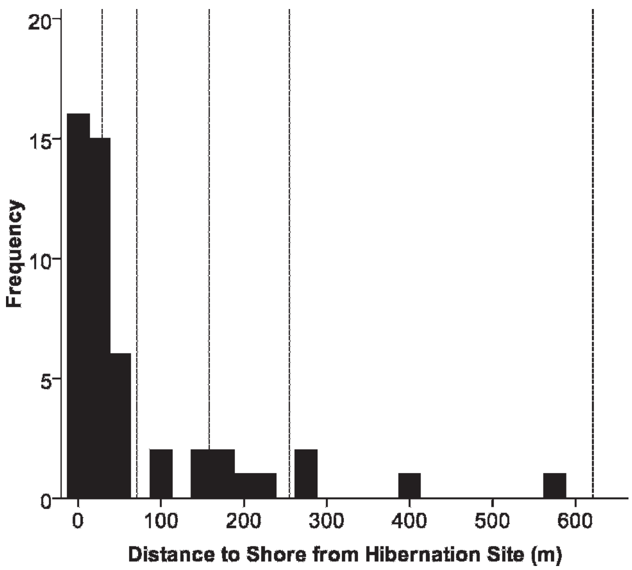

Figure 4. Distance to shore from hibernation sites for adult Lake Erie watersnakes (n = 49). Vertical dashed lines show the estimated distance inland to hibernation sites for, from left to right, 50% (≤29 m), 75% (≤71 m), 90% (≤158 m), 95% (≤255 m), and 99% (≤621 m) of the population (based on mean and variance of log-transformed values).

Characteristics of hibernation sites were variable. Most had soil and rock substrates and appeared to consist of natural openings or fissures. Access holes to some hibernation sites were apparent and may have been the result of burrowing by small mammals, shoreline erosion, or tree falls. Eleven hibernation sites were found in or near human-made structures including abandoned building foundations, drainage tile, sewage line, concrete shoreline protection material, the foundation of a cottage, and an unused wine cellar. Vegetation around hibernation sites was also variable and included mature forest, woody scrub, and grass and herbaceous vegetation (sometimes including mown lawns). Usually only one telemetered snake was observed to hibernate at a given location although other untelemetered animals were sometimes observed nearby. In three cases, two telemetered snakes hibernated within 10 m of each other.

Mortality

Of the 54 watersnakes included in this study, 29 were alive when transmitters or transmitter batteries failed. Eleven of these survivors were recaptured during annual population censuses in subsequent years (King et al. 2006a). The other 25 watersnakes were known or presumed to have died over the course of the study; 22 apparently of natural causes and 3 as a consequence of mowing, brush burning, or hibernation site disruption. Those that died of natural causes included four males and nine females that died during hibernation or shortly after spring emergence. Two females died prior to entry into hibernation. These females had recently given birth as evidenced by their thin appearance, and this may have been a contributor to their deaths. One female apparently died as the result of predation; bite marks suggest the predator was a fox, raccoon, or domestic dog. Cause of death could not be inferred for two males and four females that could not be retrieved from under large rocks.

Discussion

In describing the habitat and habits of the Lake Erie watersnake, Conant and Clay (1937) noted that

> The water snakes, for the most part, appear to be restricted to the edges of the islands. They are not numerous on sand and gravel beaches but where rocks are strewn upon the shores, where low cliffs are close to the water's edge, or where docks extend into the water they are abundant (pp 8–9).

The suggestion that the Lake Erie watersnake is largely restricted to the island peripheries is found in subsequent studies (e.g., Camin and Ehrlich 1958; King 1986) although some authors note that it ''does occasionally inhabit more inland environs'' (p 38; Kraus and Schuett 1982). Data presented here largely confirm this observation with respect to the summer active season; on average, the maximum distance inland from shore at which telemetered watersnakes were observed was just 8 m. However, the results of this study go further in documenting the linear extent of shoreline used by Lake Erie watersnakes and by providing information on the distance inland to suitable hibernation sites. Extent of habitat used during summer is highly variable, with some individuals restricting their activity to stretches of shoreline encompassing just tens of meters and others ranging over a kilometer. Furthermore, hibernation can occur well inland, which has significant conservation implications. Although on average, Lake Erie watersnakes hibernated within 29 m of shore, individual hibernation sites occurred as far inland as 580 m and 25% of the adult population was estimated to hibernate 71 m or further inland.

Fine-scale characteristics (e.g., depth, substrate) of hibernation sites used by Lake Erie watersnakes remain unknown, but given the shallow soils of the islands generally (Core 1948), hibernation sites likely occur in crevices within the bedrock or among loose rocks and other materials immediately above the bedrock. Furthermore, because the substrate over hibernation sites was sometimes as little as 1 m above lake level, it is possible that Lake Erie watersnakes are partly or fully submerged during hibernation. Submergence appears to reduce energy use and risk of desiccation and leads to increased overwinter survival in the common gartersnake *Thamnophis sirtalis* (Costanzo 1986, 1989a, 1989b), but the degree to which submergence occurs in Lake Erie watersnakes is not known.

Lake Erie watersnakes forage for fish and amphibians (primarily round gobies and mudpuppies *Necturus maculosus*), in waters adjacent to shoreline areas used in summer (Jones et al. 2009). Observations made during systematic boat surveys indicate that foraging by Lake Erie watersnakes can extend ≥200 m from shore (Figure 5) in water up to 7.5 m deep (Jones et al. 2009). Thus, while on-shore activities are restricted to a narrow band of land close to the water's edge, foraging activities extend to a wider band of the near-shore waters of Lake Erie.

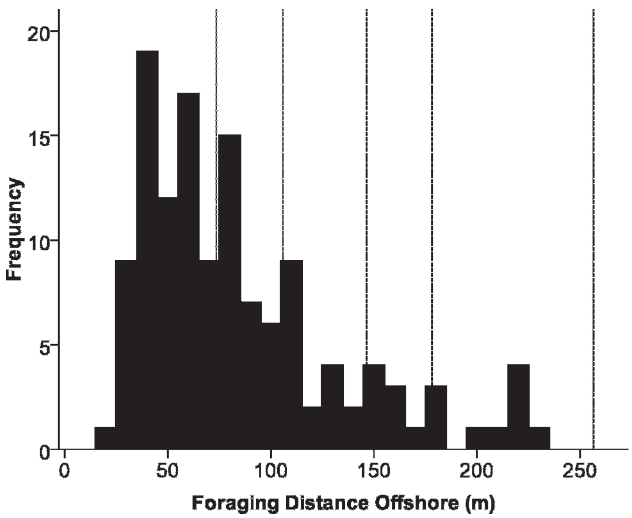

Figure 5. Distance offshore at which Lake Erie watersnakes were observed foraging (n = 130). Vertical dashed lines show the estimated distance offshore within which foraging occurred for, from left to right, 50% (≤74 m), 75% (≤106 m), 90% (≤147 m), 95% (≤178 m), and 99% (≤257 m) of the population (based on mean and variance of log-transformed values).

Spatial habitat use can be difficult to compare among telemetry studies because authors analyze data in different ways and only infrequently report detailed tracking information on individuals (Pattishall and Cundall 2008). Comparisons are further complicated by differences in the dimensionality of habitat use, even within species. For example, terrestrial habitat use by Lake Erie watersnakes in summer is essentially linear (one-dimensional) and similar to that of Northern watersnakes *Nerodia sipedon sipedon* dwelling in a stream habitat in Pennsylvania (figure 6 in Pattishall and Cundall 2009). In contrast, *N. sipedon* inhabiting marshes and wetlands exhibit planar two-dimensional habitat use (figures 2–4 in Tiebout and Cary [1987]; figure 1 in Brown and Weatherhead [1999]; figure 1 in Roe et al. [2004]; Roth and Greene [2006]). Even greater dimensionality in habitat use is seen in species living in high-relief environments where elevation (or depth) provides another habitat dimension.

The detailed data presentation of habitat use by stream-dwelling Northern watersnakes in Pennsylvania (Pattishall and Cundall 2008) allows direct comparison with this study. Much like the extent of shoreline used during summer by Lake Erie watersnakes, distances between the most upstream and downstream locations of Northern watersnakes were right-skewed (table 2 in Pattishall and Cundall 2008). In both studies, habitat use varied widely among individuals, ranging from 30 to 1,360 m in Lake Erie watersnakes (this study) and 10 to 1,425 m in Northern watersnakes (Pattishall and Cundall 2008). Northern watersnakes were more variable in habitat use (Levene's test, F = 9.95, P = 0.002, SD of natural log–transformed data = 1.8 vs. 0.78) but on average used shorter lengths of habitat than did Lake Erie watersnakes (t-test using separate variance estimates: t = −2.58, df = 73.86, P = 0.012, back-transformed means = 153 vs. 261 m; note that Pattishall and Cundall [2008] did not transform their data and so report mean stream length as 280 m). Like Lake Erie watersnakes, Northern watersnakes remained close to water, with 57% of relocations occurring within 5 m, 88% within 20 m, and 97% within 50 m of the stream (Pattishall and Cundall 2008; cf. figure 3). These similarities between stream-dwelling and lakeshore-dwelling populations are striking and contrast markedly with spatial habitat use by marsh and wetland dwelling *N. sipedon* (reviewed by Pattishall and Cundall 2008).

Conservation implications

Spatial habitat use by Lake Erie watersnakes differs markedly between the summer active season and winter hibernation, and successful management should address habitat use during both time periods. In summer, habitat use is restricted to a narrow band of terrestrial shoreline and a somewhat wider band of near-shore aquatic habitat. In contrast, winter hibernation occurs in both shoreline and inland habitats. Because there do not seem to be habitat features strongly associated with areas used in summer or for hibernation, general guidelines for human activities within these areas may represent the best way to minimize watersnake mortality.

As part of the Lake Erie watersnake recovery plan, the USFWS developed a set of Guidelines for Construction, Development, and Land Management Activities (USFWS 2003 [appendix D]; USFWS 2009b). Similar guidelines address habitat management at Middle Bass Island State Park (USFWS 2003 [appendix B]) and within conservation easements in the region (M. Seymour, USFWS, personal communication). To avoid harming watersnakes during hibernation, these guidelines recommend that no excavation occur within potential hibernation areas (defined as terrestrial habitat up to 161 m inland from shore) between 15 October and 15 April. Furthermore, during periods of hibernation egress (defined as 16 April–31 May) and ingress (defined as 15 September–14 October), excavation within potential hibernation areas should occur only when air temperatures exceed 15.5°C. Presumably, during warm weather, surface-active snakes can move quickly enough to avoid harm from excavation equipment. Because root masses may provide hibernation sites, tree removal should be limited to the above-ground portion of the tree. To avoid harming watersnakes during the active season, these guidelines recommend that mowing within potential summer habitat (defined as terrestrial habitat within 21 m of shore) between 15 April and 15 September occur at dusk with mower blades set high above the ground. By waiting until dusk, it is assumed that surface-active snakes have sought cover and are less likely to be harmed by mowing equipment. Furthermore, these guidelines specify that excavation, removal of shrubs, standing or downed trees, root masses, animal burrows, piled rocks, cliffs, or bedrock within 21 m of shore should be avoided and use of heavy machinery should be limited to paved areas. Because Lake Erie watersnakes make frequent use of docks and shoreline erosion-control structures, it is recommended that maintenance and construction of these structures should use designs that provide watersnakes with access to retreat sites (steel or timber cribs, riprap) rather than impenetrable materials (concrete, sheet steel). Finally, these guidelines specify that construction sites should be actively monitored for watersnakes before and during construction activities. The low rate of mortality among telemetered snakes attributed to human activities in this study (3 of 54 animals) suggests that these management guidelines have been effective.

Definitions of potential hibernation areas (terrestrial habitat up to 161 m from shore) and summer habitat (terrestrial habitat up to 21 m from shore) used in these guidelines were based in part on prior analyses of the telemetry data presented here (King 2003) and were selected to encompass the estimated area used by 90% of the adult population. These definitions, together with other analyses presented here, might be used to further characterize an 'ideal' Lake Erie watersnake habitat patch as also encompassing approximately 715 m of shoreline (Figure 2) and extending approximately 147 m offshore (Figure 5). Guidelines could be expanded based on habitat use by a larger proportion of adult watersnakes (e.g., 95% or 99% rather than 90%). In the absence of intentional harassment, Lake Erie watersnakes appear tolerant of human activities. Several of our long-term study sites are adjacent to seasonal and year-round residences, are within popular state parks, or encompass frequently used docks and boat ramps and still support dense (200 adults/km) Lake Erie watersnake populations (King et al. 2006a). Given the current abundance of round gobies as food and the impact this has had on Lake Erie watersnake growth and reproduction (King et al. 2006b, 2008), the habitat guidelines currently in place appear to be sufficient for persistence of stable Lake Erie watersnake populations.

Because Lake Erie watersnakes are locally abundant and human–watersnake encounters are frequent, public outreach was identified as an explicit part of the Lake Erie Watersnake Recovery Plan (USFWS 2003) and has been accomplished through active and interactive methods (public presentations, workshops, school programs) funded by federal and state agencies. Delisting of the Lake Erie watersnake, as is being proposed by the USFWS (USFWS 2010), will create additional challenges for managers charged with ensuring population persistence within a less restrictive legal framework. Adherence to the habitat management guidelines outlined above will become largely voluntary, even for projects that currently require federal consultation. We contend that continued public outreach will be helpful because Lake Erie islands are a destination for large numbers of seasonal visitors, many of whom have limited knowledge regarding snakes generally (Burghardt et al. 2009) and Lake Erie watersnakes in particular (e.g., that they are a unique feature of the regional biota, are protected, and are nonvenomous).

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