

Spatial Ecology of Northern Map Turtles (*Graptemys geographica*) in a Lotic and a Lentic Habitat

MARIE-ANDRÉE CARRIÈRE, GRÉGORY BULTÉ, AND GABRIEL BLOUIN-DEMERS¹

Department of Biology, University of Ottawa, 30 Marie-Curie, Ottawa, Ontario, K1N 6N5, Canada

ABSTRACT.—Lentic (i.e., lake) and lotic (i.e., river) environments differ in several biotic and abiotic variables such as water velocity, productivity, thermal regimes, and depth. These variables can interact with important factors such as sex, body size, and life-history stage to shape the spatial ecology of aquatic animals such as freshwater turtles. We used radio-telemetry to study seasonal movement patterns and home-range size of juvenile and adult Northern Map Turtles (*Graptemys geographica*) both in a small lake and in a large river in eastern Ontario, Canada. Adult females in the lotic environment moved longer distances and had larger home ranges than conspecifics from the lentic environment. Males and juvenile females at each site had similar patterns of space use. A seasonal effect on movement was only apparent for adult females in the lotic environment in which adult females moved longer distances during the nesting season. Differences in swimming abilities resulting from a larger body size, in natal homing, or in nest site availability are potential factors explaining the site difference in the spatial ecology of adult females. Our findings illustrate the complexity of interactions shaping patterns of space use by aquatic reptiles.

Patterns of space use by animals have implications for fundamental ecological processes such as dispersal (Armsworth and Roughgarden, 2005), habitat use (Haynes and Cronin, 2003), and predation (Fortin et al., 2005). Therefore, the study of animal movements is of central interest in ecological research. The rate of movement and the extent to which individuals move (and consequently the size of their home ranges) are mediated by many biotic and abiotic factors (Wiens et al., 1993). For example, food abundance (Compton et al., 2002), temperature (Haxton and Berrill, 2001), and habitat structure (Roe and Georges, 2008) can all influence movement and home-range size in freshwater turtles. How animals respond to such environmental factors depends, in turn, on intrinsic factors such as sex (Morreale et al., 1984), life-history stage (Blouin-Demers et al., 2007), and body size (Peters, 1983; Minns, 1995).

Freshwater ecosystems vary widely in size and structure. Specifically, lentic (i.e., lakes), and lotic (i.e., rivers) environments differ in several biotic and abiotic variables such as water velocity, productivity, thermal regimes, and depth (reviewed by Ryder and Pesendorfer, 1986). Some aquatic species are able to thrive in both lentic and lotic environments, but little is known about how such species adjust their patterns of space use as a function of habitat type. Studies comparing the spatial ecology of species in lentic and lotic environments can

provide insights on key factors shaping patterns of space use by animals. For instance, in a meta-analysis, Minns (1995) found that fishes in rivers have smaller home ranges than conspecific or heterospecific fishes of similar body size in lakes. Because rivers tend to have higher primary productivity than lakes (Ryder and Pesendorfer, 1986; Randall et al., 1995), fishes in rivers need to travel less than their counterparts in lakes to harvest resources.

Field studies comparing the spatial ecology of the same species in lakes and rivers are scarce. Such studies are important to improving our understanding of variables shaping patterns of space use by aquatic animals and how those variables interact with important factors such as sex, body size, and life-history stage. We studied seasonal movement patterns and home-range size of juvenile and adult Northern Map Turtles (*Graptemys geographica*) in a small lake and in a large river in eastern Ontario, Canada. *Graptemys geographica* is considered a river species (Moll and Moll, 2000) but also occurs in medium to large lakes (Ernst et al., 1994). The spatial ecology of this species is poorly known. Studies on the spatial ecology of Northern Map Turtles in a fluvial lake (Flaherty, 1982; Gordon and MacCulloch, 1980) and in a river (Pluto and Bellis 1986, 1988) have revealed intersexual and seasonal differences in movement patterns.

Intersexual differences in the spatial ecology of Northern Map Turtles appear to be tied to sexual size dimorphism and to reproductive behavior. *Graptemys* sp. exhibit marked sexual size dimorphism where adult females may be

¹ Corresponding Author. E-mail: gblouin@uottawa.ca

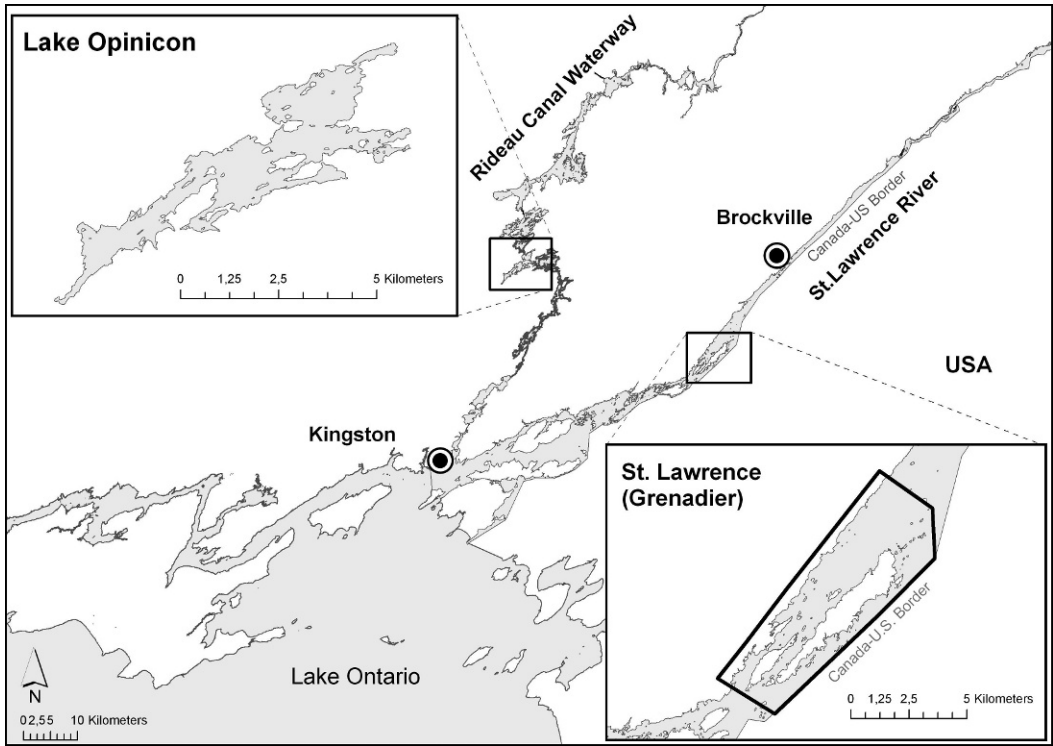


FIG. 1. Study sites of Northern Map Turtles in eastern Ontario, Canada. Lake Opinicon is small and closed, whereas the St. Lawrence River is large and open.

more than twice the length of adult males (Gibbons and Lovich, 1990). Swimming speed is dictated by body size in Northern Map Turtles (Pluto and Bellis, 1986). Water velocity can potentially restrict movements of smaller individuals (i.e., males and juveniles). Thus, relative to adult females, males and immature females may have restricted movements in rivers but not in lakes. Between sites, intersexual differences in movement patterns and home-range size may also reflect a difference in productivity (Ryder and Pesendorfer, 1986; Randall et al., 1995). Indeed, because rivers are more productive than lakes, turtles may need to move shorter distances to harvest resources and, thus, may have smaller home ranges in rivers compared to lakes.

The reproductive behaviors of each sex should also affect movement patterns and home-range size. The "reproductive strategies" hypothesis suggests that, during the nesting season, females should move more than would males to reach favorable nesting sites (Morreale et al., 1984). Within each study site, therefore, we predicted that adult females should move more during the nesting season (June and July) and that these nesting movements should be reflected in the size of their home ranges.

Differences in nesting site availability between study sites may also influence the distance traveled by adult females. The St. Lawrence River study area has few potentially suitable nesting sites, whereas Lake Opinicon has comparatively more. Therefore, adult females in the St. Lawrence River may need to move more than would those in Lake Opinicon during the nesting season. Because *G. geographica* mate in spring and fall while both sexes are at the communal hibernacula (Vogt, 1980; MAC and GB, pers. obs.), we did not expect males to increase their movements during the active season to mate as predicted by the reproductive strategies hypothesis.

MATERIALS AND METHODS

Study Areas.—We conducted this study from May to September in 2005–06. The two study sites were located approximately 40 km apart in eastern Ontario, Canada (Fig. 1). Our lentic site was Lake Opinicon situated approximately 100 km south of Ottawa, Ontario. Lake Opinicon is a small (788 ha), shallow, mesotrophic lake. Lake Opinicon is part of the Rideau Canal waterway, and locks restrict access to other bodies of water by turtles. The mean depth of

Lake Opinicon is 4.9 m (maximum = 9.2 m). Our lotic site was the St. Lawrence River between Mallorytown and Rockport, Ontario. Situated in the vicinity of a large island (Grenadier Island, area of 554 ha), this site covered an aquatic area of 2,890 ha and was entirely open, having no physical barrier restricting the upstream and downstream movements of turtles. The relatively large St. Lawrence River provides many habitat types ranging from rugged granite shores to dense cattail marshes. The water depth ranges from less than 1 m to more than 25 m.

Radio-Telemetry and Data Collection.—Turtles were captured mainly with basking traps and by snorkeling near areas of aggregation. Sex was determined by size, carapace shape, and preanal tail length. Juvenile females were defined as females with a carapace length < 200 mm, a criterion based on the smallest gravid female captured. Subsets of captured individuals from three reproductive classes (juvenile females, adult females, and adult males) were fitted with radio-transmitters (Hohloh SI-2FT 16 g, battery life of 28 months; SI-2FT 12 g, battery life of 18 months; and SB-2FT 6 g, battery life of 12 months) at each site. Over the two years of the study, 49 turtles (17 adult females, 15 juvenile females, and 17 adult males) were followed in Lake Opinicon, and 31 turtles (12 adult females, 9 juvenile females, and 10 adult males) were followed in the St. Lawrence River. We used stainless steel bolts to attach the transmitters to the rear marginal scutes of the carapace. Nontoxic aquarium silicone was used to cover the bolts and the transmitter edges for additional adhesion and for contouring to reduce snagging by macrophytes. Transmitters (including bolts, nuts, and silicone) represented maximally 5% of the turtle's body mass.

Turtles were released at their site of capture the following day and were then tracked every 2–3 days using a telemetry receiver and a directional antenna. At each location, we recorded the Universal Transverse Mercator (UTM) coordinates (3D differential receiver status, NAD83 datum) with a GPSmap76 (Garmin International, Inc., Olathe, KS) at an estimated accuracy of <3 m.

Movement Patterns.—We derived movement statistics from 43 turtles (15 adult females, 15 juvenile females, and 13 males) in Lake Opinicon and from 28 turtles (11 adult females, 9 juvenile females, and 8 males) in the St. Lawrence River. Premature transmitter failure (3 males and 2 juvenile females), predation (2 males and 1 adult female), and winterkill (2 males) precluded the collection of sufficient

movement data for the remaining individuals. In Lake Opinicon, 3 adult females and 2 males were followed both years; thus, we had data for 18 turtle-years for adult females, 15 turtle-years for juvenile females, and 15 turtle-years for adult males. In the St. Lawrence River, 9 adult females and 3 juvenile females were followed for two years, resulting in 20 turtle-years for adult females, 12 turtle-years for juvenile females, and 8 turtle-years for males. Following a few individuals over two seasons resulted in some pseudoreplication, but randomly excluding individuals so that each individual was only represented once did not change our conclusions.

We measured distances moved between locations with the Animal Movements Extension 2.0 (Hooge and Eichenlaub, 2000) in ArcView 3.2 (ESRI, 2000b). Movements were measured as straight-line distances between relocations. *Graptemys geographica* are highly aquatic, only using land to nest or bask and, thus, are unlikely to cross land during normal daily activities. Therefore, any straight-line movement crossing land was modified to represent the shortest distance in water between points. We calculated distances moved per day as the distance moved between relocations divided by the number of days elapsed since the last location. We then averaged these distances across the entire active season for mean distance moved per day and across each month for mean distance moved per month. We averaged distances moved for each individual before analyses.

We first examined the effect of site and reproductive class on the mean distance moved per day. Then, to determine whether movement patterns varied by month throughout the active season, we examined the mean distance moved per day in each month while controlling for reproductive class at each study site. Analyses examining the mean distance moved per day included all turtle years ($N = 88$). Analyses examining movement per month used data from 2006 only ($N = 49$) because all individuals were tracked regularly throughout the active season (June, July, and August), which was not the case in the first year of the study. Movement data for the first months of the first year were not available for all individuals because some turtles received their transmitters later in the active season.

Home Ranges.—We estimated the aquatic home range (excluding all land) for all individuals using the minimum convex polygon method (MCP). The MCP method is the most commonly used approach to estimate animal home ranges (Powell, 2000). Each MCP is

calculated by creating the smallest possible convex polygon that encompasses all known locations for an individual. Row and Blouin-Demers (2006) demonstrated that MCPs accurately represent the maximum home-range area for reptiles. We calculated MCPs using Hawth's Tools (Beyer, 2004) an animal movement extension for ArcMAP 9.0 (ESRI, 2000a).

We maximized the accuracy of our MCP estimates by maintaining fixed sampling intervals and by controlling the number of data points used. Our fixed sampling interval (2–3 days) should have allowed turtles to traverse their home range between locations, thus minimizing autocorrelation (Hansteen et al., 1997). As evidenced by asymptote analysis, cumulative addition of locations over time resulted in a series of plateaus rather than an asymptote. Therefore, we calculated home ranges only for individuals that were tracked for an entire active season (June, July, and August). Based on this criterion, we calculated home ranges for 49 turtles in Lake Opinicon and 27 turtles in the St. Lawrence River. We again separated the data by turtle-years to examine the effect of reproductive class and site on home-range size. For Lake Opinicon, we accumulated 19 turtle-years for adult females, 18 for juvenile females, and 16 for males. For the St. Lawrence River, we accumulated 20 turtle-years for adult females, 12 for juvenile females, and 7 for males.

Statistical Analyses.—All statistical analyses were performed with JMP version 5.0.1 (SAS Institute, Statistical Analysis Systems, Cary, NC, 2002). Log- or square-root transformations were performed on some variables to meet the assumptions of normality. All means are reported ± 1 SE, and we accepted significance of tests at $\alpha = 0.05$. We used two-way ANOVAs to examine differences in movement patterns and home-range size. When we found significant main effects or interactions, we conducted Tukey HSD post hoc comparisons.

RESULTS

Movement Patterns.—Daily and seasonal movement patterns only varied among reproductive classes at the lotic site. We used a two-way ANOVA to determine whether reproductive class (juvenile females, adult females, and males) or site (lentic or lotic) had an effect on the mean distance moved per day (log-transformed). Following a significant interaction between reproductive class and site ($R^2 = 0.40$, $F_{5,82} = 12.2$, $P < 0.001$), the Tukey HSD post hoc comparison revealed that adult females moved significantly more in the St. Lawrence River

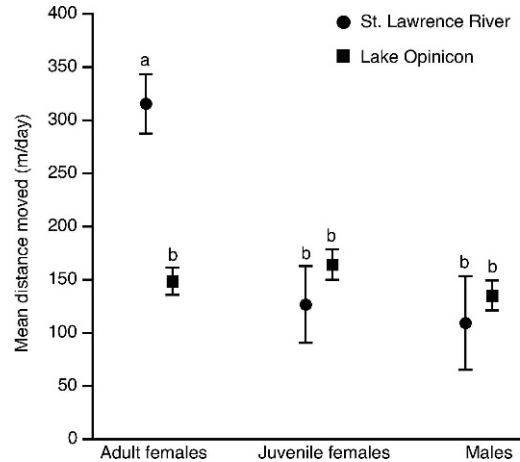


FIG. 2. Mean distance moved per day (m/day, \pm SE) for each reproductive class of Northern Map Turtles followed by radio-telemetry in Lake Opinicon and in the St. Lawrence River, Ontario, Canada. Means with the same letters are not significantly different.

than in Lake Opinicon (Fig. 2). Adult females traveled on average 315 m/day in the St. Lawrence River, while they traveled on average 149 m/day in Lake Opinicon.

We looked for differences in movement patterns within an active season by determining whether the mean distance moved per day (log-transformed) varied monthly (May to August) while controlling for reproductive class at each site. Two-way repeated-measures ANOVAs were run separately by study site because we documented differences in distances moved between sites. In Lake Opinicon, there was no interaction between month and reproductive class ($R^2 = 0.17$, $F_{6,57} = 1.7$, $P = 0.15$). The mean daily distance moved did not differ between months ($R^2 = 0.17$, $F_{3,57} = 1.17$, $P = 0.33$) or between reproductive classes ($R^2 = 0.17$, $F_{2,57} = 1.4$, $P = 0.27$). In the St. Lawrence River, however, there was a significant interaction between month and reproductive class ($R^2 = 0.51$, $F_{6,96} = 2.3$, $P = 0.04$). The Tukey HSD post hoc comparison revealed that adult females moved more than males and juvenile females in June in the St. Lawrence River (Fig. 3).

Home Ranges.—We examined the effect of reproductive class and site on home-range size (square-root transformed) using a two-way ANOVA. Following a significant interaction between site and reproductive class ($R^2 = 0.2$, $F_{2,86} = 4.5$, $P = 0.01$), the Tukey HSD post hoc comparison revealed that adult females in the St. Lawrence River had significantly larger home ranges than did males at that site (Fig. 4), but home-range size for juvenile fe-

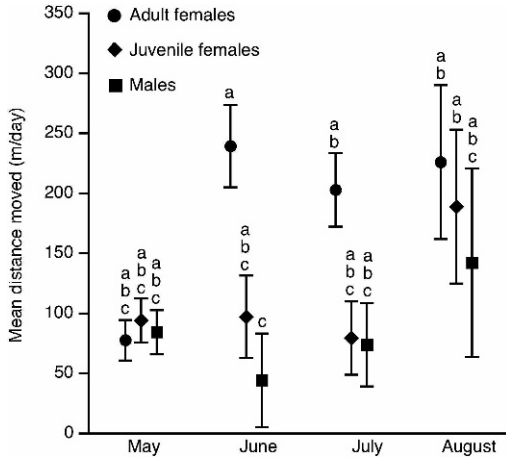


FIG. 3. Mean distances moved per day (m/day, \pm SE) by three reproductive classes of Northern Map Turtles followed by radio-telemetry in the St. Lawrence River, Ontario, Canada for each month of the active season. Means with the same letters are not significantly different.

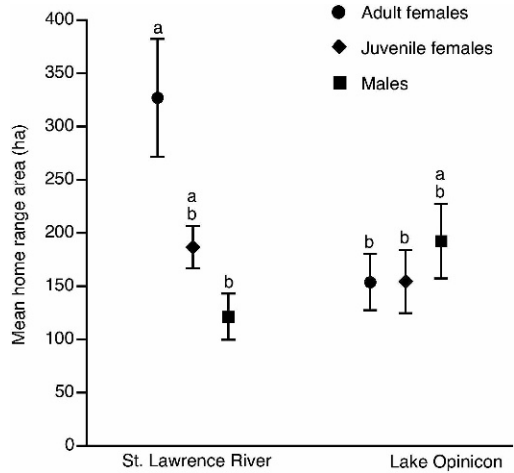


FIG. 4. Minimum convex polygon home-range area (ha, \pm SE) for each reproductive class of Northern Map Turtles followed by radio-telemetry in Lake Opinicon and the St. Lawrence River, Ontario, Canada. Means with the same letters are not significantly different.

males was not significantly different from that of males or adult females. No significant differences were observed in Lake Opinicon.

DISCUSSION

We examined the spatial ecology of three reproductive classes of map turtles in both a lentic and a lotic environment. In the lentic environment (Lake Opinicon), we found no difference in movement patterns or home-range size between the reproductive classes (adult females, juvenile females, and males). In contrast, in the lotic environment (St. Lawrence River), we found that adult female *G. geographica* moved longer distances and had larger home ranges than did juvenile females and males. We are fully cognizant of the limitations imposed on our conclusions because we had a single lotic site and a single lentic site; therefore, we are unable to separate site effects from habitat type effects. Nevertheless, this study is a useful first step toward understanding the potential effects of habitat type on movement patterns in aquatic reptiles.

Movement Patterns.—Adult female map turtles are much larger than males and juvenile females. A direct consequence of this larger body size is a higher energy requirement (Andrews and Pough, 1985). The longer distances moved by adult females compared to males and juvenile females could be attributable to differences in energy requirements. Such a trend is well documented in mammals (McNab,

1963) where larger species use larger areas, seemingly to harvest the resources necessary for them to meet their greater energy requirements. However, this hypothesis assumes that food availability limits energy intake, an assumption unlikely to hold in Northern Map Turtles at our study sites. Indeed, the recent introduction of zebra mussels in North America has increased resource availability dramatically for Northern Map Turtles (Lindeman, 2006; Bulté and Blouin-Demers, 2008). Females ingest large quantities of zebra mussels (Lindeman, 2006; Bulté and Blouin-Demers, 2008). In both our lentic and our lotic sites, introduced zebra mussels are abundant (Ricciardi et al., 1996; Bulté et al., 2008); therefore, adult females do not have to travel long distances to feed on this prey. Hence, food availability is unlikely to be driving movement patterns of adult females at our study sites and certainly does not explain the difference observed between sites. However, movements may be influenced by swimming capacity. Because swimming capacity increases with body size in map turtles (Pluto and Bellis, 1986), larger individuals may simply be less restricted in their movements because they can swim farther or better negotiate swift waters. Differences in swimming abilities could explain differences in movements in the open, lotic site where adult females may be able to roam further or travel to areas inaccessible to smaller turtles. These differences in swimming abilities would not create differences in distances moved in a small lentic environment.

Traveling long distances may also be necessary for females to seek out appropriate nesting sites. Based on the reproductive strategies hypothesis (Morreale et al., 1984), we expected adult females to move more than would males and juvenile females during the nesting season to reach favorable nesting sites. This pattern was only observed in the St. Lawrence River in June. Some females traveled as much as 5 km to reach their nesting site. Long-distance movements in turtles have often been related to finding suitable nesting sites (Obbard and Brooks, 1980; Jones, 1996; Litzgus and Mousseau, 2004) because finding an optimal nesting location results in higher fitness for the offspring (Gibbons et al., 1990). The shores of the St. Lawrence River in our study area are mostly granitic. Therefore, there are only a few potential nesting sites close to the water and females travel long distances to use these nesting sites. The lack of difference in movement patterns between the reproductive classes in Lake Opinicon may be the result of a greater availability of nesting sites. Although we did not quantify nesting site availability formally, Lake Opinicon has several small nesting sites along the shoreline. Thus, females do not have to move extensively to reach these sites.

Nesting site availability may not be the only reason why lotic adult females move longer distances than lentic adult females. The difference observed between the sites may be indicative of the interplay between female natal homing (females return to their natal sites to nest) and the dispersal potential of the habitat. Many turtles, including the congeneric *Graptemys kohnii*, exhibit natal homing (Freedberg et al., 2005). Because dispersal over long distances is more likely in a lotic environment because of the "openness" of the habitat and water velocity, females living in rivers may be more likely to settle in areas further from their natal site. Consequently, females from the lotic site may be more likely to have to move longer distances to return to their natal site to nest.

Because Northern Map Turtles mate in the spring and fall at their communal hibernacula (Vogt, 1980; MAC and GB, pers. obs.), we did not expect males to increase their movements during the active season to locate mates. In accordance with this expectation, we found that male map turtles were more sedentary than females over the active season at both study sites. This pattern has been documented in Northern Map Turtles (Flaherty, 1982; Gordon and McCulloch, 1980) as well as in False Map Turtles (*Graptemys pseudogeographica*; Bodie and Semlitsch, 2000). The lack of mate searching and nesting migration in juvenile females may also explain their sedentary behavior.

Home Ranges.—We observed high individual variation in home-range size, a trend that is consistent with many other studies on freshwater turtles (Pluto and Bellis, 1988; Kramer, 1995; Jones, 1996; Galois et al., 2002). As was the case for daily and seasonal movement patterns, differences in home-range area between reproductive classes were found only in the lotic environment. Adult females in the St. Lawrence River had larger home ranges than males. Larger home ranges in females are common in freshwater turtles (Doody et al., 2002; Galois et al., 2002; Litzgus and Mousseau, 2004). Differences in home-range size (and movement patterns) may be in part explained by intersexual and ontogenetic differences in habitat use. Intersexual and ontogenetic differences in habitat use have been linked to differences in diet in Texas Map Turtles (*Graptemys versa*) inhabiting a river (Lindeman, 2003). Northern Map Turtles exhibit habitat use differences in the St. Lawrence River (Carrière, 2007) but not in Lake Opinicon (Bulté et al., 2008). Thus, intersexual differences in home-range size and movement patterns may be linked to intersexual differences in habitat use in the St. Lawrence River.

Although Pluto and Bellis (1988) found that males had larger home ranges than females, their home-range size estimates were based on basking surveys. Basking surveys underestimate the total area used by individuals because turtles spend a considerable amount of time underwater. Using radio-telemetry, we found that turtles were located 77% of the time underwater. We believe that patterns of intersexual differences in home-range size between studies probably reflect methodological differences. As discussed above, the larger home ranges of adult female map turtles in the lotic environment seem to result from their nesting excursions.

Our study is the first comprehensive examination of the spatial ecology of *G. geographica* in both a lentic and a lotic environment. Our findings indicate that patterns of space use by *G. geographica* are shaped by complex interactions among sex, age, and habitat structure. Future studies should focus on overcoming logistical difficulties of assessing large numbers of juveniles and adults of each sex in multiple lotic and lentic ecosystems.

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