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Movement Patterns, Activity, and Home Range of the Eastern Spiny Softshell Turtle (*Apalone spinifera*) in Northern Lake Champlain, Québec, Vermont

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ABSTRACT.—**We studied movement patterns, activity, and home range of the eastern spiny softshell turtle (*Apalone spinifera*) in northern Lake Champlain (Québec, Canada; Vermont) from 1996 to 1999. This turtle population is at the northern limit of its range and considered threatened. Of the 30 individuals captured and marked, 15 females and eight males were equipped with radio-transmitters and monitored from two weeks to 29 months. Mean annual home range size for females (32.06 km^2, $N = 11$) was significantly larger than for males (2.75 km^2, $N = 4$). Home ranges generally consisted of a spring-summer concentration area (0.90 km^2) and a fall-winter concentration area (1.80 km^2), plus the area traversed between these concentration areas. In general, movements did not vary significantly from May to September, but turtles were less active after mid-September. Three hibernacula and three nesting sites were identified. Seventy five percent of the radio-tracked individuals were concentrated in a small area surrounding one hibernaculum from September to April. We hypothesize that habitat fragmentation, both natural and resulting from human activities, was in part responsible for the large home range and long movements observed. Results indicate that, to conserve this spiny softshell turtle population, the seasonal concentration areas need strict protection, although a lakewide approach promoting the preservation of natural habitats is also necessary.**

The ecology of the spiny softshell turtle (*Apalone spinifera*) has been studied mainly in the Mississippi River drainage system and in stream and river ecosystems (Webb, 1962; Vose, 1964; Dunson, 1967; Robinson and Murphy, 1978; Williams and Christiansen, 1981; Cochran and McConville, 1983; Graham and Graham, 1997; Plummer and Burnley, 1997; Plummer et al., 1997; DonnerWright et al., 1999). However, knowledge of *A. spinifera* in the colder, more northern portion of its range is limited to a study conducted in Vermont in the late 1980s in the Lamoille River, a tributary of Lake Champlain (Graham and Graham, 1997).

The Québec spiny softshell turtle population is at the extreme northern limit of the species' distribution and is isolated from other popula-

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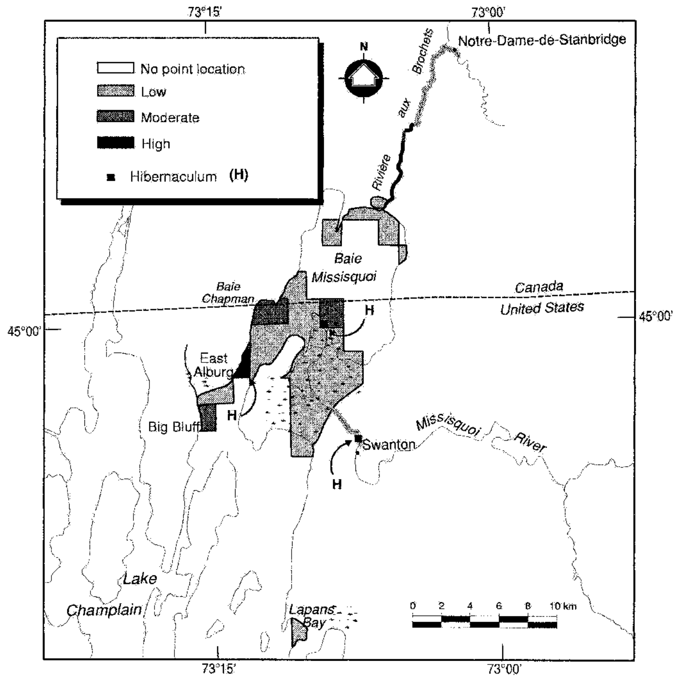

FIG. 1. Study area and use intensity of different quadrats in northern Lake Champlain by *Apalone spinifera* with identified overwintering sites. Intensity categories represented are absence of location points; low (1 to 20 location points); moderate (21 to 100 location points); high (> 100 location points).

tions. Turtle surveys conducted in the early 1990s (C. Daigle and M. Lepage, unpubl.) confirmed the spiny softshell turtle's presence only in Lake Champlain despite historical records from other areas in southern Québec (Bleakney, 1958; Lovrity and Denman, 1964; Bider and Matte, 1996). Spiny softshell turtles currently occur mainly in two areas of Lake Champlain, the Lamoille River and adjacent lake, and the Missisquoi Bay area surveyed in our study. The species historically also was documented farther south along the Vermont side of Lake Champlain (Thompson, 1853; Babitt, 1936; Graham, 1989). In 1991, *A. spinifera* was listed as Threatened in Canada by the Committee on the Status of Endangered Wildlife in Canada (Shank, 1999). In 1992, the species was proposed to be listed as Threatened or Vulnerable in Québec (Beaulieu, 1992). In 1996, the Ministère de l'Environnement et de la Faune du Québec formed a spiny softshell turtle recovery team. A status report was produced (J. Bonin, unpubl.) and a recovery plan was developed. Because knowledge on this population was limited, a priority action of the recovery plan was to document the status of the Lake Champlain population. In 1996, a study was initiated to document the use of the lake by the only known visible population in the province and to identify critical areas in need of special protection (e.g., nesting and hibernation sites). In view of the 1996 and 1997 results, and the Threatened status in Vermont, collaboration was initiated with the Vermont Fish & Wildlife Department and the U.S. Fish and Wildlife Service in 1998. In 1999, the species was listed as Threatened in Québec.

Herein we present annual activity and movement patterns, home range, and habitat use by *A. spinifera* in northern Lake Champlain. This study aimed to provide baseline data critical to the population's persistence and to contribute to a better understanding of the species' ecology in the extreme northern portion of its range.

MATERIALS AND METHODS

The study was conducted from 1996 to 1999 in northern Lake Champlain, Québec and Vermont (73°09′W, 45°01′N; Fig. 1). The northeastern part of the lake receives water from two major tributaries, the Rivière aux Brochets (Pike River) and the Missisquoi River. Part of the Champlain Sea some 10,000 years ago, the region's surface substrate is mostly sand and clay. The bedrock is mainly shale with outcrops and cliffs forming part of the natural lakeshore. Both the Missisquoi River and Rivière aux Brochets flow through agricultural lands in the St. Lawrence Lowlands region. The lower course of these two rivers (10–15 km) is in more natural forest habitat (E. Thompson, unpubl.) with the mouths completely (Missisquoi National Wildlife Refuge) or partly protected (Réserve écologique de la Rivière aux Brochets). The Rivière aux Brochets is 50–70 m wide between the mouth and the first riffles 6 km upstream and narrows to 30–40 m over the next 8 km upstream. The Missisquoi River is 70–120 m wide in the study area. The three branches of its delta are 20–40 m wide. The depth of northwestern Lake Champlain averages between 4 and 5 m (U.S. Lake Survey—Lake Champlain, Chart 171, 1962). The air temperature ranged between a minimum of −4°C and a maximum of 31°C from May to October 1996 to 1998. The lake and rivers are covered with ice for two to three months in winter. On the Québec side, 78% (21.3 km) of the 27.3 km of lakeshore has been modified (cottages, marina, public beach, campground), 46% (12.6 km) impacted by concrete and block walls. On the Vermont side down to Lapans Bay, 52% (84.8 km) of the 163.6 km of shoreline (including islands) has been altered (E. Thompson, unpubl.).

We captured turtles with baited hoop-traps, by swimming with a floating blind and a dip-net (Bider and Hoek, 1971), or with a dip-net on the shore or from a boat. The capture effort was concentrated between the end of May and the beginning of July in 1996 and 1997, and during July in 1998. For each individual, we measured plastron length (PL), carapace length (CL) and width (CW) with calipers (± 0.5 mm), and body weight with a spring balance (Pesola or Chatillon). Sexes were determined based on a combination of size, tail length and cloaca position, and shell color pattern and texture (Ernst et al., 1994). The turtles were considered adult or mature according to previous studies (Webb, 1962; Robinson and Murphy, 1978) where males were mature at PL > 79 mm and female at PL > 180 mm. Turtles were individually marked with a PIT-tag (Datamars Passive Transponder System ID-100), and released at the point of capture.

In 1996, five females were equipped with L.L. Electronics transmitters (Model LF-1-2/3A-RS-18, Mahomet, IL) attached on the rear side of the carapace with braided nylon fishing line. In the following years Holohil Systems Ltd transmitters (Model AI-2M or SI-2SP, Ottawa, Canada) were used and attached with stainless steel wire. The transmitter battery lifespan was approximately 12 months for the males and 16 months for the females. A portable receiver (Lotek SRX 400) was used with a 1.12-m long Yagi type antenna (Cushcraft Corp.) installed on a mast or a smaller hand-held Yagi type antenna (Lindsay Products Ltd.).

Telemetry was conducted mostly by boat and occasionally from shore. An aircraft was used when terrestrial contact was lost with a radio-transmitter. Locations obtained by boat were generally precise (within 5 m) or resulted from direct observation of the turtle. When a close approach was not possible, in particular with the aircraft (approximately 200 m radius around the point) or from the shore, locations were considered approximate. In 1996, telemetry monitoring was conducted twice a week from May to the end of July and once a week from August to November. In 1997, telemetry surveys were conducted twice a week from mid-June to the beginning October, and once every two weeks until 20 November. In 1998, the turtles were first located on 9 February, and once a week from 1 May until 21 October, with daily monitoring of three females on the Rivière aux Brochets from 1–19 June. In 1999, turtle locations were obtained by aircraft on 10 February, once a week from the end of April to the end of October, and once every two weeks until the end of November. In 1998 and 1999, daily monitoring of females in June was conducted to locate the nesting sites. For conservation reasons and in accord with Vermont's endangered species law, exact locations of the nesting sites are not disclosed.

For each location or observation, we recorded the turtle's behavior (basking, underwater immobility, swimming), meteorological conditions (wind, cloudiness, air temperature), habitat characteristics such as water depth and temperature, aquatic or riverine dominant vegetation species and abundance, and substrate. The geographic position was recorded with a Geographic Positioning System (Garmin GPS 75, ± 25 m) and located on a map. A bathymetry survey (Lowrance X16 sonar) was conducted at two hibernating sites where water current (Scientific Instrument, Inc.) and dissolved oxygen (Oxymeter YSI, model 51B) were measured.

Seasonal movements were calculated by pooling data from the different years, excluding approximate locations. Months were divided into three periods, approximately equal, the last period being 10 or 11 days. Taking the individual's earliest location in each period, the distance to the next consecutive location was calculated using the software CALHOME (J. G. Kie, Forestry Sciences Lab, Fresno, CA, 1994). We obtained 18 periods starting 1 May and ending 31 October. Individual distances were pooled for each period.

Annual home range size was calculated using the minimum convex polygon method (Mohr, 1947), with 95% of the point locations per individual, using CALHOME (Kie et al., 1996). The home range was calculated when point locations were available for 11 months minimum to cover the annual activities. In cases of multiple locations of the same individual in a day, only the first point was considered (White and

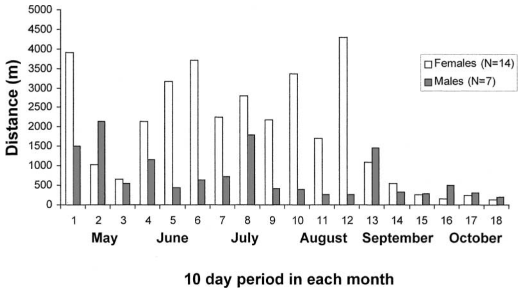

FIG. 2. Male and female *Apalone spinifera* mean movements from May to October in northern Lake Champlain.

Garrott, 1990). Point locations obtained by aircraft or from long distances were not included. The surface area was corrected by removing land from the home range area using a standardized point grid (Bruning areagraph, chart # 4850, precision ± 10%). Size of the individual concentration areas inside the annual home range was calculated using the harmonic mean measure (Dixon and Chapman, 1980) with 80% of the telemetry point locations.

The use intensity of the different areas was determined by using all the point locations from 1996 to 1999. The study area was divided into 1–min–by–1–min quadrats (2.48 km^2) using a latitude and longitude grid. The potential habitat surface (water and wetland) was calculated for each quadrat with point locations. The density of points was calculated in these quadrats relative to the potential aquatic habitat. For the purpose of representation, the range of density was divided in four categories: absent, low (1–20 location points), moderate (21–100 location points), and high density (> 100 location points).

Statistical analyses were conducted with SigmaStat (Jandel Scientific Software, San Rafael, CA, 1994) and SAS (SAS Institute, Inc., Cary, NC, 1996). Movements were analyzed through two-way ANOVA with multiple comparisons (test of fixed effects and test of effect slices). The water depth data were analyzed through ANOVA using the Mixed Procedure with rank transformation and differences of Least Squares Means. Means are presented with standard deviation in text and tables. Significance was determined as $P < 0.05$.

RESULTS

Movements and Activities.—Fifteen females and eight males were equipped with radio transmitters. Five females were captured in Chapman Bay in 1996, and four males and two females (including a recapture) in 1997; three females in the Rivière aux Brochets in 1997; and six females and four males in the Missisquoi River delta in 1998. The period of monitoring ranged from two weeks to 29 months. A total of 993 telemetry fixes was obtained with 765 precise point locations, 152 by aircraft, and 76 approximate point locations by boat or from the shore. The male ($N = 7$) and female ($N = 14$) mean movements were calculated for 18 periods (Fig. 2). An ANOVA revealed that turtle mobility differed significantly between males and females ($F = 4.77$, $P = 0.035$) and between periods ($F = 2.02$, $P = 0.01$). In general, the mean distance moved did not significantly vary between May and September ($P > 0.05$), but the turtles were less active after mid-September ($P < 0.05$). The multiple comparisons indicated that the chronology of movements tended to differ between males and females ($P = 0.08$). This difference was more pronounced in August when females seemed to travel longer distances than males ($P < 0.05$). The mean distance varied during the year for females ($P < 0.001$), but seemed constant for males ($P = 0.40$).

Turtle activities were grouped into three categories: basking, immobile underwater, and swimming (Table 1). There was a significant difference between male and female activity frequencies ($\chi^2 = 20.7$, $P < 0.001$). Males were more often located immobile underwater than females. For both sexes, basking was the less observed activity, and from all the observations 56% were on shore, 20% on a trunk, 14% on a rock, and 10% on floating vegetation. There was a significant difference in the water depth at point locations from April to November ($F = 50.6$, $P = 0.0001$) when turtles were underwater or swimming (Fig. 3). The mean water depth was the lowest in May (1.47 ± 0.83 m, $N = 31$), June (1.62 ± 0.81 m, $N = 54$), July (1.40 ± 0.89

TABLE 1. Male and female *Apalone spinifera* activities (%) recorded at the time of telemetry location in northern Lake Champlain.

Activity	Female	Male	Total
Basking	68 (13.0)	9 (6.0)	77 (11.5)
Immobile underwater	386 (73.5)	126 (86.5)	512 (76.3)
Swimming	71 (13.5)	11 (7.5)	82 (12.2)
Total point locations	525	146	671

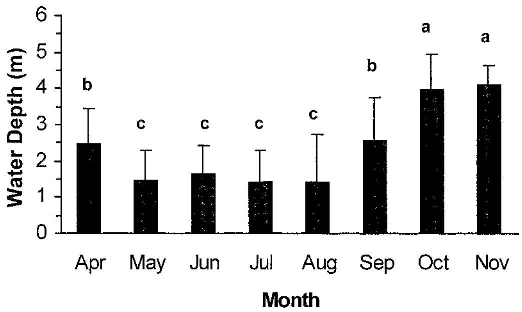

FIG. 3. Mean water depth at point locations for eight male and 15 female *Apalone spinifera* from April to November in northern Lake Champlain. Vertical lines are for standard deviation. Letters above bars indicate significant differences in mean water depth among months; months with the same letter are not significantly different.

m, N = 48), and August (1.43 ± 1.30 m, N = 72). It increased in September (2.54 ± 1.22 m, N = 102) to reach a maximum in October (3.97 ± 0.96, N = 68) and November (4.10 ± 0.53 m, N = 21) when the turtles were at their overwintering site. The water depth at the point locations in April (2.48 ± 0.98 m, N = 102) was intermediate and similar to September.

Only two radio-tagged females were observed nesting. A full nesting sequence, including a 7-km upstream movement to the nesting site on Rivière aux Brochets, was closely monitored for one radio-tagged female (199704) in June 1998 (Daigle et al., in press). Another radio-tagged female (199806) was observed nesting on 14 June 1999 on a Vermont site. Mating between a radio-tagged female (199802) and an untagged male was observed taking place on the Missisquoi River shoreline on 21 August 1998.

Home Range.—The annual home range area was calculated for 11 females and four males (Table 2). There was no significant correlation between the number of point locations used and the home range area (Spearman's R = 0.442, P = 0.09). The individuals were monitored for periods varying from 317 to 863 days. The mean annual home range area was 32.06 ± 30.70 km^2 (N = 11; range 1.77–110.28 km^2) for females and 2.75 ± 2.99 km^2 (N = 4; range 0.44–6.92 km^2) for males. The annual mean home range was significantly larger for females (Mann-Whitney U-test: t = 12, P < 0.015). There was no significant correlation between annual home range size and carapace length for females (Spearman's R = −0.0545, P = 0.860) or for males (Spearman's R = −1.0, P = 0.083).

Most home ranges included two centers of intense activity corresponding to two periods of time, one from August to April and the other from May to July (Table 2). The mean size of the August to April period area was 2.11 ± 1.81 km^2 (N = 11) for females and 0.1 km^2 (N = 2) for

TABLE 2. Telemetry monitoring period, number of telemetry point locations, annual home range size, center of activity size in August to April and in May to July, and linear home range size for four males and 11 females *Apalone spinifera* in northern Lake Champlain.

Turtle no.	Carapace length (mm)	Period monitored (days)	No. of point locations	Annual home range size (km^2)	Activity center harmonic means (km^2) August to April	Activity center harmonic means (km^2) May to July	Linear home range size (km)
Females							
199604	300	863	59	11.17	0.33	0.61	6.0
199703	276	490	68	36.98	2.53	0.22	17.9
199704	324	420	61	110.28	4.15	0.35	25.0
199705	359	474	72	19.69	0.47	0.15	19.8
199707	212	385	44	1.77	0.04	0.16	5.6
199801	345	502	39	56.16	3.77	2.33	23.0
199802	368	495	44	18.00	1.89	2.12	10.0
199803	397	487	49	14.61	1.47	1.09	7.5
199805	334	478	35	43.43	5.82	2.57	17.0
199806	375	472	45	8.31	0.88	0.51	7.3
199807	302	477	50	32.27	1.87	0.23	11.8
Female means	326.5 ± 52.4	460	51	32.06 ± 30.70	2.11 ± 1.81	0.94 ± 0.94	13.7 ± 7.0
Males							
199706	161	317	38	2.92	0.10	0.18	5.0
199804	170	373	41	0.44	—	—	2.86
199809	166	331	31	0.72	—	—	1.43
199810	156	331	31	6.92	0.10	1.17	6.3
Male means	163.2 ± 6.0	338	35	2.75 ± 2.99	0.10	0.67 ± 0.70	3.89 ± 2.17

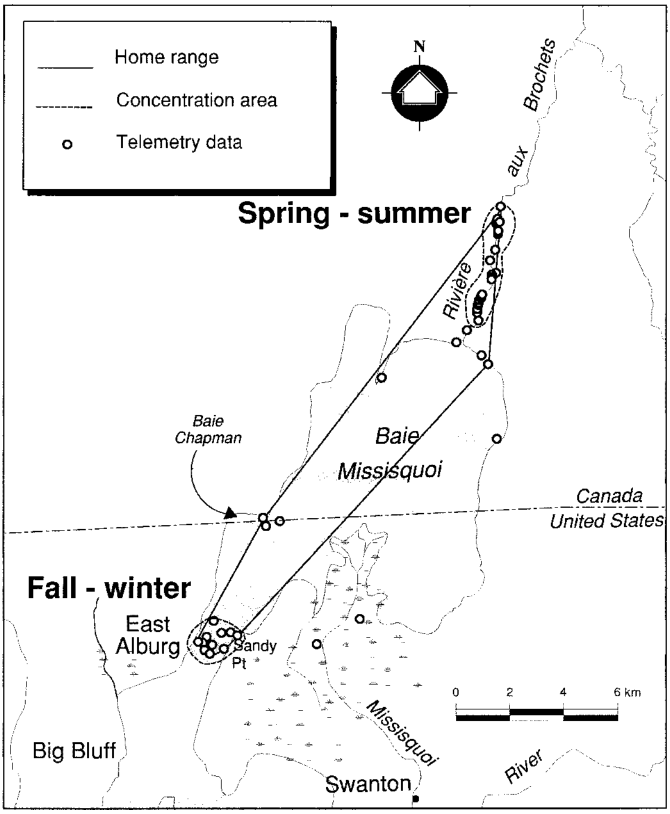

FIG. 4. Annual home range and concentration areas for one female (199703) *Apalone spinifera* in northern Lake Champlain.

males. The mean size of the May to July period area was for female 0.94 ± 0.94 km² (N = 11) and for male 0.675 ± 0.70 km² (N = 2). An example of a female home range with the concentration areas is presented (Fig. 4).

Linear home range size was 13.7 ± 7.0 km (N = 11) for females and 3.89 ± 2.17 km (N = 4) for males (Table 2). The mean extreme distance was significantly longer for females (Mann-Whitney U-test: $t = 12$, $P < 0.015$). In 70% of the individuals (seven females and two males) the distance between the most distant points reflected the distance between the two activity centers.

Habitat Use Intensity.—A total of 791 point locations was used to determine the intensity of use of the study area (Fig. 1). Three hibernacula were identified, two on a river and one in the lake (Table 3). The Swanton hibernaculum located 10 km upstream on the Missisquoi River was used by one tagged female in 1997, and three males overwintered in the delta in 1998. Ten of the females (91%) and two of the males (40%) used the East Alburg bridge site for overwintering, representing 75% of turtles tracked to their hibernaculum. From those turtles, at least nine females overwintered in this site two years in a row. On 28 September 1999, a total of

TABLE 3. Characteristics of three hibernacula used by *Apalone spinifera* in northern Lake Champlain.

Site	Swanton	Missisquoi River delta	East Alburg bridge
Water body	River	River	Lake
Number of tagged turtles	1	3	12
Maximum depth	5.2 m	2.5 m	5.0 m
Main substrate (%)	Sand (80%)	Sand (90%)	Silt (90%)
Dissolved oxygen	11.0 ppm	—	12.0 ppm
Date collected	20 November	22 October	20 November

20 turtles was detected at this site (14 basking, 6 with radio signals). In addition to being an overwintering concentration site, this area was used by different tagged turtles all year long but more intensively from the end of August to May.

The other high-density use quadrat included the lower 5 km of the Rivière aux Brochets (Fig. 1). Three radio-tagged females used this river and its mouth two years in a row from May to the end of August. In June 1997, at least five females were on the lowest part of the river, three equipped with transmitters and two others seen basking. Another radio-tagged female used the bay around the river mouth in 1999.

Two major nesting sites were identified on the lakeshore. One of them was intensively monitored in June 1995, and 16 spiny softshell nests were found (J. Brisebois and P. Galois, unpubl. data). Four unmarked females were observed digging on the site in 1996, and eight females were captured in this area in June 1996 and 1997. At the other site in 1999, one radio-equipped female and two unmarked females were observed digging and 13 nests were found. One female (199704) used a nesting site on the upper part of the Rivière aux Brochets in 1998 (Daigle et al., in press).

Injuries and Mortality.—One female (199601) was found dead on 15 July 1996, 46 days after its initial capture. The cause of death was not determined, but the turtle was in good general condition and full of eggs. A fisherman found one male (199702) dead of unknown cause (not collected) in late June 1997, less than two weeks after its capture. One female (199705) radio-tracked in 1997 and 1998 was found dead, without its radio, on the Rivière aux Brochets shoreline in July 1999. It had deep lacerations, probably caused by a boat propeller.

Discussion

Movements and Activities.—Spiny softshell turtles we observed were not as sedentary as often reported (Webb, 1962; Plummer and Shirer, 1975; Plummer and Burnley, 1997; Plummer et al., 1997). In Lake Champlain, long movements seemed frequent at different times of the year and more noticeable in early spring and at the end of August. Turtles left overwintering sites in early May and quickly reached the spring-summer area. Despite intensive efforts in June to document nesting and identify nesting sites, only two radio-tagged females were observed digging a nest. In general it seems that nesting sites were located in the spring-summer use area except for three females that went out of their spring-summer area for a short period of time. During spring and summer, the turtles dispersed in different areas over a large territory. The female mean movements stayed relatively high during the summer compared to those of males. Movement toward the fall-winter area took place around the end of August.

This high mobility of softshell turtles might be explained by the low availability of suitable habitat. In Lake Champlain, a short summer activity season, harsh winter conditions, and the species biological requirements (Ultsch et al., 1984) likely favored selection of overwintering sites that provided the most positive energy balance. On the Lamoille River, Graham and Graham (1997) observed a similar yearly pattern in the movements of three females, but with a 3- to 4-km distance traveled upstream to reach the overwintering site, distances shorter than the 13.7-km mean we obtained for females. The East Alburg bridge overwintering site appears to attract the majority of the adult female turtles in this population and likely provides benefits that make a 13.7 km trip worthwhile. Radio-tagged males seemed less dependent on this site. In contrast, Plummer and Burnley (1997) observed no particular movement toward a hibernaculum. Turtles in their study hibernated at lower depths than in our study but were in an area with a milder climate than in northern Lake Champlain.

Home Range.—Movement patterns resulted in large annual home ranges with spring-summer and fall-winter activity centers. The great distance between these two centers had a considerable influence on the total home range size. For example, the three females using the Rivière aux Brochets in the summer overwintered 20 km to the south. The individual home range sizes were highly variable. Males seemed to use a restricted home range compared to females. This difference was largely due to the larger distances between female concentration areas. These data contrast with those of home range reported in the literature. Plummer et al. (1997) obtained male and female home range close to 1 ha in a stream, which was much smaller (270 times) than those obtained in the present study. When considering only the activity center area size, the present home ranges are still larger than those reported for *Apalone spinifera* and *Apalone muticus* (Plummer and Shirer, 1975; Plummer et al., 1997). For most of the individuals, the home range included different waterbodies such as lake, river, creeks, and marsh. As suggested by Plummer et al. (1997), home range size might also be affected by the size of the body of water. Most of the telemetry locations we obtained were in shallow water near the shore, and no tagged turtle was found in the middle of the open lake. This suggests that turtles were mostly moving along the shore between the different activity areas. Some annual home ranges including large patches of the lake might overestimate home range size. Some of the females moved long distances to reach a nesting site or an overwintering site. In most cases, the path they used was not recorded. Telemetry data also indicate that the female summer home range might vary in location from year to year. The large size of some home range certainly reflects these data.

Use Intensity.—Habitat use intensity in Lake Champlain was not uniform, perhaps because data were obtained for animals from only three capture sites. Monitoring of turtles captured in other sites might have given a better picture of habitat use. However, capture effort was concentrated where turtles were most frequently seen, and the radio-tagged individuals led us to other concentration areas, such as nesting and hibernation sites, some unknown before the study.

Habitats used provided the turtles with specific resources such as nesting sites, overwintering sites, and probably food, shelter, optimal temperature conditions, and opportunity for social interactions. The heterogeneous distribution of these resources might explain part of the observed variability in the use of the different parts of the lake and its tributaries. Shoreline habitat fragmentation has certainly increased in the past years through habitat modification and human activities and might have caused this clumped use pattern. Therefore, the apparent heterogeneous use of the lake might reflect the confinement of turtles to the only remaining suitable sites. Sites used by the turtles were generally undisturbed habitats or those with few alterations, for example, the Missisquoi River, the Rivière aux Brochets, and the Big Bluff area (E. Thompson, unpubl.). Some areas where turtles were not detected were unsuitable natural places like rocky steep shoreline or highly modified and disturbed areas characterized by intensive human summer activities on the shore and on the water, for example, the northwest portion of the lake (E. Thompson, unpubl.).

One of the most critical softshell habitats occurs at the East Alburg bridge, where 75% of turtles tracked to their hibernaculum gathered for hibernation from the late August until early May (approximately nine months). Reasons for turtles gathering for such a long period at this particular site are unclear. There are no available data on the possible use of this area by spiny softshell turtles before the construction of the bridge and its causeway in the late 1930s. At least nine of the radio-tagged females, of different ages and captured at different sites, showed fidelity to this hibernaculum. This narrow part of the lake is one of the deepest areas of Missisquoi Bay and is more similar to a river habitat than a lake habitat. In addition, we hypothesize that the long rocky causeway (a 1.1-km long rock structure with a 170-m bridge section in the middle) provides an abundance of food and basking sites useful in preparation for hibernation. In addition winter wind pushes the ice from the north against the causeway, so that the south side of the causeway, where turtles concentrate in winter, tends to be ice-free earlier in spring. The combination of these local conditions may create highly suitable conditions for overwintering. Further research is certainly needed to better assess the specificity of the bridge site in comparison to other potential overwintering sites.

The Rivière aux Brochets was the other intensively used area. Before this study, softshell observations on the Rivière aux Brochets were scarce. Even though intensive monitoring in June 1998 might bias results about the habitat use on this river, telemetry revealed that the species was using it and the Missisquoi Bay around its mouth from May to September. The telemetry monitoring also confirmed that nesting occurs along this river.

The variation in individual use of activity areas was intriguing. For example, four males were captured in the Missisquoi River and stayed in the river delta area all summer. Three of them hibernated in the delta, whereas one left the river in August for the bridge site and came back to the river the next spring. Of three females captured in the Rivière aux Brochets, two hibernated at the bridge site, whereas one went to the Missisquoi River to hibernate after staying more than a week in early September south of the bridge. As noted by Fletcher in Ontario (pers. comm.), long movements are not fully explained by the habitat fragmentation, because some individuals passed areas used by other individuals to reach other tributaries or lake sections.

Conservation Implications.—Before this study, available information on the lake populations was scattered observations of the species and the study by Graham and Graham (1997). Our study has confirmed and documented the use of the northern part of Lake Champlain and its tributaries by *A. spinifera*. It revealed that the turtles, particularly females, were moving long distances to fulfill their biological requirements and used a variety of areas in the lake and its tributaries. Any factor that might affect or impede movements between these areas, such as dams on the rivers, habitat alteration, or intense human activities on water and shore, could affect the population by limiting its access to the few suitable feeding, nesting or hibernating sites remaining (Shively and Jackson, 1985; Dodd, 1990; DonnerWright et al., 1999).

Injuries related to human activities are of great concern for this species. In addition to the mortality presented, reports of *A. spinifera* hooked by anglers or injured by boats and fishing gears are, not surprisingly, accumulating (P. Galois and M. Ouellet, unpubl. data). These recreational activities are particularly intensive in the shallow waters of bays and rivers, which are also used by the turtles from May to August. Available data suggest that spiny softshell turtles in Lake Champlain are apparently in very small numbers when compared to more southern populations (Cagle, 1942; Lagler, 1943; Cagle and Chaney, 1950; Breckenridge, 1955; Cochran and McConville, 1983; DonnerWright et al., 1999). Increased mortalities associated with these activities could further threaten this population (Klemens, 2000; Galois and Ouellet, in press).

Concerted actions of governmental and nongovernmental organizations, and local conservation groups and municipalities from Canada and the United States are required, for example, to regulate recreational activities in shallow waters. These actions would benefit the turtles as well as other aquatic wildlife. Also, the lake was not used uniformly by the species. Areas used by turtles are scattered over a large territory and separated by areas that seemed little-used or even unused by the monitored turtles. Considering the level of modification of the lake shoreline and habitats, protection of *A. spinifera* in Lake Champlain depends more specifically on preservation of remaining natural habitat, and possibly the restriction of human activities in critical areas. A few habitat sites were used by a relatively large number of turtles, and any significant event altering these sites might have a negative impact at the population level. The East Alburg bridge area and an important nesting site in Québec are such critical areas that do not benefit from any particular protection but need immediate protection. How critically important turtle habitats are protected and managed in both Canada and the United States will likely determine the fate of this international population of spiny softshell turtles.

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Literature Cited

Babitt, L. H. 1936. Soft-shelled turtles in Vermont. Bulletin of the Boston Society of Natural History 78:10.

Beaulieu, H. 1992. Liste des espèces de la faune vertébrée susceptibles d'être désignées menacées ou vulnérables. Ministère du Loisir, de la Chasse et de la Pêche du Québec, Québec, PQ, Canada.

Bider, R. J., and W. Hoek. 1971. An efficient and apparently unbiased sampling technique for population studies of painted turtles. Herpetologica 27:481–484.

Bider, R. J., and S. Matte. 1996. The Atlas of Amphibians and Reptiles of Québec. St. Lawrence Valley Natural History Society, Ministère de l'Environnement et de la Faune, Québec, PQ, Canada.

Bleakney, S. 1958. The significance of turtle bones from archaeological sites in southern Ontario and Québec. Canadian Field-Naturalist 72:1–5.

Breckenridge, W. J. 1955. Observations on the life history of the soft-shelled turtle *Trionyx ferox*, with especial reference to growth. Copeia 1955:5–9.

Cagle, F. R. 1942. Turtle populations in southern Illinois. Copeia 1942:155–162.

Cagle, F. R., and A. H. Chaney. 1950. Turtle populations in Louisiana. American Midland Naturalist 43:383–388.

Cochran, P. A., and D. R. McConville. 1983. Feeding by *Trionyx spiniferus* in backwaters of the upper Mississippi River. Journal of Herpetology 17:82–86.

Daigle, C., P. Galois, and Y. Chagnon. In Press. Nesting activities of an eastern spiny softshell turtle, *Apalone spinifera*. Canadian Field-Naturalist.

Dixon, K. R., and J. A. Chapman. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

Dodd Jr., C. K. 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Sternotherus depressus*. Biological Conservation 54:33–45.

DonnerWright, D. M., M. A. Bozek, J. R. Probst, and E. M. Anderson. 1999. Responses of turtle assemblage to environmental gradients in the St. Croix River in Minnesota and Wisconsin, U.S.A. Canadian Journal of Zoology 77:989–1000.

Dunson, W. A. 1967. Relationship between length and weight in the spiny softshell turtle. Copeia 1967:483–484.

Ernst, C. H., J. E. Lovich, and R. W. Barbour. 1994.

Turtles of the United States and Canada. Smithsonian Institution Press, Washington, DC.

GALOIS, P., AND M. OUELLET. In Press. Health and disease in Canadian reptile populations. *In* C. N. L. Seburn and C. A. Bishop (eds.), Conservation and Status of Reptiles in Canada. Herpetological Conservation. Society for the Study of Amphibians and Reptiles, Bethesda, MD.

GRAHAM, T. E. 1989. Map and softshell turtles from Vermont. Bulletin Maryland Herpetological Society 25:35–39.

GRAHAM, T. E., AND A. A. GRAHAM. 1997. Ecology of the eastern spiny softshell, *Apalone spinifera spinifera*, in the Lamoille River, Vermont. Chelonian Conservation and Biology 2:363–369.

KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1996. CALHOME: a program for estimating animal home ranges. Wildlife Society Bulletin 24:342–344.

KLEMENS, M. W. 2000. Turtle conservation. Smithsonian Institution Press, Washington, DC.

LAGLER, K. F. 1943. Food habits and economic relations of the turtles of Michigan with special reference to fish management. American Midland Naturalist 29:257–312.

LOVRITY, J., AND N. DENMAN. 1964. An eastern spiny soft-shelled turtle from Québec Province. Canadian Field-Naturalist 78:63–64.

MOHR, C. O. 1947. Table of equivalent population of North American mammals. American Midland Natutalist 37:223–249.

PLUMMER, M. V., AND J. C. BURNLEY. 1997. Behavior, hibernacula, and thermal relations of softshell turtles (*Trionyx spiniferus*) overwintering in a small stream. Chelonian Conservation and Biology 2: 489–493.

PLUMMER, M. V., AND H. W. SHIRER. 1975. Movement patterns in a river population of the softshell turtle, *Trionyx muticus*. Journal of Herpetology 11:87–90.

PLUMMER, M. V., N. E. MILLS, AND S. L. ALLEN. 1997. Activity, habitat, and movement patterns of softshell turtles (*Trionyx spiniferus*) in a small stream. Chelonian Conservation and Biology 2:514–520.

ROBINSON, K. M., AND G. G. MURPHY. 1978. The reproductive cycle of the eastern spiny softshell turtle (*Trionyx spiniferus spiniferus*). Herpetologica 34: 137–140.

SHANK, C. C. 1999. The committee on the status of endangered wildlife in Canada (COSEWIC): a 21-year retrospective. Canadian Field-Natutalist 113: 318–341.

SHIVELY, S. H., AND J. F. JACKSON. 1985. Factors limiting the upstream distribution of the Sabine map turtle. American Midland Naturalist 114:292–303.

THOMPSON, Z. 1853. Appendix to the natural history of Vermont. Published by the author, Burlington, VT.

ULTSCH, G. R., C. V. HERBERT, AND D. C. JACKSON. 1984. The comparative physiology of diving in North American freshwater turtles. I. Submergence tolerance, gas exchange and acid-base balance. Physiological Zoology 57:620–631.

VOSE, R. N. 1964. Nesting habits of the soft-shelled turtles (*Trionyx* sp.). Procedings of the Minnesota Academy of Science 32:122–124.

WEBB, R. G. 1962. North American recent soft-shelled turtles (Family Trionychidae). University of Kansas Publications, Museum of Natural History 13:429–611.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, CA.

WILLIAMS, T. A., AND J. L. CHRISTIANSEN. 1981. The niches of two sympatric softshell turtles, *Trionyx muticus* and *Trionyx spiniferus*, in Iowa. Journal of Herpetology 15:303–308.

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