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The Effects of Flooding on the Spatial Ecology of Spotted Turtles (*Clemmys guttata*) in a Partially Mined Peatland

Katharine T. Yagi¹ and Jacqueline D. Litzgus¹

Many studies have focused on the effects of anthropogenic habitat alterations on animals, but little attention has been given to the effects of natural changes in habitat. The purpose of our study was to examine the effects of flooding caused by Beaver (*Castor canadensis*) dams on the spatial ecology of the federally endangered Spotted Turtle (*Clemmys guttata*), in a bog in Ontario that was historically drained for peat extraction. We hypothesized that home range sizes and daily distances traveled would be greater after flooding and that habitat selection would change because turtles would exploit the increase in aquatic habitats post-flooding. Using 12 years of mark-recapture data, radio telemetry, and GIS software, we compared movements and habitat selection before and after flooding. Distances traveled and home range sizes were larger post-flood compared to pre-flood conditions, indicating that turtles were opportunistically exploring the new aquatic habitat. During pre-flooding, turtles primarily selected the drainage ditches created to facilitate peat extraction; these were the only aquatic habitat available. After flooding, there was a strong preference for newly flooded areas and drainage ditches, showing that turtles exploited the increase in available aquatic habitat. Our findings indicate that natural habitat alteration resulting from Beaver dam flooding may be beneficial for Spotted Turtles, although observations also suggest that nesting habitat may be limited due to the flooding, and further research is needed to determine the effect of the flooding on recruitment into the population.

• HE amount of space used and habitats selected by an animal are primary aspects of its ecology and are important indicators of resource availability (Carfagno and Weatherhead, 2008). As such, environmental conditions can directly influence animal behavior and movement patterns (Huey, 1982; Blouin-Demers and Weatherhead, 2001; Row and Blouin-Demers, 2006a). Animals that live in isolated areas tend to have restricted movement patterns (Schtickzelle and Baguette, 2003; Iglay et al., 2007; Pittman and Dorcas, 2009). Isolation occurs when the natural habitat is degraded and fragmented, usually as a result of the construction of roads, urban landscapes, and farm fields (Cushman, 2005; Ryan et al., 2008). Many studies have focused on the effects of anthropogenic habitat alterations on animals, including turtles. For example, several studies have examined the effects of anthropogenic disturbances on turtle spatial ecology (Dodd, 1990; Leighton et al., 2008; Harden et al., 2009). Habitat changes can affect freshwater turtles, mainly because of their seasonal patterns of habitat selection and dependence on stable aquatic habitats for hibernation (Litzgus et al., 1999; Beaudry et al., 2009; Edge et al., 2010).

Habitat selection studies aim to examine the likelihood of finding an animal in a particular habitat type, when a certain range of habitats are available (Johnson, 1980; Morrow et al., 2001; Alldredge and Griswold, 2006). Habitat selection is regarded as the disproportionate use of a certain habitat relative to its availability (Johnson, 1980; Aebischer et al., 1993; Mysterud and Ims, 1998). Understanding which habitats an animal chooses throughout its life will help to identify what types of habitats are necessary for populations

of that species to survive in the long term. Habitat selection has been examined for a broad range of animal species (Carter et al., 1999; Harvey and Weatherhead, 2006; Bonnot et al., 2009). Reptiles and amphibians tend to use smaller areas than birds and mammals of similar sizes, usually because they are less mobile, have smaller energy requirements, and their fitness is influenced primarily by environmental conditions (Nagy et al., 1999; Carfagno and Weatherhead, 2008).

Little attention has been given to the effects of natural habitat changes on animal spatial ecology (Ernst, 1974; Brodie and Semlitsch, 2000; Dodd and Dreslik, 2008). Dams constructed by Beavers (Castor canadensis) cause flooding resulting in natural changes to an area, including the creation of new wetlands (Johnston and Naiman, 1987). Beaver impoundments have been found to stabilize stream flow and create deep pools with warmer temperatures that provide winter habitat for aquatic species (Johnston and Naiman, 1987; Collen and Gibson, 2001). Although the creation of a new wetland can have a positive influence by increasing wetland species biodiversity (Johnston and Naiman, 1987), the presence of Beaver dams in areas in close proximity to humans has been considered undesirable because flooding can damage roads, crop lands, and human residences (Collen and Gibson, 2001). A few studies have examined the effects of Beaver dams on aquatic organisms, such as the community structure of fishes and the population density of invertebrates (Hanson and Campbell, 1963; Stock and Schlosser, 1991), but no studies have examined the effects of Beaver dams on the spatial ecology of turtles.

We examined the effects of flooding caused by Beavers on the spatial ecology of Spotted Turtles (*Clemmys guttata*)

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located in a historically mined peatland in Southern Ontario, Canada. Recent attention has been given to studies of the life history, behavior, and spatial ecology of Spotted Turtles (Haxton and Berrill, 2001; Litzgus, 2006; Rasmussen and Litzgus, 2010) because of their provincially and federally endangered status in Canada (COSEWIC, 2004). Home range sizes of Spotted Turtles have been documented to vary from 0.2 ha to 34.4 ha (Lewis and Faulhaber, 1999; Milam and Melvin, 2001; Litzgus and Mousseau, 2004a), and their largest daily movements tend to be in the spring and late summer (Lovich, 1988; Haxton and Berrill, 2001; Rasmussen and Litzgus, 2010). Some Spotted Turtles exhibit aestivation behavior during which individuals become inactive for a variable period of time to avoid overheating and desiccation during late summer (Ernst, 1982; Milam and Melvin, 2001; Litzgus and Mousseau, 2004a). This behavior may also be triggered by a shortage of food (Ward et al., 1976; Land and Bernier, 1995). Spotted Turtles have been documented to aestivate in a variety of habitats, including muskrat burrows (Ernst, 1976), sphagnum swamps, in vegetative debris on rock outcrops, forests (Litzgus and Brooks, 2000), and under leaf litter and woody debris (Litzgus and Mousseau, 2004a). Using historical radio telemetry data collected by the Ontario Ministry of Natural Resources (OMNR) before flooding and data we collected after flooding, we examined changes in home ranges, seasonal movement patterns, habitat selection, and behavior of Spotted Turtles in response to this natural habitat change. We predicted that Spotted Turtle home range sizes would increase and that daily distances traveled would be greater after flooding because the increased water level would make more of the site available to the turtles. We also predicted that turtles would show preference for the new aquatic habitat because the increased water level would provide more wetland habitat for turtles to exploit and occupy. Finally, we predicted that turtles would aestivate less often after flooding because the cues that trigger aestivation behavior (hot and dry conditions) would be removed by the increased presence of aquatic habitat.

MATERIALS AND METHODS

Study site.—The study site is a partially mined peatland located on the Niagara Peninsula of Southern Ontario, Canada (Fig. 1; the exact location of the site is not given to protect the turtles from collection). The study site is also located within the prehistoric floodplains of Lake Erie, making the surrounding region optimal for cropland and susceptible to flooding (Gayler, 1994). The Niagara region has a mean annual precipitation level of 1003.2 mm, and the mean daily temperature in January is -4.2° C and increases to 21.6°C in July (Environment Canada, 2010).

The study site covers 1460 ha, making it the largest remaining *Sphagnum*-dominated, ombrotrophic peatland in the region (Pengelly et al., 1997). Historical dominant vegetation consisted of bog species such as Leatherleaf (*Chamaedaphne calyculata*) and *Sphagnum* spp. The outer edges of the bog consisted of swamp-like forest habitat where water levels fluctuated seasonally. After the site was drained and mined for peat (mid 1930s to early 1990s), dominant vegetation species shifted to Highbush Blueberry (*Vaccinium corymbosum*), Black Chokeberry (*Aronia melanocarpa*), European Birch (*Betula pendula*), and Trembling Aspen (*Populus tremuloides*; Yagi and Frohlich, 1998). The

site is currently surrounded by rural development (e.g., crop lands and quarries) and some urban development.

Over 60 years of peat extraction within the study site was made possible by the placement of a series of drainage ditches throughout the interior and along the edges of the bog (Yagi and Frohlich, 1998). These ditches maintained the peatland in a relatively dry state, leaving the site prone to bush fires, and the only standing water was found in the deep drains and in a few ponds dug out by the peat-miners (Yagi and Frohlich, 1998). The remaining standing water became the primary source of aquatic habitat for many organisms (Yagi and Frohlich, 1998). In 1997, the Niagara Peninsula Conservation Authority (NPCA), OMNR, and Nature Conservancy of Canada (NCC) purchased 74% of the peatland and began to manage and restore the site (Niagara Peninsula Conservation Authority, 1997). In 1998, the OMNR began to collect data on species of concern in the site, including the Spotted Turtle.

In fall 2005, Beaver dispersed into the local watershed and were recorded in the interior of the bog (M. Browning, pers. comm., 2009). Beaver constructed many dams in the main drainage ditches within and around the bog. This Beaver activity caused significant flooding in the extracted interior of the site and initiated changes in the dominant vegetation. By 2008, approximately 47% of the extracted interior was covered by flooded areas, causing a vast change in the appearance and vegetation composition of the site (Fig. 1).

Mark-recapture and radio telemetry .-- In 1998, the OMNR initiated a long-term mark-recapture study of the Spotted Turtle population in the study site. Turtles were captured with dip nets and by hand, and individually marked by filing notches in the marginal scutes of the carapace (Cagle, 1939) and plastron. Individuals were sexed based on secondary sex characteristics (Ernst and Lovich, 2009). Mark-recapture data were used to estimate population size (N) for pre-flooding (N_{pre}) and post-flooding (N_{post}) conditions using the Lincoln Index (Fowler et al., 1998): N = (m*n)/r, where *m* is the number of individuals marked in the first sample, *n* is the number of individuals captured in the second sample, and r is the number of re-captured individuals in the second sample. Population size was estimated for each year (1999 to 2009) and then an average population size estimate was calculated for pre-flooding (1999 to 2005) and post-flooding (2006 to 2009). Population density estimates were calculated for pre-flood and postflood conditions by dividing population size by the corresponding population range sizes (see below) for both flooding conditions. Sex ratios before and after flooding were examined using Chi-squared tests.

During pre-flooding (2000 to 2005), a total of seven adult Spotted Turtles (six females, one male) were outfitted with 12 g Holohil temperature-sensitive radio transmitters (Model SI- 2T, Carp, ON) and radio tracked throughout their active season (April–October). The transmitter did not exceed 7% of the turtle's body mass. Transmitters were attached to the carapaces of adult turtles with thin brass wire threaded through small holes drilled into the posterior marginal scutes. Due to lost transmitters and mortalities, all seven turtles were not tracked continuously from 2000 to 2005. Nonetheless, the data collected from each turtle represented behavioral and spatial data from the entire preflooding time period. On average, turtles were tracked once every two weeks.



Fig. 1. A comparison of the study site in the Niagara region of Ontario, Canada during pre-flooding (A) and post-flooding (B) conditions. The only permanent aquatic habitat available before flooding was the water present in the drains. The post-flooding map shows a drastic increase in water levels (Flooded zone) caused by Beaver (*Castor canadensis*) damming. Many previously independent drains were merged together as a result of the flooding.

Habitat acronym	Habitat type	Habitat descriptions (dominant plant type)
OP	Open peat	Sparse vegetation, some raspberry (<i>Rubus idaesus strigosus</i>)
CG	Cotton grass	Early-successional vegetation (Eriophorum vaginatum)
YB	Young birch	Early-successional birch (Betula pendula)
SPH	Sphagnum	Sphagnum spp. regeneration
SHR	Shrub	Highbush Blueberry (Vaccinium corymbosum), Black Chokeberry (Aronia melanocarpa)
FOR	Forest	Mature birch (Betula pendula), Trembling Aspen (Populus tremuloides)
TMP	Temporary pool	Vegetation variable, water temporary
SFZ	Shallow flooded zone	Mixed aquatic vegetation, water depth $<$ 40 cm
DFZ	Deep flooded zone	Emergent aquatic vegetation, water depth 40–70 cm
DR	Drains	Water depth >70 cm
PON	Pond	Vegetation variable, water depth $>$ 70 cm

 Table 1. Definitions Used to Classify Habitats at the Study Site in Niagara District, ON. Using the Ecological Landscape Classification (ELC) criteria

 (Lee et al., 1998), we defined fine resolution habitat types in order to assess habitat selection by Spotted Turtles (Clemmys guttata).

In 2008 (post-flooding), 12 turtles (six males, five females, and one sub-adult) were outfitted with 3.6 g Advanced Telemetry System (ATS) radio transmitters (Model R1680, Isanti, MN). The transmitters were attached to the posterior marginal scutes of the carapace using a five-minute curing epoxy and smoothed over with a waterproof putty epoxy to prevent the transmitter snagging in vegetation. Transmitters with epoxy never weighed more than 7% of the turtle's body mass. Turtles were tracked at least once/week from May (initial turtle capture date) to November, or until they began hibernation. Turtles were tracked once/month during hibernation to determine hibernacula locations. In 2009 (post-flooding), seven more turtles (two males, four females, one sub-adult) were captured and outfitted with ATS transmitters, making a total of 19 radio-tagged turtles for the post-flooding data collection period. Turtles were tracked 2-3 times/week in 2009, from emergence from hibernation (March) until entrance into hibernation (November). For all radio telemetry studies pre- and postflooding, at each location point, the date and time, turtle behavior, habitat description, and GPS location were recorded. The proportion of aestivation behavior (number of observations of aestivation out of total number of behavior observations) was compared between flooding conditions using a paired *t*-test.

Movement patterns and home ranges.—Because time of year (i.e., season) has a significant effect on turtle movements (Litzgus and Brooks, 2000; Arvisais et al., 2004; Litzgus and Mousseau, 2004a), the activity patterns for turtles were assessed annually and throughout different seasons. Movement data were divided into five seasonal time periods: hibernation (22 November 2008-21 March 2009), prenesting (22 March 2009-18 May 2009), nesting (19 May 2009-30 June 2009), post-nesting (1 July 2009-3 August 2009; 10 October 2009-21 November 2009), and aestivation (4 August 2009–9 October 2009). The movement data were separated by sex so that male and female movement patterns within each season could be compared. The preflooding data only had one male; therefore, comparisons between the sexes were made only using the post-flooding data.

Daily mean distances traveled were calculated for each radio-tagged turtle during each season for both pre- and postflooding conditions. The shortest distance between consecutive location points was measured using ArcGIS (v 9.2, ESRI, Isanti, MN) and divided by the intervening number of days to obtain the mean distance moved per day. If distance data were not normally distributed, a log₁₀ transformation was performed on the data and normality was verified with a Shapiro-Wilk test. A repeated measures analysis of variance (rmANOVA), with turtles as replicates and seasons as the repeated measurement, was used to determine if mean daily distances traveled were affected by flooding conditions and seasons (Statistica 6.1, Tulsa, OK). Because there was only one radio-tagged male during pre-flooding, the sexes were pooled for analyses comparing flooding conditions, and a separate rmANOVA was used to examine differences between the sexes for post-flooding only. Tukey's HSD *post hoc* analysis was used to determine which seasons were different within each flooding condition.

To estimate home range sizes, annual minimum convex polygons (MCPs) and seasonal MCPs were created for each turtle for both pre- and post-flooding conditions. MCPs were estimated using the Hawth's Tools extension in ArcGIS (v3.27, ESRI, Isanti, MN). A Shapiro-Wilk test was used to ensure the data were normally distributed; if the data were not normally distributed, they were log₁₀ transformed. MCPs were compared between flooding conditions and among seasons using rmANOVA.

Habitat selection.—The predominant habitat type at the study site is classified by the Ecological Landscape Classification (ELC) system as a Shrub Bog (Lee et al., 1998). Because habitat use by Spotted Turtles is at a finer scale than what has been classified under the ELC, we demarcated the bog interior into 11 habitat categories. These habitat types were classified using the same methodology as ELC classification technique, which defines habitat categories based on soil type and dominant plant species (Table 1).

The available habitats and habitats used by turtles were quantified during pre- and post-flooding conditions, and habitat selection was examined using the Euclidean distance-based method (Conner and Plowman, 2001). Habitat selection analyses involved demarcating population ranges using MCPs and individual home ranges using 95% kernels in ArcGIS. Habitats within the population range were considered to be the available habitats for turtles. During pre-flooding, the population range was drawn as a MCP encompassing all locations for all seven radio-tagged turtles and covered an area of 48.1 ha. To include all 95% kernels for all turtles in the population range, it was necessary to add an 83 m buffer to this MCP. The 83 m buffer was the largest measured distance from the MCP boundary to the outer boundary of the 95% kernels, calculated in ArcGIS. The resulting area (72.8 ha) was the designated available habitat for the population during pre-flooding. For postflooding, the population range MCP for all 19 radio-tagged turtles covered an area of 179.5 ha. Determined in the same manner as for pre-flooding turtles, a 63 m buffer was added to the population range MCP to include all 95% kernels; the resulting area (215.5 ha) was designated as the available habitat for the population during post-flooding. Using ArcGIS, available habitat types within the population range were drawn as shape files for both pre-flooding and postflooding conditions. Areas (ha) of each habitat type were calculated using area measurement tools in ArcGIS. Habitat use was quantified using a kernel home range estimator, a non-parametric method that produces a geographical distribution estimating the probability of finding an animal at any particular location within its home range (Worton, 1989). For each individual turtle, the area of the 95% kernel was determined using the Hawth's Tool extension in ArcGIS and adjusted to equal the 100% MCP of the same turtle (Row and Blouin-Demers, 2006b). This was done by adjusting the value of the smoothing factor (h) and keeping the raster cell size small (at a value of 3-4). Kernel smoothing factors for each turtle were adjusted so that the 95% kernel did not differ by more than 5% from the size of the corresponding 100% MCP.

Different elements of habitat must be measured at appropriate spatial and temporal scales that are relevant to the species of interest (Girvetz and Greco, 2009). Habitat selection can occur at different spatial scales, referred to as 1st, 2nd, and 3rd order selection (Johnson, 1980). The 1st order selection scale refers to the selection of the species' population range from its geographic range, the 2nd order selection scale indicates the selection of the home ranges of individuals from the population range, and the 3rd order selection scale refers to selection of location points within an individual's home range (Johnson, 1980). Habitats at larger resolutions are considered to be available to the animal at finer resolutions; therefore, at each scale, habitats are selected from those habitats available one level up in the hierarchy (Bissonette et al., 1997). In our study, habitat selection was quantified at the 2nd and 3rd order scales. For pre-flooding, 599 random points (i.e., equivalent to the total number of radio locations during pre-flooding) were created within the population range MCP using Hawth's Tool. The average distance from each random point to the nearest boundary of each habitat type was measured using the Near Tool extension in ArcGIS. For post-flooding, 858 random points (i.e., equivalent to the total number of radio locations during post-flooding) were made within the population range MCP and the average distance from each random point to the nearest boundary of each habitat type was measured. These average distances represent habitat availability (r_i) at the 2nd order scale. Habitat use at the 2nd order scale was quantified by creating random points within each turtle's 95% kernel. The number of random points used for each turtle's kernel was equal to the number of radio locations recorded for the individual. Again, the average distance from each random point to the nearest habitat type was calculated. These distances represent habitat use (u_i) at the 2nd order scale. For 3rd order analysis, the random points from the 95% kernels for each turtle become the r_i values and the actual radio locations for each turtle become the u_i values.

For each selection scale, a vector of ratios (*d*) was calculated for each turtle, where $d = u_i/r_i$. These ratios were compared to an expected vector of ratios given a value of 1. A low value of d (d < 1) indicates that the animals were closer to the habitat type than expected (habitat selection), whereas a high value of d (d > 1) indicates that the animals were farther away from the habitat type than expected (habitat avoidance; Conner and Plowman, 2001). Ratio data were log_{10} transformed when their distributions did not conform to the assumption of parametric statistical analyses. For analyses of both 2^{nd} and 3^{rd} order habitat selection, an rmANOVA was used to test if habitat use ratios differed from a value of 1, where individual turtles were the replicates and the habitat types were the repeated measure.

There were not enough data points for each turtle during each season to calculate seasonal 95% kernels for measuring habitat selection for each season at the 2nd order scale. Therefore, comparisons within seasons were only made at the 3rd order spatial scale for both flooding conditions. If there was a significant difference in turtle proximities to habitat types than random at the 2nd order selection scale, then further analysis was done at the 3rd order selection scale. An rmANOVA was used to compare turtle locations to random locations for each season at the 3rd order selection scale, using habitat type as the repeated measurement. Sex was added as a grouping variable only for post-flooding conditions to determine if there was a difference in turtle proximity to habitat types between males and females. Tukey's HSD post hoc analyses were used to determine which habitat types were selected within each season.

In order to compare habitat selection between flooding conditions, we created four broad habitat categories by combining the 11 categories described above (and in Table 1) so that there would be an equal number of habitat types available between both flooding conditions. To determine if there were any seasonal differences between flooding conditions, we used 3rd order selection data. We averaged the ratio data (d) collected for drains, ponds, and temporary pools available from pre-flooding conditions into the same category as the shallow flooded zones and deep flooded zones available in post-flood conditions, under a habitat category called "aquatic." Similarly, we averaged the shrub and forest habitat types into one category called "upland," and averaged the Sphagnum, Cotton Grass, and young Birch all into one category called "early succession." The open peat habitat type was left as its own category called "degraded." These combined data were analyzed with an rmANOVA separately within each season, with individual turtles being replicates and habitat categories being the repeated measurement.

RESULTS

Mark–recapture and radio telemetry.—Annual population size estimates ranged from 65 to 173 turtles across the 12-year study (Fig. 2). The pre-flooding mean population size (N_{pre}; 1999 to 2005) was 115 individuals (SE = 7) and population density was 1.6 turtles/ha. The post-flooding mean population size (N_{post}; 2006 to 2009) was 143 individuals (SE = 5) and population density was 0.7 turtles/ha. The post-flooding population size estimate was not significantly different from the pre-flooding estimate ($t_9 = -1.24$, P = 0.25). However, population density was significantly lower during post-flooding compared to pre-flooding ($t_9 = 3.25$, P = 0.01).

Pre-flood

Post-flood

Fig. 2. Spotted Turtle (*Clemmys guttata*) population size estimates (N) in a historically mined peat land in Southern Ontario from 1999 to 2009. Pre-flood conditions define years 1999 to 2005, and post-flood conditions define years 2006 to 2009. The black squares indicate the mean population estimate. Error bars denote standard error.

The population sex ratio before flooding was 1M:1.05F, and this was not statistically different than 1M:1F ($\chi^2_1 = 0.003$, P = 0.96). During post-flooding conditions, the sex ratio was 1M:0.83F, which also was not different than 1M:1F ($\chi^2_1 = 0.031$, P = 0.86).

Individual Spotted Turtles were tracked on average 85.6 times (SE = 11.8) for the duration of the pre-flooding telemetry study (six years). These historical data (i.e., GPS locations and behavior) showed that 90% of the telemetry observations represented turtle activity in aquatic habitats (DR, TMP, PON; Table 1), and 10% of the observations indicated turtle activity in terrestrial habitats. Four adult female turtles out of the seven radio-tagged turtles were found dead, three likely due to predation because turtles were found partially eaten (head or limbs missing) in terrestrial locations (Coyotes [Canis latrans] and Raccoons [Procyon lotor] are common at the site), and one likely due to overheating and desiccation because it was found dead on the bottom of a dried-out drain. From these observations, pre-flooding (1998 to 2004) mortality rate was estimated to be 57%. In 2008 (post-flooding), 12 turtles were radiotagged, and each one was tracked on average 9.6 times (SE = 1.31), while in 2009, 19 turtles were tracked on average 39.1 times each (SE = 1.37). Post-flooding, 99% of the turtle telemetry observations represented turtle activity in aquatic habitat (DR, PON, SFZ, DFZ; Table 1) and 1% of the observations indicated turtle activity in terrestrial habitats. No telemetry turtles were found dead from May 2008 to December 2009; thus, the mortality rate post-flooding was 0%.

There was a significantly greater proportion of observations of radio-tagged turtles aestivating before flooding (mean \pm SE = 0.22 \pm 0.05) compared to after flooding (0.02 \pm 0.01; t_{24} = 12.33, P < 0.001). During pre-flooding, aestivation behavior was observed as early as 18 June and as late as 25 October. Telemetry turtles were found aestivating in a variety of habitat types such as in the damp soil of dried temporary pools, under dense Raspberry (*Rubus idaesus strigosus*) and Blueberry bushes, and at the bottoms of

Fig. 3. Mean daily distances traveled by Spotted Turtles (*Clemmys guttata*) in a historically mined peat land in Southern Ontario from 1998 to 2000 (pre-flood; gray diamonds) and 2008 to 2009 (post-flood; black squares). Comparisons were made within each of five seasons, between pre-flooding and post-flooding conditions. Error bars denote standard error.

Nesting Post nesting Aestivation

30

25

20

15

10

5

C

Hibernation Pre nesting

Daily distance travelled (m day⁻¹)

drains. During post-flooding, there were only six observations of radio-tagged turtles aestivating in both the 2008 and 2009 field seasons combined. These turtles were observed aestivating in Cotton Grass tussocks (*Eriophorum vaginatum*), Blueberry bushes, Leatherleaf shrubs, and in Sphagnum moss hummocks.

Movement patterns and home ranges.—Turtles showed different movement patterns between flood conditions. The average daily distance traveled during pre-flood conditions by females was 4.5 m/day (N = 6, SE = 1.7), and was 6.0 m/ day (SE = 4.4) for the one tagged male. During post-flooding conditions, males moved a mean distance of 18.3 m/day (N = 8, SE = 4.3), and females moved a mean distance of 16.5 m/day (N = 9, SE = 3.0). There was no significant difference in daily distances traveled between males and females during post-flooding ($t_{16} = 0.25$, P = 0.80). There was a significant interaction effect between season and flooding condition ($F_{4.88} = 5.0$, P < 0.001); daily movements increased in response to flooding condition and season. There was no difference in daily distance traveled between flooding conditions during hibernation (Tukey's HSD P = 1.00, but there were significant movement differences between flooding conditions during the prenesting (P < 0.01), nesting (P < 0.005), post-nesting (P < 0.005) 0.005), and aestivation seasons (P < 0.001; Fig. 3).

Population range size for all tracked turtles (N = 7) during pre-flooding was 48.1 ha, which was significantly smaller than the population range size for all tracked turtles (N =19) during post-flooding (179.5 ha; $t_6 = 14.44$, P < 0.001). There was a significant difference in annual home range size between pre-flood (mean = 3.2 ha, SE = 0.01) and postflood conditions (mean = 7.1 ha, SE = 0.2; $F_{1,20}$ = 5.34, P <0.05). Home range size also differed among seasons ($F_{4,88}$ = 64.8, P < 0.001), and the interaction between season and flooding condition was significant ($F_{4,88} = 3.38$, P < 0.01). During post-flooding, no difference between males and females was detected in annual home range size ($F_{1,20}$ = 0.216, P = 0.65), and home range size did not differ between the sexes in any season ($F_{4.60} = 1.55$, P = 0.20). The smallest home range for both flood conditions was during hibernation (0 ha). The largest home range during pre-flooding was 8.8 ha for a female, which occurred during pre-nesting, and



1.0 ha for the male, which occurred during post-nesting. The largest home ranges during post-flooding were 14.1 ha for a female and 15.5 ha for a male, both of which occurred during the post-nesting season.

Habitat selection.—During both pre-flooding and post-flooding conditions, there was evidence of significant habitat selection at both the 2^{nd} order and 3^{rd} order spatial scales. There was an obvious change in the types of habitat available during post-flooding compared to pre-flooding (Fig. 1). Turtles generally selected drains and open peat during pre-flooding; whereas, during post-flooding, they selected aquatic habitat, including the newly flooded areas and drains (Fig. 4).

Habitat selection during pre-flooding.—At the 2nd order spatial scale, annual home ranges were at proximities to habitat types that were significantly different from random proximities to habitat types available within the population range ($F_{1,12} = 39.2$, P < 0.001). There was also a significant interaction between ratio type (actual vs. random) and habitat type ($F_{8,96} = 5.91$, P < 0.001), meaning that turtles were selecting certain habitat types over others within the population range. Turtles selected drains (Tukey's HSD P < 0.05) and open peat (P < 0.05) within their home ranges over the other habitat types available within the population range.

At the 3rd order spatial scale, we detected seasonal habitat selection (Table 2). Turtles were closer than random to drains (Tukey's HSD P < 0.001) and open peat (P < 0.001) during hibernation, open peat (P < 0.05) during pre-nesting and nesting (P < 0.05), drains (P < 0.01) and open peat (P < 0.05) during post-nesting, and drains (P < 0.05) and open peat (P < 0.05) during aestivation (Fig. 4A).

Habitat selection during post-flooding.—At the 2nd order spatial scale, annual home ranges were at proximities to habitat types that were significantly different than random proximities to habitat types available within the population range ($F_{1,30} = 92.7$, P < 0.001). There was also a significant interaction effect between ratio type (actual vs. random) and habitat type ($F_{9,270} = 22.1$, P < 0.001), suggesting that turtles were selecting certain habitat types over others within the population range. Turtles selected primarily shallow flooded zones (Tukey's HSD P < 0.001), deep flooded zones (P < 0.001), and drains (P < 0.05) over the other habitat types available within the population range. There was no difference between the sexes in habitat selection at this spatial scale ($F_{1,30} = 0.013$, P = 0.91).

At the 3rd order spatial scale, we detected seasonal habitat selection (Table 2). There was no significant difference in turtle proximity to habitat types between males and females for all seasons: hibernation ($F_{1,30} = 2.88$, P = 0.10), prenesting ($F_{1,30} = 1.62$, P = 0.21), nesting ($F_{1,30} = 2.49$, P = 0.13), post-nesting ($F_{1,30} = 1.47$, P = 0.26), and aestivation ($F_{1,30} = 0.02$, P = 0.90). Turtles selected primarily drains (Tukey's HSD P < 0.001) and shallow flooded zones (P < 0.01) during hibernation, shallow flooded zones (P < 0.001) during pre-nesting and nesting (P < 0.005) during post-nesting, and shallow flooded zones (P < 0.001) and shallow flooded zones (P < 0.001) and shallow flooded zones (P < 0.001) during post-nesting, and shallow flooded zones (P < 0.001) during aestivation (Fig. 4B).

Comparison of habitat selection between flooding conditions.— Habitat selection changed between flooding conditions. During pre-flooding, turtles selected aquatic, upland, and degraded habitat (Fig. 4A); whereas, post-flooding, turtles selected mainly aquatic habitat (Fig. 4B). There was no difference in habitat selection between pre-flood and post-flood conditions during hibernation ($F_{1,22} = 0.06$, P = 0.81), pre-nesting ($F_{1,22} = 0.68$, P = 0.42), and post-nesting ($F_{1,22} = 1.06$, P = 0.31). However, there was a significant difference in habitat selection between pre- and post-flooding conditions during the nesting ($F_{1,22} = 5.88$, P < 0.05) and aestivation seasons ($F_{1,22} = 5.79$, P < 0.05; Table 3). Based on the lowest mean *d* ratio calculated for each habitat category, during both the nesting and aestivation seasons, turtles were closest to degraded habitat during pre-flood conditions and closest to aquatic habitat during post-flood conditions (Table 3).

DISCUSSION

Mark-recapture and radio telemetry.-The estimated population size was larger during post-flooding compared to preflooding, but the difference was not statistically significant. The lack of statistical significance may be explained by the high variability among annual estimates (Fig. 2). Nonetheless, many (16) new adult turtles were found post-flooding, likely because the greater number of radio-tagged turtles increased our coverage of the site and therefore increased the chance of opportunistically encountering turtles that were not radio-tagged. Finding several unmarked adult turtles in a population that has been studied for 12 years suggests that these turtles may have immigrated to the site from proximate unsurveyed sites. Interestingly, all the new turtles were found in the newly flooded areas. In fact, during post-flooding, all turtles used the new flooded areas which increased connectivity among drains, including some of the more isolated drains from which the new turtles may have traveled.

That the density of turtles at our site was significantly lower during post-flooding is a result of the fact that a larger area was being used by the turtles because the flooding made more of the bog available to the turtles. A lower population density can suggest that there is less competition for food and space within preferable habitat (Hariston et al., 1960; Case and Gilpin, 1974; Jirotkul, 1999), implying that flooding has been beneficial for the Spotted Turtles in our study population. However, there is little evidence of density-dependent responses (e.g., survivorship and fecundity) in turtle populations (Burke et al., 1998; Brook and Bradshaw, 2006; Enneson and Litzgus, 2009). Therefore, a change in population density may have little to no effect on Spotted Turtle population dynamics within our study site.

The sex ratio of adult turtles in our population was not different than 1:1 pre- or post-flooding. Similarly, equal sex ratios have been documented in other Spotted Turtle populations (Graham, 1995; Litzgus and Mousseau, 2004b). Populations with equal sex ratios are considered healthy (Fisher, 1930). Turtle populations in fragmented or disturbed sites have been found to have skewed sex ratios (Ernst, 1974; Dodd and Dreslik, 2008; Bennett et al., 2009). Although flooding can be considered a disturbance, in our study, sex ratios remained equal, suggesting that the disturbance has not had a negative effect on the Spotted Turtles in our population.

Aestivation was observed significantly less often during post-flooding compared to pre-flooding. These observations support our prediction that flooding increased the presence of suitable conditions (e.g., habitat and temperatures) in



Fig. 4. Seasonal habitat selection at the 3rd order spatial scale during pre-flood conditions (A) and post-flood conditions (B). Mean Spotted Turtle (*Clemmys guttata*) proximities to each habitat type (Table 1) during each season at the 3rd order spatial scale are shown. Ratios (*d*) close to 1 suggest that turtles were not selecting the habitat; ratios close to 0 suggest that turtles were selecting the habitat. * indicates habitat types that were selected (*d* ratio not significantly different than 0).

Nesting

Post-nesting

Aestivation

0.02

0.52

0.17

was detected in post-flood conditions during the hibernation, pre-nesting, and nesting seasons.									
	Pre-flood		Post-flood						
Season	F value	P value	F value	P value					
Hibernation	$F_{1,12} = 0.54$	0.48	$F_{1,30} = 75.6$	< 0.001					
Pre-nesting	$F_{1,12} = 0.11$	0.74	$F_{1.30} = 4.55$	0.01					

0.78

< 0.05

< 0.01

Table 2. Summary of ANOVA Results for the Analysis of 3rd Order Seasonal Habitat Selection by Spotted Turtles (*Clemmys guttata*) during Pre-flood and Post-flood Conditions. Habitat selection was detected in pre-flood conditions during the post-nesting and aestivation seasons. Habitat selection was detected in post-flood conditions during the hibernation, pre-nesting, and nesting seasons.

which turtles could remain active. Although most of the Spotted Turtles in our study did not aestivate in the postflooding period, a few turtles still displayed the behavior. One possible explanation for the persistence of aestivation is that it has not been selected out of the species' behavioral repertoire. Aestivation might have been necessary historically for survival farther south where the species likely originated. The aestivation behavior of Spotted Turtles in Ontario that we observe today may be residual behavior from the species' evolutionary history when it was exposed to different climatic conditions (Graham, 1995). Another possibility is that aestivation occurs in response to food shortages (Ward et al., 1976) or after the animal has met all of its dietary requirements for the season (Litzgus and Brooks, 2000). Turtles likely continued to display aestivation behavior post-flooding due to a combination of factors (e.g., evolutionary history, individual habits, and food requirements), but the majority of turtles did not aestivate, suggesting that having more available preferred habitat plays a major role in reducing the occurrence of the behavior.

 $F_{1,12} = 0.08$

 $F_{1,12} = 7.56$ $F_{1,12} = 9.21$

Movement patterns and home ranges.—Population range size, individual home range sizes, and daily distances traveled all increased post-flooding. Because the same areas in the site were searched for turtles during both flooding conditions, we believe that the increase in population range size was not caused by the increase in number of turtles found, but rather caused by the increased availability of aquatic habitat. The greater home range sizes and daily distances traveled post-flooding relative to pre-flooding support our prediction that

turtle movements would increase with the increase in available aquatic habitat. In addition, a previously unoccupied part of the site, specifically the southwest end, was used by turtles after flooding and flooding here increased connectivity among drains. Prior to flooding, turtle movements were confined mainly to the only available aquatic habitat at the time, the drains. The use of these drains restricted turtle home range sizes. Smaller movements by turtles within their home ranges prior to flooding also reflect this restriction of available habitat.

 $F_{1.30} = 5.77$

 $F_{1,30} = 0.43$

 $F_{1,30} = 1.96$

When considering a species living in a highly fragmented habitat, the ability of the animal to meet its resource requirements depends partially on the connectivity between available habitat patches (Taylor et al., 1993). If the drainage ditches were the only adequate Spotted Turtle habitat during pre-flooding, then the drains could be viewed as habitat fragments. Habitat fragmentation can cause animals to aggregate near edges, resulting in increased interactions between predators and prey, which can increase prey mortality (Soulé et al., 1988; Bender et al., 1998; Harden et al., 2009). Turtles may appear to be aggregating near habitat edges in our case because of the long and narrow structure of the drains themselves, such that turtles in a drain (usually 2-3 m wide) will always be relatively close to the drain edge. In our study, mortality rate was relatively high during preflooding, and there was no mortality observed during postflooding. The decrease in predator-induced mortality postflooding may have resulted from the increased water level that removed the drain edge effect and connected drains of the study site interior, making terrestrial areas used by predators less connected with the Spotted Turtle's preferred

Table 3. Comparison of Habitat Selection by Spotted Turtles (*Clemmys guttata*) in the Nesting and Aestivation Seasons at the 3rd Order Spatial Scale, between Pre- and Post-Flooding Conditions. The mean proximities (*d*) to each habitat category are reported here, and habitat types are ranked from smallest to largest ratio ($d = u_i/r_i$). A low value of d (d < 1) indicates turtles were closer to the habitat type than expected (habitat selection), whereas a high value of d (d > 1) indicates that turtles were farther away from the habitat type than expected (habitat avoidance; Conner and Plowman, 2001).

	Pre-flood		Post-flood	
Season	Habitat category	d	Habitat category	d
Nesting	degraded	0.59	aquatic	0.67
0	aquatic	0.82	upland	0.86
	upland	0.84	early succession	0.86
	early succession	0.92	degraded	0.91
Aestivation	degraded	0.56	aquatic	0.77
	upland	0.77	upland	0.81
	aquatic	0.80	early succession	0.82
	early succession	0.89	degraded	0.91

habitat, allowing for better predator avoidance (<u>Fahrig and</u> Merriam, 1985).

Habitat selection.—Turtles displayed habitat selection at both the 2nd and 3rd order spatial scales during both flooding conditions and among seasons at the 3rd order scale. Furthermore, habitat selection changed from pre-flooding to post-flooding. Turtles selected degraded habitat (open peat) and drains during pre-flooding but switched to aquatic habitat (new shallow flooded zones and drains) during postflooding. The apparent selection for open peat during preflooding might be an artifact of selection for drains because open peat was closely associated with drains. During peat extraction, drains were excavated and the peat was left in long piles alongside the drains. There was generally a lack of vegetation in the extracted areas, leaving most of the space around the drains as open peat. Our findings indicate that turtles preferred aquatic habitats and exploited the increase in available aquatic habitat post-flooding, supporting our prediction that turtles would prefer the new aquatic habitat over the available terrestrial habitat. These findings also suggest that flooding improved habitat quality within the study site.

Different habitats were selected seasonally during the two flooding conditions. Drains were selected for hibernation during both flood conditions. The drains were much deeper than the flooded areas, and could therefore provide a more thermally stable site for hibernation, and turtles may show fidelity to hibernation sites (Litzgus et al., 1999) which may be why drains were still the preferred hibernation habitat post-flooding. Turtles hibernate in aquatic habitats to maintain thermally stable body temperatures and to avoid freezing during the winter (Ultsch, 2006). Blanding's Turtles (Emydoidea blandingii) in Algonquin Provincial Park, Ontario selected hibernation sites that were stable at around 0°C (Edge et al., 2009) and Spotted Turtles hibernate in sites with temperatures that do not deviate far from 0°C (Litzgus et al., 1999; Rasmussen and Litzgus, 2010). In our study, all but three Spotted Turtles hibernated in drains post-flooding: two individuals hibernated in the new flooded area and one individual hibernated in a flooded area adjacent to a drain.

We found changes in habitat selection during the aestivation and nesting seasons between flood conditions. Habitat selection during the aestivation season post-flooding changed to aquatic habitats in which turtles remained active. Turtles may choose to remain active in their preferable aquatic habitat rather than seeking out aestivation sites during the late summer because remaining active means more opportunities for feeding. More feeding translates into increased storage of resources to invest in hibernation and future reproduction. These results coincide with our observational results of decreased aestivation frequency post-flooding, and give support to our prediction that Spotted Turtles would aestivate less often due to the increased availability of preferred habitat.

During the nesting season, turtles selected degraded (open peat) during pre-flooding and selected aquatic (shallow flooded zones) during post-flooding. Historical nesting sites, which were located on the open peat of drain banks (OMNR, unpubl. data), may have been lost due to the Beaver flooding, and open peat habitat became limited around drain edges. Thus, nest sites may have become a limited resource after flooding. In 2009, one female was observed ovipositing 6 m from a drain in an area of saturated peat and raised moss hummocks, with flooded areas nearby. Five eggs were found in the nest, and four out the five eggs hatched successfully, indicating that at least some recruitment is occurring despite the flooding. Spotted Turtles may be able to utilize the new vegetation growing in newly flooded areas as nesting habitat, especially moss hummocks in shallow flooded zones. This may explain why during post-flooding, turtles were selecting flooded areas during the nesting season.

In summary, flooding caused by Beaver dams at our site increased Spotted Turtle mobility in terms of daily movements and home range size; allowed turtles to remain active longer, presumably allowing them to feed and acquire more energy reserves; and caused significant shifts in habitat selection with turtles displaying a distinct preference for the newly flooded habitat. These findings indicate that Spotted Turtles are opportunistic, and because Beaver cycles are much shorter than Spotted Turtle life spans (Litzgus, 2006), they also indicate that the turtles can survive, and indeed benefit, from such natural habitat changes. However, as a result of the flooding, female Spotted Turtles may be spending more time searching for appropriate nesting habitat during the pre-nesting and nesting seasons. Future work should examine the effects of flooding on the nesting ecology and recruitment of Spotted Turtles.

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