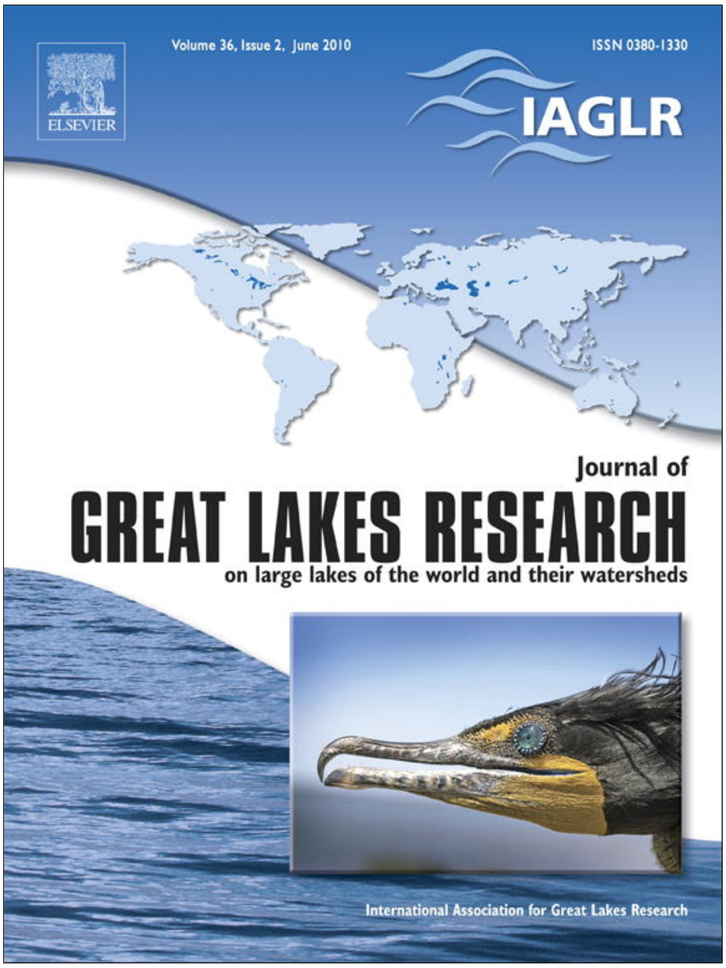
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Relationship of road density and marsh condition to turtle assemblage characteristics in the Laurentian Great Lakes

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ABSTRACT

Human-induced degradation of coastal wetlands often leads to altered trophic dynamics and species assemblages. Here we use data from 77 coastal marshes in three Laurentian Great Lakes collected between 2001 and 2007 to examine the relationship between human disturbance (road density and wetland quality) and characteristics of aquatic turtle assemblages, including species richness and abundances. Painted turtles (*Chrysemys picta*) were encountered disproportionately in degraded wetlands and the probability of occurrence decreased with improved site quality. Abundance of painted turtles peaked, however, at intermediate road density in surrounding 1- and 2-km buffers. Across all sites, species richness was highest and common snapping turtles (*Chelydra serpentina*) were most abundant in wetlands with intermediate water quality. The common musk turtle (*Sternotherus odoratus*) was absent from degraded wetlands in the lower lakes (Erie and Ontario) that fell within their historical range, but reached high abundances in marshes of Georgian Bay and the North Channel, a region with relatively low human disturbance. Analysis of sex ratios in painted turtles revealed a significant male bias in an area with high road density, while the sex ratio did not differ significantly from 1:1 in a less developed region, consistent with reports of high female mortality in urban areas.

Introduction

Wetland-dependent species often respond predictably to changes in watershed and wetland integrity within the Laurentian Great Lakes. The diversity and abundance of amphibians and wetland-dependent birds, as well as the condition and abundance of some fish species are often used as indicators of changes to ecosystem health in the Great Lakes basin (e.g. Shear et al., 2003; Seilheimer and Chow-Fraser, 2006; Brazner et al., 2007; Howe et al., 2007; Price et al., 2007). Study of the response of reptiles to changes in Great Lakes health, however, has been largely restricted to the effects of elevated contaminant levels (e.g. Bishop and Gendron, 1998; Bishop et al., 1998), and little attention has been given to the overall effects of human-induced changes to watershed and wetland habitat on species abundances and diversity.

Human alteration of terrestrial landscapes can affect the survival and recruitment of freshwater turtles. Modified landscapes may provide nesting habitat (Marchand and Litvaitis, 2004a), but higher abundances of predators such as raccoons (*Procyon lotor*) in human-altered habitats can lower nest success (Marchand and Litvaitis, 2004b; Browne and Hecnar, 2007). An increase in predator abundance and exposure to high road densities and traffic volumes can also increase mortality of hatchlings and adults undergoing terrestrial movements (Gibbs and Shriver, 2002; Beaudry et al., 2008). Because the life-history traits of turtles include high adult survival, late sexual maturity and low reproductive output, even slight increases in adult mortality can have devastating effects on recruitment rates (Brooks et al., 1991; Congdon et al., 1993, 1994). Females of most species are particularly vulnerable to predation and road mortality because they travel overland to nest and may be attracted to road-side nesting sites (e.g. Steen et al., 2006). Consequently, studies at both regional and larger scales in North America have reported male-biased sex ratios in urban areas for a number of species (Steen and Gibbs, 2004; Aresco, 2005; Gibbs and Steen, 2005; Steen et al., 2006).

Urban and agricultural development can also affect the aquatic habitats of turtles. An increase in road density and proportion of human-altered land in the watershed has been associated with nutrient enrichment and overall reduced water quality in coastal wetlands of the Great Lakes (Chow-Fraser, 2006; Trebitz et al., 2007; DeCatanzaro et al., 2009). The common snapping turtle (*Chelydra serpentina*) and painted turtle (*Chrysemys picta*) may benefit from nutrient enrichment of water from agricultural and urban runoff because of increased primary production and food availability that increases fecundity and growth rates (Brown et al., 1994; Lindeman, 1996). Blanding's turtles (*Emydoidea blandingii*) may also benefit from some nutrient enrichment and increase in productivity (Ernst et al., 1994), but high nutrients and suspended solids inputs from urban and agricultural lands can eventually reduce submergent habitat (Lougheed et al., 2001) upon which this species depends (Ross and Anderson, 1990; Ernst et al.,

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1994). Similarly, it has been noted that the common musk turtle (*Sternotherus odoratus*) declines in areas that have undergone extensive agricultural and urban development, possibly due to loss of habitat resulting from draining and degradation of wetlands (Edmonds, 2002).

To date, most studies that link human disturbance to abundances of freshwater turtles have dealt with a single species (e.g. Brown et al., 1994; Lindeman, 1996; Marchand and Litvaitis, 2004a) or have had a narrow geographic focus (e.g. Rizkalla and Swihart, 2006; Browne and Hecnar, 2007). No study has yet explored broad-scale relationships between abundances of multiple species and habitat degradation at the scale of several Laurentian Great Lakes. Our primary goal was to determine how measures of anthropogenic disturbance (road density and ecological indices) relate to presence/absence, abundances and species richness of turtle assemblages in coastal wetlands of Lakes Ontario, Erie and Huron. A second objective was to compare the sex ratio of a common turtle (the painted turtle) in areas of low (southeastern Georgian Bay) and high (western Lake Ontario) road density. We predict a disproportionate number of males in marshes in the area of high road density because females are expected to suffer higher road mortality.

Methods

Site distribution

Turtle capture records were taken from a synoptic coastal wetland database. This database contains information on water quality, macrophytes, fish and by-catch for over 200 georeferenced coastal wetlands sampled between 2001 and 2007, and has been used to develop ecological indices to assess the impact of human activities on wetland quality (Chow-Fraser, 2006; Seilheimer and Chow-Fraser, 2006, 2007; Croft and Chow-Fraser, 2007). Although turtles were not targeted during this study, they were frequently trapped in fyke nets used to survey the fish community. In total, turtle records exist for 5 wetlands in Lake Erie, 16 wetlands in Lake Ontario, 2 wetlands in the main Lake Huron basin and 54 wetlands in Georgian Bay and the North Channel (Fig. 1).

Trapping

Sampling took place annually between late May and early September. All captures were made with unbaited, paired fyke nets. During synoptic surveys, three pairs of nets (two pairs of large nets (4.25 m length, 1 × 1.25 m front opening) and one pair of small nets (2.1 m length, 0.5 × 1 m front opening)) were deployed at each site. These nets were set parallel to the emergent zone and left for approximately 24 h (Seilheimer and Chow-Fraser, 2006). While fyke nets are considered an effective method for sampling turtles in lakes and wetlands (Lagler, 1943; Vogt, 1980; Dreslik et al., 2005; Smith and Iverson, 2006), the nets were deployed to target the fish community. In 2007, we compared this set-up with one that was designed specifically to sample turtles that used a single pair of unbaited paired fyke nets with a 1 m × 1.25 m front opening and 2.5 m wings, connected by a 14 m lead set parallel to a basking site (a fallen tree or rock face) ($n = 6$). The deployment type did not significantly affect species richness (Paired t-test; $t = 0.60$; $p = 0.576$) or number of basking (Paired t-test; $t = 0.00$, $p = 1.00$) or non-basking species (Paired t-test; $t = 1.58$, $p = 0.175$) caught. Due to greater efficiency (higher catch per net pair), the latter method was used during the sex-ratio surveys in 2007. All individuals caught were identified at the species level, and carapace length was measured and used to classify turtles as adults or juveniles. In 2007, we used secondary sex characteristics to determine the sex of adult turtles (see Ernst et al., 1994).

Because our trapping methods were limited to fyke nets alone, which were set over a single trap night per site, not all individuals or species using a given wetland were encountered during the surveys. Thus, the synoptic survey data likely underestimates species richness, and species occurrences and abundances. However, because effort was consistent across sites, by-catch data provided a means to compare relative species abundances and richness across sites.

Wetland quality assessment

Two environmental indices of wetland quality, the Water Quality Index (WQI; Chow-Fraser, 2006) and the Wetland Macrophyte Index

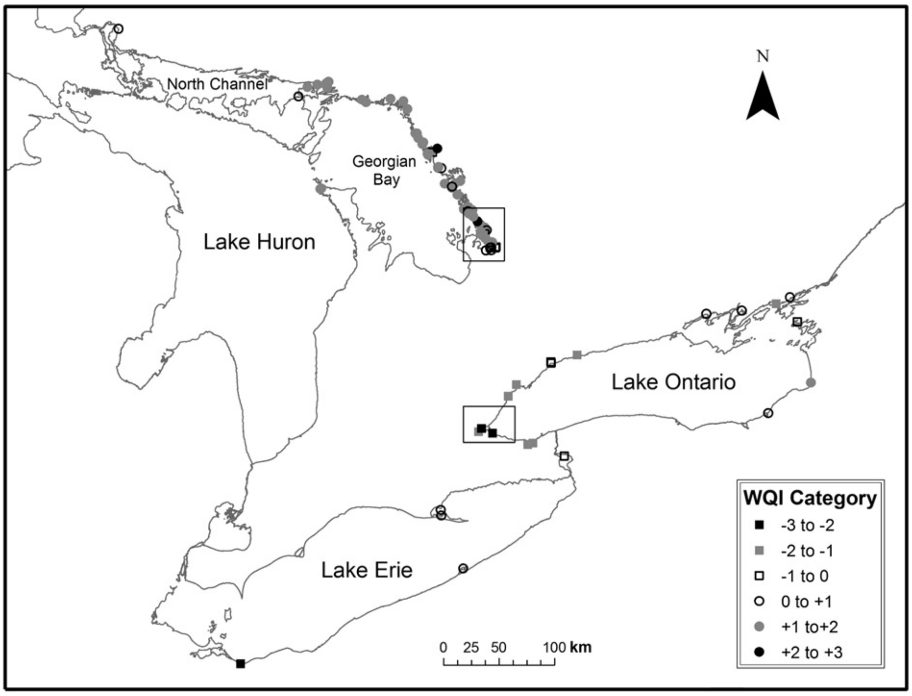

Fig. 1. Distribution and quality (based on WQI scores) of 77 coastal wetlands sampled during synoptic surveying between 2001 and 2007. Boxes highlight the areas targeted for sex ratio surveys in 2007.

(WMI; Croft and Chow-Fraser, 2007) were used to quantify the ecological condition of each marsh. The WQI uses 12 water-quality variables to assess the degree of degradation of Great Lakes coastal marshes that can be attributed to human activities. Values range from -3.0 (highly degraded) to $+3.0$ (excellent quality), and the index is significantly negatively correlated with the proportion of altered land (agriculture and urban) in wetland watersheds (Chow-Fraser, 2006). The WMI is a biotic index that can be used as a surrogate for water quality and that is highly correlated with the WQI (Croft and Chow-Fraser, 2007; Seilheimer et al., 2009); it provides a quantitative measure of wetland condition on a scale of 1.0 (highly degraded) to 5.0 (excellent quality) based on the presence of macrophyte species and their associated tolerance to water quality degradation (Croft and Chow-Fraser, 2007, 2009).

Wetlands in our database span a wide range of water-quality conditions (Fig. 1). The majority of the sites having a WQI score of >1 ("very good" and "excellent" condition) were located in Georgian Bay and the North Channel, while degraded sites (WQI scores <0) were mainly located in the lower lakes (Lake Erie and Lake Ontario). Wetlands with a WQI score <-1 ("very degraded" and "highly degraded") were predominantly located in the western end of Lake Ontario.

Road density

We calculated road density (road length per unit area; RD) in 1-km and 2-km buffers around each sampling point in the database. These buffer distances were selected because it is uncommon for these species to travel more than 2 km over land (Rowe and Moll, 1991; Steen and Gibbs, 2004; Baldwin et al., 2004), and the use of multiple buffer widths allows us to compare the relative strength of relationships produced by the two sizes. Road network shapefiles for the U.S portion of the Great Lakes were obtained from ESRI Streetmap USA. In the Canadian portion of the Great Lakes, we used the most recent road network shapefiles available from the National Topographic Database (NTDB; Natural Resources Canada).

Study sites for sex ratio analysis

In 2007, we targeted a relatively undeveloped region (southeastern Georgian Bay in the Georgian Bay Township) and a heavily urbanized region (Hamilton and Burlington in western Lake Ontario; Fig. 1) to study how sex ratios of the painted turtle, a species that is abundant in both study areas, differ in areas of high and low road density. The 2006 human population density in Hamilton/Burlington was over 100-fold greater than that in southeastern Georgian Bay, and total road density was over 30-fold higher (Table 1). In both areas, non-limited access roads comprised the majority (>95%) of the road networks.

Statistical analysis

Data were analyzed in JMP 4.0 (SAS Institute Inc., Cary, NC, USA). We obtained sufficient catch of painted turtles, common snapping turtles, and common musk turtles to test the relationships of these species' abundances to habitat quality and road density. When multi-year data were available (was the case for 8 wetlands), average abundance was used for that site. Abundances were $\log_{10}$-transformed to approach normality and reduce heteroscedasticity in the regression analyses.

Table 1
Road density (limited access (LA) and non-limited access (NLA)) and population density estimates for the focus regions used in the sex ratio analysis. Road density was estimated from NTDB road network shapefiles, and population density estimates were obtained from 2006 Statistics Canada census data.

	SE Georgian Bay	W Lake Ontario
NLA road density (m/ha)	2.731	81.206
LA road density (m/ha)	0.018	3.307
Total road density (m/ha)	2.749	84.513
Population density (persons/km^2)	4.4[a]	505

[a] Estimate for the Georgian Bay township, doubles (at least) during summer months.

ANOVA was used to test for differences in wetland disturbance parameters as well as mean turtle abundance (all species combined) and species richness among the three lakes (Erie, Ontario, and Huron). Due to small sample sizes in Lakes Erie and Ontario, we grouped these two lakes under the term "lower lakes" for subsequent analyses; these lakes have similar climate and bedrock properties that are distinct from landscapes of Georgian Bay and the North Channel. Georgian Bay and the North Channel are also unique in that most human impact comes from recreational shoreline development, whereas urban and agricultural development are the predominant land uses in the lower lakes.

A logistic function was used to regress species presence against WQI, WMI and RD (at 1- and 2-km buffers). We then computed linear regressions of turtle abundance (for each species) on WQI, WMI and RD (1- and 2-km buffers) for all sites ($n=77$), and separately for Georgian Bay/North Channel ($n=54$) and the lower lakes (Erie and Ontario; $n=21$). We similarly regressed species richness and the proportion of the catch that was painted turtles against WQI, WMI, and RD. Where linear fits for the data were either poor or not statistically significant, we tested for significance of second-order polynomial regressions.

We used chi-square goodness-of-fit tests to determine whether the observed sex ratios of painted turtles differed significantly from a 1:1 ratio in Georgian Bay and in western Lake Ontario. Only adult turtles whose sex could be confidently determined were used in the sex-ratio comparison. Data from individuals trapped in fyke nets set for synoptic surveys in the two regions in 2007 were included to increase the sample size.

Results

Road density and wetland quality

WQI and WMI index scores were highly correlated ($r=0.88$, $p<0.001$) across all sites. Road density was also highly negatively correlated with both the WQI ($r=-0.76$, $p<0.001$ for 1-km buffer and $r=-0.74$, $p<0.001$ for 2-km buffer) and the WMI ($r=-0.71$, $p<0.001$ for 1-km buffer and $r=-0.70$, $p<0.001$ for 2-km buffer). RD was significantly higher around Lake Ontario marshes than it was around Lake Huron and Lake Erie marshes (Table 2). In the case of wetland quality, however, index scores of Lake Erie marshes were more similar to those of Lake Ontario marshes, and both of these lakes had marshes with significantly lower index scores than Lake Huron.

Species distributions

We captured 709 turtles belonging to five species from 77 wetlands during the synoptic surveys (Table 3). This included 419 painted turtles, 227 common musk turtles, 38 common snapping turtles, 15 northern map turtles (*Graptemys geographica*), and 10 Blanding's turtles. All five of these species occurred in both Lake Erie and Lake Huron (including Georgian Bay and the North Channel), while only painted turtles, common snapping turtles and Blanding's turtles were recorded in Lake Ontario wetlands during these surveys (Table 4). Mean turtle abundance and species richness obtained at wetlands were not statistically different for the different lakes (ANOVA; $p=0.449$ and $p=0.127$, respectively; Table 4). In surveys of the focus regions in 2007, we captured an additional 179 individuals, including 137 painted turtles, 19 common musk turtles, 6 common snapping turtles, 15 northern map turtles, 1 Blanding's

Table 2
Summary of wetland conditions and road density in surrounding 1- and 2-km buffers for the three lakes. Means (and ranges) are provided. ANOVA was used to determine significant differences among lakes and the Tukey–Kramer test was used to determine significant differences between pairs of means. Means sharing the same superscript letter are statistically homogeneous.

Lake	Wetlands	WQI	WMI	RD (m/ha; 1 km buffer)	RD (m/ha; 2 km buffer)
Ontario	16	−0.82 ^{A} (−2.31 to 1.28)	1.95 ^{A} (1.00 to 3.08)	40.73 ^{A} (7.16 to 102.29)	41.26 ^{A} (4.87 to 116.38)
Erie	5	−0.36 ^{A} (−2.42 to 0.70)	2.06 ^{A} (1.00 to 2.52)	12.96 ^{B} (0.00 to 41.63)	12.90 ^{B} (0.00 to 28.32)
Huron[a]	56	1.37 ^{B} (−0.46 to 2.28)	3.49 ^{B} (2.45 to 4.10)	4.83 ^{B} (0.00 to 40.27)	4.71 ^{B} (0.00 to 35.84)

[a] Includes the main basin and Georgian Bay and the North Channel.

Table 3
Summary of turtle captures by species during basin-wide synoptic surveys (77 wetlands) between 2001 and 2007, including the number of sites they occurred at, the total catch across all sites, and the range (and mean) of abundances (AB) obtained at a single site. Total catch of additional turtles obtained during surveys of the focus regions (8 sites in western Lake Ontario (LO), 11 in southeastern Georgian Bay (GB)) in 2007 are also given.

Common name	Species	Synoptic surveys			Focus region surveys	
		Total sites	Total catch	Range (and mean) AB	Total catch GB	Total catch ON
Painted	*Chrysemys picta*	64	419	0–35 (5.44)	47	90
Common musk	*Sternotherus odoratus*	37	227	0–25 (2.95)	19	0
Common snapping	*Chelydra serpentine*	17	38	0–7 (0.49)	4	2
Northern map	*Graptemys geographica*	7	15	0–5 (0.19)	9	6
Blanding's	*Emydoidea blandingii*	6	10	0–5 (0.13)	1	0
Red-eared slider	*Trachemys scripta elegans*	0	0	–	0	1
Total			709		80	99

turtle and 1 red-eared slider (*Trachemys scripta elegans*; exotic; Table 3). Fig. 2 shows the locations where each species was trapped.

Relating species abundances to wetland quality and road density

The painted turtle was the most abundant species both in terms of the number of individuals caught and the number of sites at which it occurred (Table 3). Painted turtles occupied both high-quality and poor-quality wetlands, but the probability of presence decreased with increasing WQI (logistic regression; $\chi^2 = 15.21$, $p<0.001$) and WMI ($\chi^2 = 18.01$, <0.001) scores. Probability of presence also increased with increasing RD (1-km buffer $\chi^2 = 20.02$, $p<0.001$; 2-km buffer $\chi^2 = 19.95$, $p<0.001$). Painted turtle abundance had negative linear relationships with WQI and WMI scores, and positive linear relationships with RD when all sites were considered; however, second-order polynomial fits were stronger than the linear fits in all cases, particularly for the relationships with RD at both buffer widths (Table 5), where abundance was highest in wetlands surrounded by intermediate to high RD but decreased in sites surrounded by very high RD. Within the high-quality wetlands of Georgian Bay/North Channel, painted turtle abundance showed negative linear relationships with indices of wetland quality (highest abundances in wetlands showing more degradation) and positive linear relationships with RD, but abundance was not significantly related to disturbance measures in the lower lakes.

Table 4
Summary of means (and ranges) of total turtle abundance and species richness for wetlands of each lake. ANOVA did not reveal significant differences among lakes for either parameter. The species found in each lake are also given.

Lake	Abundance[a]	Species richness	Species present (ranked by occurrence)
Ontario	11.8 (1–35)	1.4 (1–2)	Painted, snapping, Blanding's, map[b], red-eared slider[b]
Erie	8.6 (1–15)	2.2 (1–3)	Painted, snapping, Blanding's, map, musk
Huron	8.5 (1–30)	1.8 (1–4)	Painted, musk, snapping, map, Blanding's

[a] Abundances of all species combined, obtained during a single trap night per wetland site.
[b] Not recorded in the synoptic database, but trapped during sex ratio surveys.

The common musk turtle was the second most abundant species recorded in our study (Table 3), but was found exclusively in Georgian Bay and eastern North Channel, with the exception of one marsh on Lake Erie (located in Presque Isle State Park). Within Georgian Bay and the North Channel, some marshes contained very high abundances of this species (up to 25 individuals obtained during a single trap night); however, abundance showed no relationship with either the WQI or the WMI, nor was it significantly related to RD (Table 5).

The common snapping turtle was the third most abundant species in the synoptic database (Table 3). Most sites with high abundances (up to 7 individuals obtained during a single trap night) of common snapping turtles had intermediate values with respect to wetland quality and RD. At the largest scale (all sites), second-order polynomial fits best explained the relationships between common snapping turtle abundance and the WQI, WMI, and RD, but was only significant for the WQI (Table 5). Within Georgian Bay/North Channel, this species also showed a significant second-order polynomial relationship with both the WQI and RD at 1-km. Within the lower lakes, snapping turtles were not found in the most degraded wetlands, and abundance showed a significant positive linear relationship with wetland quality (WQI and WMI).

The other two species in the synoptic database (the northern map turtle and Blanding's turtle) were rarely caught during the 7 years of sampling (Table 3), and catch was insufficient to determine the relationship between species abundances and disturbance.

Relating species richness and proportion painted to wetland quality and road density

Across all sites, turtle species richness showed a significant second-order polynomial relationship with indices of wetland quality (WQI and WMI; Table 6). Species richness tended to be highest in wetlands of "good" quality (WQI between 0 and +1; WMI between 2.51 and 3.00). In Georgian Bay and the North Channel, species richness was negatively linearly related to indices of wetland quality and positively related to RD, while in the lower lakes, species richness was positively linearly related to wetland quality. Across all sites, the proportion of catch that was painted turtles was negatively linearly related to wetland quality and positively linearly related to RD; the relationships to WQI and WMI were stronger than the relationships to RD in surrounding 1- and 2-km buffers.

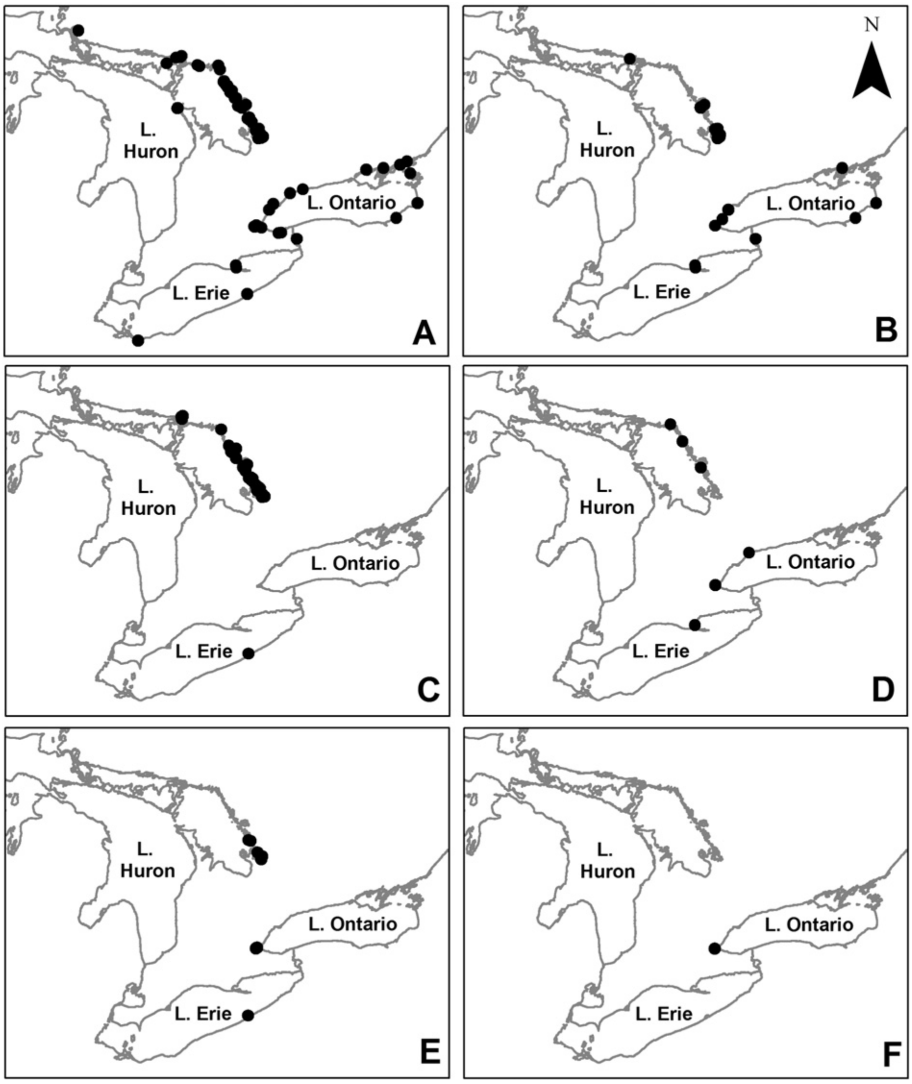

Fig. 2. Distribution of the painted turtle (A), common snapping turtle (B), common musk turtle (C), Blanding's turtle (D), northern map turtle (E), and red-eared slider (F). Sites include captures from the synoptic database (2001–2007) and the sex-ratio survey database (2007).

Sex ratios in focus regions

Of all captures made in the focus regions in 2007, 87 of the painted turtles in Lake Ontario and 57 of the painted turtles in Georgian Bay were sexually mature. Painted turtles in western Lake Ontario had a significantly male-biased sex ratio (3.1:1; $\chi^2 = 24.44$, $p < 0.001$), while in Georgian Bay the sex ratio (1.3:1) did not differ significantly from 1:1 ($\chi^2 = 0.86$, $p = 0.353$; Fig. 3).

Discussion

Turtle species abundances and disturbance

The painted turtle

Our results indicate that painted turtles can reach high abundances in degraded wetlands of human-altered landscapes. This may be the result of a combination of factors. The increase in nesting site

Table 5
Relationships of turtle species abundances to WQI and WMI scores and road density (RD; calculated in 1- and 2-km buffers) for all sites, and for Georgian Bay/North Channel (GBNC) and the Lower Lakes (LL) separately. Direction of the relationship is indicated in parentheses in front of the r^2. When second-order polynomial relationships were stronger than the linear fit, the associated r^2 values are indicated after the linear fit, in parentheses.

Region	Species	WQI	WMI	RD (1 km)	RD (2 km)
Overall $n = 77$	Painted	(−) 0.170*** (0.235****)	(−) 0.171*** (0.267****)	(+) 0.086** (0.270****)	(+) 0.089** (0.280****)
	Common musk	–	–	–	–
	Common snapping	N.S. (0.148**)	N.S.	N.S.	N.S.
GBNC $n = 54$	Painted	(−) 0.226***	(−) 0.224***	(+) 0.229***	(+) 0.203***
	Common musk	N.S.	N.S.	N.S.	N.S.
	Common snapping	N.S. (0.144*)	N.S.	N.S. (0.140*)	N.S.
LL $n = 21$	Painted	N.S.	N.S.	N.S.	N.S.
	Common musk	–	–	–	–
	Common snapping	(+) 0.229*	(+) 0.323**	N.S.	N.S.

N.S. = not significant, $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{****}p < 0.0001$.

Table 6

Relationships of turtle species richness and proportion painted to WQI and WMI scores and road density (RD; calculated in 1- and 2-km buffers) for all sites, and for Georgian Bay/North Channel (GBNC) and the Lower Lakes (LL) separately. Direction of the relationship is indicated in parentheses in front of the r^2. When second-order polynomial relationships were stronger than the linear fit, the associated r^2 values are indicated after the linear fit, in parentheses.

Region	Species	WQI	WMI	RD (1 km)	RD (2 km)
Overall $n=77$	Species richness	N.S. (0.123**)	N.S. (0.095*)	N.S.	N.S.
	Proportion painted	(−) 0.163***	(−) 0.199****	(+) 0.126**	(+) 0.134***
GBNC $n=54$	Species richness	(−) 0.077*	(−) 0.114*	(+) 0.081*	(+) 0.105*
	Proportion painted	N.S.	N.S.	N.S.	N.S.
LL $n=21$	Species richness	(+) 0.317**	(+) 0.270*	N.S.	N.S.
	Proportion painted	N.S.	N.S.	N.S.	N.S.

N.S. = not significant, *$p<0.05$, **$p<0.01$, ***$p<0.001$, ****$p<0.0001$.

availability (sites with an open canopy and no overstorey vegetation) associated with urban and agricultural development is believed to benefit this species (Baldwin et al., 2004; Marchand and Litvaitis, 2004a). Wetlands in human-altered landscapes also tend to exist as isolated remnants, and low emigration rates may contribute to high abundances (Galat et al., 1998; Rizkalla and Swihart, 2006). Finally, increased food availability (such as chironomid larvae and pupae) in nutrient-rich wetlands can contribute to increased growth rates, reduced time to maturity and increased fecundity (Knight and Gibbons, 1968; Lindeman, 1996).

The inverse relationship between painted turtle abundance and wetland quality and positive relationship between abundance and road density were highly evident in Georgian Bay and the North Channel. While these linear relationships were also significant across all sites in the database, second-order polynomial fits were stronger, and in the lower lakes, where the majority of wetlands are already considered degraded to some extent, these relationships were no longer observed. This may in part reflect different effects of agricultural and urban development on turtle survival and recruitment, since both of these can lower WQI and WMI scores of downstream wetlands. High turtle mortality on roads in areas with very high road densities (e.g. Gibbs and Shriver, 2002; Beaudry et al., 2008) may explain why, across all sites, the polynomial fits between painted turtle abundance and road density were strongest.

The common snapping turtle

The common snapping turtle is a species of special concern in Canada (COSEWIC, 2009). We found it to be most abundant in wetlands with intermediate water quality, suggesting that this species may benefit from some landscape alteration and moderate wetland degradation, but may be negatively impacted by extensive alteration of habitat. Other studies have observed that snapping turtles thrive in eutrophic wetlands because of increased food availability that allows for more rapid growth and a higher reproductive output (Galbraith et al., 1988; Brown et al., 1994). In our study, we had a low catch of snapping turtles in the most degraded wetlands. Within the lower lakes (Lake Erie and Lake Ontario), snapping turtle abundance was positively linearly related to wetland quality. This is in spite of potentially higher growth rates and reproduction in productive, degraded wetlands, and may be the result of high mortality from road traffic or predation surrounding these highly urbanized or agriculturally-impacted sites (Congdon et al., 1994; Oehler and Litvaitis, 1996; Marchand and Litvaitis, 2004b; Steen and Gibbs, 2004). It is also likely that since the funnel openings of our fyke nets were small (rarely did we catch adult snapping turtles with carapace length >250 mm), we may have underestimated the presence and abundance of this species at the highly degraded sites, where populations could be dominated by larger individuals due to rapid growth rates or low recruitment. Using baited hoop nets with larger funnel openings is generally the most efficient method of detecting this species (e.g. Brown et al., 1994; Browne and Hecnar, 2007).

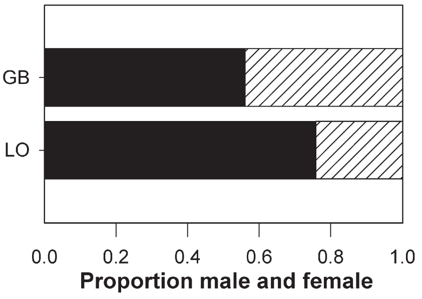

Fig. 3. Proportion of adult painted turtles that were male (solid) and female (diagonals) trapped in western Lake Ontario (LO; $n=87$) and southeastern Georgian Bay (GB; $n=57$) in 2007.

The common musk turtle

The common musk turtle, a federally threatened species (COSEWIC, 2009), was caught almost exclusively in wetlands of eastern Georgian Bay and the North Channel; within this region, we detected no significant relationship between wetland condition and musk turtle abundance. The common musk turtle relies on wetland vegetation for shelter, foraging and basking activities (Ernst, 1986; Ernst et al., 1994; Edmonds, 2002; Ford and Moll, 2004), with submergent vegetation being a particularly important habitat component (Ernst, 1986; Edmonds, 2002). The high-quality wetlands in Georgian Bay provide favourable habitat for this species because they have low nutrients and water turbidity that allow for abundant growth of submersed aquatic vegetation. In comparison, degraded wetlands of the lower lakes tend to have high water turbidity that prevents growth of submerged species (Lougheed et al., 2001). The absence of the common musk turtle in many lower lakes marshes could therefore be partially a byproduct of the impact of human-induced impairment of water quality on the macrophyte community.

Due to documented historical sightings of common musk turtles along the lower Great Lakes shorelines, including much of Lake Erie and Lake Ontario (Lamond, 1994; Oldham and Weller, 2000), we do not think this species is naturally more prevalent in northern latitudes or Precambrian Shield landscapes. We also trapped this species in moderate abundance (5 individuals trapped over one trap-night) at a site in southern Lake Erie with good water quality (Presque Isle State Park), and it is the fifth most common species trapped at Point Pelee National Park in northern Lake Erie, where some habitat protection exists (Browne and Hecnar, 2007).

The northern map turtle and Blanding's turtle

The northern map (special concern; COSEWIC, 2009) and Blanding's (threatened (Great Lakes/St. Lawrence population); COSEWIC, 2009) turtles were relatively rare in the synoptic database. We noted that on several occasions, northern map turtles were observed basking in a wetland but were not caught in our traps, suggesting that fyke nets may not have been an effective means to sample this species. This species is generally best sampled using basking traps (Browne and Hecnar, 2005, 2007). Very little is known about the status of populations of the northern map turtle (Roche, 2002), and although we found them to occur in similar abundances in both degraded marshes of western Lake Ontario as well as good quality wetlands of southeastern Georgian Bay, much more research is required to determine the tolerance of this species to habitat conditions. The Blanding's turtle was also found in both high-quality and degraded wetlands, and in some areas this species is recognized as an indicator of highly productive, nutrient-rich waters (Herman et al., 1993). Although it is thought to be in decline in the Great Lakes, we cannot draw any conclusions regarding the sensitivity of this species to habitat alteration because too few individuals were caught during our surveys.

Proportion of painted turtles and species richness

In degraded wetlands, the catch consisted almost entirely of a single species—the painted turtle; this reflects the relatively high tolerance of this species to human-altered habitats. Consistent with the intermediate disturbance hypothesis (Connell, 1978), species richness increased with minor disturbance, but decreased in severely degraded wetlands, with the peak in richness occurring in sites of “good” quality. Wetlands of intermediate quality in areas of moderate human disturbance are capable of supporting species that benefit from disturbance (such as the painted turtle) as well as species that are sensitive to disturbance (such as the common musk turtle), whereas a shift in wetland quality in either direction appears to result in conditions that are unfavourable for one or more species.

Potential use of freshwater turtles as ecological indicators

Wetland condition and road density explained a significant amount of variation in abundances of some species, although a considerably large amount of variation remained unexplained. Many factors can affect turtle abundance, independent of wetland condition and human disturbance, and this may limit our ability to use abundances of turtle species as reliable indicators of wetland health. For example, it has been found that the common musk turtle and the painted turtle occur in higher abundances in wetlands with a high percentage of organic matter in the substrate (DeCatanzaro and Chow-Fraser unpub. data). Furthermore, wetland condition (measured using the WQI or WMI) is affected similarly by agricultural and urban development (Chow-Fraser, 2006; Croft and Chow-Fraser, 2007), and since many aquatic and semi-aquatic turtles spend a considerable portion of their annual activity cycle on land, whether the landscape development is predominantly urban or agricultural can potentially impact species abundances. For instance, it is likely that adult turtles in urban and suburban areas with high road densities will suffer higher land-based mortality than those in agricultural settings, particularly if more road crossings are necessary to reach suitable nesting habitat (see Eigenbrod et al., 2008).

Another impediment to using turtle species assemblages as indicators of wetland health stems from the long lifespan of turtles (anywhere from 15–100+ years). Populations of turtles are unable to respond to environmental changes as readily as short-lived, rapidly reproducing organisms like zooplankton and many amphibians (Klemens, 2000). Wetlands can undergo relatively rapid changes in condition (over the course of a decade or less) as a result of restoration efforts or landuse development projects, while it may take several decades for turtle assemblages to respond. In particular, the continued presence of adults can make it difficult to identify populations that are threatened by low recruitment in the absence of a thorough study of population structure (Browne and Hecnar, 2007). In addition, once a species has been extirpated from wetlands in an area, remediation of one or a few wetlands is unlikely to result in re-colonization of the wetland by this species if it lacks a healthy neighbouring source population.

Despite these limitations, turtle assemblages may offer some insight into ecosystem integrity. We suspect that relating species abundances to disturbance gradients based on different landuse types and habitat fragmentation could produce stronger empirical relationships, and this needs to be explored in future research. Using probability of occurrence of a species may also be useful. Price et al. (2007) and Howe et al. (2007) have suggested using presence of disturbance-sensitive species to calculate multi-species indicators of ecological condition. Using this approach to examine the probability of occurrence for species like the painted turtle, which is most commonly encountered in degraded wetlands, for wetlands of different condition or disturbance levels may provide some utility for evaluating wetland health.

Sex ratios

The high male-to-female sex ratio that we observed in western Lake Ontario is consistent with data collected in other urban regions, and which has often been attributed to high female mortality on roads (e.g. Steen and Gibbs, 2004; Aresco, 2005; Steen et al., 2006). This phenomenon is known to occur in many aquatic and semi-aquatic turtle species, since females of most species spend more time on land than do males, and are often attracted to roadsides to nest (Aresco, 2005; Steen et al., 2006). Browne and Hecnar (2007) observed an increase in the male: female sex ratio in painted turtles over the past 30 years at Point Pelee National Park, Lake Erie, and suspected that road mortality was a contributing factor. Since we observed only a small (non-significant) male bias in the sex ratio of painted turtles in southeastern Georgian Bay, where road networks are sparse, we suggest that a natural tendency for a more even sex ratio exists for this species.

We recognize that sampling biases can also contribute to a perceived skew in adult sex ratios. While different sampling methods can more efficiently trap male or female turtles (e.g. Ream and Ream, 1966; Browne and Hecnar, 2007), we used the same method in both regions, so any bias due to trapping method was consistent. Since our study coincided with the nesting season, we have to assume that part of the male-biased catch may be due to the movement of females on land. Although we sampled both areas over the same time period, slight variations in the timing of nesting migrations due to differences in latitude and climate of the two areas could have affected our results. This may be a particular concern because we sampled only two areas of the Great Lakes, and they had considerable latitudinal separation. Environmental factors that influence nest temperature can also influence the sex ratio of hatchlings, since warmer nest temperatures tend to produce more females (Ewert and Nelson, 1991). We would have expected, however, that the reduced forest vegetation cover (Marchand and Litvaitis, 2004a) and warmer weather in the Lake Ontario region would have reduced the ratio of males to females in this area relative to Georgian Bay. Future work should focus on gathering sex ratio data across a broader range of road density conditions in the Great Lakes region to confirm the role of road mortality as a cause of male-biased sex ratios.

Implications for conservation

Our study is the first to establish clear relationships between turtle species abundances and human disturbance across multiple wetlands in the Great Lakes region. Many turtle species are federally and provincially at risk, and understanding their response to habitat disturbance will be crucial for guiding conservation efforts. Our data indicate that painted turtles are the most tolerant of wetland degradation and a high proportion of painted turtles in a wetland turtle assemblage may result from degraded conditions produced by extensive watershed land use alteration. Our results provide evidence, however, that this species may begin to decline in abundance in overly developed areas with a very high surrounding road density. If the perceived male bias in the sex ratio of painted turtles in western Lake Ontario is indeed accurate, high rates of adult female mortality in urbanized areas may contribute to this effect. Our data also suggest that the common snapping turtle does poorly under heavily disturbed conditions in the lower lakes; this contrasts some studies which have found this species to be abundant in highly degraded habitats (Galbraith et al., 1988; Brown et al., 1994). Finally, we found that the common musk turtle thrives in the good-quality, relatively undisturbed wetlands found in Georgian Bay and the North Channel, but this species was not encountered in many wetlands in the lower lakes. Protection of these high-quality Georgian Bay marshes will help ensure persistence of this species.

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