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Relationships between muskrat density and avian and anuran richness in Great Lakes coastal wetlands

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Abstract

Wetlands in southern Ontario are at risk of degradation and alteration due to human activities. This is a concern because wetlands provide essential habitat for species from a range of taxa, such as birds and anurans (frogs and toads). One wetland-dwelling species whose decline may be linked to loss of wetland wildlife habitat is the muskrat (*Ondatra zibethicus*). The decline of muskrats may also be linked to declines of other species because muskrats engage in activities that could support taxa such as birds and anurans by increasing habitat heterogeneity. We investigated whether bird and anuran species richness is related to muskrat density or if it is better predicted by land cover variables that describe the wetland and surrounding area at 30 coastal wetlands on Lake Ontario. We estimated bird and anuran species richness using data from the Great Lakes Marsh Monitoring Program and the Great Lakes Coastal Wetland Monitoring Program, and muskrat density based on muskrat house counts. Our results suggest that muskrat activity did not predict richness of anurans or birds overall; however, it did predict richness for the subset of birds that nest in emergent aquatic vegetation. Our results indicate that muskrat abundance in emergent marshes may increase habitat quality for birds that nest in emergent vegetation but may not have a measurable effect on anuran diversity in these same wetlands.

Introduction

Wetlands play a critical role in climate change mitigation (Russi et al. 2013), hydrological regulation (Finlayson et al. 2005), and biodiversity support (Mitra et al. 2003). Despite the various functions that wetlands serve, the past 200 years have seen a 60% reduction in wetlands in southern Ontario, with some areas experiencing more than 80% wetland loss (Snell 1987; Penfound and Vaz 2022). Wetland loss and degradation is primarily attributed to human activities, such as filling, dredging, agricultural runoff, and altered hydrological regimes (Roman et al. 1984; Crowder and Bristow 1988; Herdendorf 1992; Mitsch and Gosselink 2000; Timmermans et al. 2008). The loss of wetlands has affected a wide diversity of taxa, as wetlands provide habitat for many species, including waterfowl, anurans, and muskrats (Herdendorf 1992; Prince et al. 1992; Mitra et al. 2003; Gibbs 1995).

Muskrats (*Ondatra zibethicus*) are thought to be important in North American wetlands. Considered by many to be ecosystem engineers (Higgins and Mitsch 2001; Mott et al. 2013; Kua et al. 2020), muskrats engage in activities that alter the structure of wetlands, such as building houses, excavating bank dens, and clearing emergent vegetation (Boutin and Birkenholz 1987; Connors et al. 2000; Kua et al. 2020; Bomske and Ahlers 2021). These activities have been associated with many benefits to wetland animal habitats. For example, muskrats have been linked to increased habitat heterogeneity (Kaminski and Prince 1981; Kua et al. 2020) and interspersion of open water and emergent vegetation (Weller and Spatcher 1965; Kaminski and Prince 1981; Boutin and Birkenholz 1987). Muskrat activity has also been linked to higher species richness of plants (Nyman et al. 1993; Kua et al. 2020), species richness and densities of waterfowl (Kaminski and Prince 1981) and marsh birds (Weller and Spatcher 1965), and abundance of fish (Nummi et al. 2006). Additionally, muskrat houses support aquatic macroinvertebrates, particularly chironomid midges (de Szalay and Cassidy 2001). Numerous species have also been observed directly using muskrat dwellings for shelter, nesting, and loafing or basking (Kiviat 1978). Finally, muskrats have been shown to increase nitrification and soil aeration in wetlands (Connors et al. 2000). Therefore, a decline in muskrat populations may lead to reduced wetland function and overall habitat quality, which may have negative impacts on other wetland species.

Despite occupying a large range across North America, muskrats have declined in many locations (Benoit and Askins 1999; Roberts and Crimmins 2010; Brietzke 2015; Ahlers and Heske 2017; Ward and Gorelick 2018; Gregory et al. 2019; Sadowski and Bowman 2021). The cause of these widespread declines is unknown (Greenhorn et al. 2017; Sadowski and Bowman, 2021); however, muskrat populations have been strongly linked to water level management (Toner et al. 2010; Greenhorn et al. 2017; Ward and Gorelick 2018). Sudden and long-term fluctuations in water levels leading to floods or low-water conditions both have the potential to reduce muskrat populations (Errington 1939; Phaneuf 1979; Toner et al. 2010; Ward and Gorelick 2018). In many places, water levels are stabilized to facilitate shoreline development, power generation, and transportation (Clamen and Macfarlane 2020). This reduces natural variability of water levels in wetlands, which has been shown to promote the growth of invasive plants, especially *Typha* x *glauca*, a hybrid between the native Broad-leaved Cattail (*Typha latifolia*) and the European Narrow-leaved Cattail (*Typha angustifolia*) (Wilcox et al. 1984; Shay et al. 1999; Boers et al. 2007; Wilcox et al. 2008; Boers and Zedler 2008). Moreover, *Typha* x *glauca* invasions are associated with decreases in plant diversity (Shay et al. 1999; Tuchman et al. 2009), which reduces overall habitat quality for groups such as marsh birds and aquatic macroinvertebrates (Schummer et al. 2012). For example, the decades-long stabilization of Lake Ontario water levels has been associated with a large-scale *Typha* invasion in coastal wetlands, which has reduced vegetation diversity, structural complexity, and plant species richness (Mitchell et al. 2011; IJC 2016). Furthermore, *Typha* invasions are linked to a reduction in the interspersion of open water and emergent vegetation (Harris and Marshall 1963; Wilcox et al. 2008; Schummer et al. 2012; Markle et al. 2018; Smith et al. 2021). This loss of interspersion may have negative consequences for muskrats, which thrive in wetlands with high interspersion (Proulx and Gilbert 1983; Boutin and Birkenholz 1987). An autumn drawdown is another aspect of water-level management that negatively affects muskrat abundance, as it results in house freeze-outs over winter (Bellrose 1950). Additionally, sustained reductions in water levels may also lead to a loss of suitable aquatic habitat, thereby reducing muskrat populations (Ward and Gorelick 2018). Regardless of the cause, muskrat declines may have wider impacts on wetland biodiversity. Through their many wetland-altering activities, muskrats could increase and maintain the abundance and reproductive success of other wetland taxa, such as birds and anurans, which thrive in the wetland conditions created by muskrats (e.g., Rehm and Baldassare 2007).

We evaluated the relationship between muskrat density and other components of wetland biodiversity to determine whether the loss and decline of muskrats might have broader biodiversity implications. Using data from coastal wetlands of Lake Ontario, Canada, we investigated whether bird and anuran species richness is related to muskrat density or whether species richness is better predicted by other land cover variables such as wetland size, wetland type, and anthropogenic development (e.g., Brown and Dinsmore 1986; Benoit and Askins 1999; Vierling 1999; Vierling 2000; Guadagnin and Maltchik 2007; Tozer et al. 2010). We hypothesized that muskrats positively influence bird and anuran species richness by maintaining favourable levels of open water-vegetation interspersion and preferred vegetation structure and diversity. We predicted that models that include muskrat density as a predictor variable will perform better than models that only include land cover variables as predictors of species richness.

Methods

Estimating Muskrat Density

We used muskrat house counts from Greenhorn et al. (2017) as a proxy for muskrat activity in Lake Ontario coastal wetlands. Greenhorn et al. (2017) surveyed 43 coastal wetlands along the north shore of Lake Ontario for the presence of muskrat houses and feeders (smaller structures used for shelter during winter feeding) from January to March 2014 (Greenhorn et al. 2017). The surveyed marshes were located between Hay Bay near Napanee, Ontario in the east (44° 9' 55" N, 76° 54'18" W) and the Rouge River in Scarborough, Ontario (43° 47'50" N, 79° 7'35" W) in the west (Greenhorn et al. 2017) (Fig. 1).

Within each wetland, 10 1-ha grid cells of muskrat habitat (estimated from available imagery) were randomly selected to be surveyed; cells were not considered to be habitat if greater than 80% of the cell was open water or land, or if the dominant vegetation type was not cattail (Greenhorn et al. 2017). Muskrat houses suspected to be active were counted via ground surveys from January to March 2014. Surveyors distinguished houses from other muskrat-built structures by using a minimum height threshold of 40 cm above the ice, suggested by Dozier (1948). If a structure was greater than 40 cm but the structure type was unknown (e.g., houses versus feeders), surveyors measured the distance to the nearest house using ArcMap (ESRI 2011); if this distance was more than 36 m, the structure was classified as a house. Otherwise, it was classified as an unknown structure. Only structures confidently assigned as houses were selected for muskrat density estimates as multiple secondary structures (such as winter-feeding sites) are usually associated with a single house (for full methodology see Greenhorn et al. 2017).

Estimating Bird and Anuran Richness

We estimated bird and anuran species richness using data from the Great Lakes Coastal Wetland Monitoring Program (CWMP) delivered by Central Michigan University and dozens of partner organizations in collaboration with the United States Environmental Protection Agency (greatlakeswetlands.org) and the Great Lakes Marsh Monitoring Program (GLMMP) delivered by Birds Canada (birdscanada.org/gl_mmp). These data were collected by trained participants following the CWMP or GLMMP protocols. We focused on CWMP and GLMMP data collected in 2013 because the muskrat houses counted in winter 2014 were reflective of muskrat activity during the summer of 2013.

Both the CWMP and GLMMP used nearly identical sampling protocols for anurans (Timmermans et al. 2008), in which participants visited survey stations to estimate relative abundance of calling anurans. For both sampling protocols, stations were surveyed three times throughout the spring and early summer to ensure the breeding season of all anuran species were sampled. Surveys occurred at least 15 days apart and were determined by nighttime air temperature (above 5°C, 10°C, and 17°C for each consecutive survey). Surveys occurred at night between 30 minutes after sunrise to midnight, and only under ideal conditions (wind at a Beaufort scale of 0–3 or 0–19 km/hr and no persistent or heavy precipitation). During each survey, stations were sampled by estimating the abundance of each anuran species calling within a three-minute period. The CWMP used a circular sampling station area, whereas the GLMMP used a front-facing semicircular sampling station area (for full methodology see Bird Studies Canada 2009a, Bird Studies Canada 2009b, and Walpole et al. 2012).

Bird richness for both CWMP and GLMMP were also collected using nearly identical sampling protocols (Grabas et al. 2008). Two surveys were conducted per station per year between 20 May and either 5 July for GLMMP or 10 July for CWMP. Stations were monitored either in the morning or evening. Morning surveys were conducted between 30 minutes before sunrise and 10:00 a.m., and evening surveys were conducted between 4 hours before sunset and dark. Surveys were conducted by a single surveyor and lasted 15 minutes, with passive observations made in the first and last 5 minutes, and call playback for the middle 5 minutes. Surveys were only conducted in suitable conditions (wind at a Beaufort scale of 0–3 or 0–19 km/hr, no precipitation, good visibility; for full methodology see Bird Studies Canada 2009b).

We filtered the data to account for differences in sampling protocol between the CWMP and GLMMP. The GLMMP surveys used a forward-facing half-circle plot, whereas the CWMP used a full-circle plot that was parsed into front and back. Both the GLMMP and CWMP used plots with a radius of 100 m. For consistency, we filtered all survey data to use only the front (forward-facing) plots at each station. Additionally, we accounted for differences in the number of stations per wetland and the number of visits per station. Within our study wetlands, the number of anuran and bird sampling stations ranged from 1–18 and 1–16, respectively. Two visits were made to each bird station, but the number of visits was variable for anuran stations. Most anuran stations were visited three times, but 14% were visited twice and 11% were visited once. To account for these differences, we standardized the bird and anuran species richness values using a richness index. To find the species richness index for each wetland, we calculated the average richness per station (total bird or anuran richness divided by the number of visits) and then found the average across all stations within a wetland (total average bird or anuran richness across all stations divided by the number of stations).

Species Richness Modeling

We created linear models to evaluate the relationship between bird and anuran richness and our set of predictor variables using R Studio (R Core Team 2022). When evaluating bird richness, we assessed the relationship between species richness and our predictor variables for all avian species recorded, and for a subset of bird species representing those that nest in emergent vegetation (Cadman et al. 2007), which may therefore be more strongly influenced by muskrat activity within a wetland. Associations between pairs of variables were tested with Pearson correlation tests (continuous vs continuous).

During the 2014 muskrat surveys Lake Ontario water levels were regulated at the Moses Saunders Power Dam under International Joint Commission Plan 1958 (Clamen and MacFarlane 2020). Given this, and that Greenhorn et al. (2017) found a significant relationship between variables representing connectedness to Lake Ontario and muskrat density, we constructed models to specifically assess the relationship between bird and anuran species richness and either muskrat activity (house density or presence) or wetland connectedness (wetland type or openness to Lake Ontario), with wetland size and road cover as covariates (Table 1). Our data regarding muskrat activity, wetland connectedness, wetland area, and road cover are directly from Greenhorn et al. (2017).

Table 1
Variables tested in relation to wetland species richness for birds and anurans in 2013 among coastal wetlands in southern Ontario.

Variable	Description	Predicted Direction of Relationship
Muskrat Activity	1. *Density*: Muskrat (*Ondatra zibethicus*) house counts conducted on-site in winter 2013/2014 (houses/ha)	+
	2. *Presence*: Muskrat density reduced to presence/absence only (y/n)	+
Connectedness	1. *Openness*: Whether the wetland has a water connection to Lake Ontario, either directly or via tributaries or canals, and regardless of land barriers (y/n)	-
	2. *Wetland Type*: Wetland classification as assigned by Greenhorn et al (2017), in accordance with the Great Lakes Coastal Wetland Monitoring Program (Albert et al. 2003):	
	a) Open Coastal (OC): Wetland is directly adjacent to Lake Ontario, with no land barriers	-
	b) Drowned River Mouth (DRM): Wetland is located at a river mouth; may be partial barrier to Lake Ontario	-
	c) Barrier Beach (BB): Wetland is separated from Lake Ontario by a significant land barrier	+
Wetland Size	Area of wetland estimated from ArcGIS shapefile (ha)	+
Urbanization	*% Road*: Percentage of surrounding road cover within a 2km buffer (% road pixels)	-

Muskrat activity was first represented as muskrat density which was a continuous variable derived from muskrat house counts conducted in winter 2013/2014 by Greenhorn et al. (2017). House counts were converted to density values (number of houses/ha) prior to modeling. We also represented muskrat activity as a binary variable with muskrat houses having either been recorded in a wetland (1) or not (0), henceforth referred to as muskrat presence.

Connectedness was either represented as a binary variable, which we called openness, or as a categorical variable called wetland type (Table 1). For the binary variable openness, wetlands were classified as being either directly connected to Lake Ontario (1) or not (0). For the categorical variable, wetlands were classified as either open coastal (OC), drowned river mouth (DRM), or barrier beach (BB) (Greenhorn et al. 2017). Almost all OC and DRM wetlands were assigned an openness value of 1 as they were connected to the lake; however, there was variation in whether or not BB wetlands are connected to the lake via channels. Most, but not all, BB wetlands were not connected to the lake (Table 1).

Both wetland area and roads have previously been demonstrated to affect the abundance and reproductive success of wetland-breeding birds and anurans (e.g., Benoit and Askins 1999; Guadagnin and Maltchik 2007; Fahrig and Rytwinski 2009; Tozer et al. 2010; Rytwinski and Fahrig 2012; van der Hoek et al. 2019). Wetland area and surrounding road cover were calculated by Greenhorn et al. (2017). Wetland area was derived from delineated polygons (Albert et al. 2003) and road cover was estimated by counting the number of road pixels in a 2 km buffer around the wetland (aerial photographs taken by SOLRIS; Ontario Ministry of Natural Resources 2015). A 2-km buffer was chosen by Greenhorn et al. (2017) because road density within this buffer size has been shown to have the greatest effect on wetland species (Findlay and Houlahan 1997). Prior to modeling, wetland area (in ha) was log-transformed to account for the well-described relationship between species richness and area (Rosenzweig 1995), in which larger areas support larger numbers of species. This species-area relationship has been demonstrated in wetland birds (Cerda-Peña and Rau 2023) and amphibians (Parris 2006).

We constructed 4 models (one model each for muskrat density, muskrat presence, openness, and wetland type plus road and wetland area as covariates in each model; Table 1) for each species group (birds: all, anurans, birds: wetland nesters). Models were fit under a Gaussian distribution and for each we calculated Akaike's information criterion (AICc) to perform model selection and to calculate R^2 to evaluate model fit using the "AICcmodavg" package (Mazerolle 2023) for R Studio (R Core Team 2022).

Of the 42 wetlands taken from Greenhorn et al. (2017), 11 wetlands were removed from the dataset as they did not have corresponding anuran or bird data. Additionally, while Corner Marsh and Duffin's Creek were treated as independent wetlands by Greenhorn et al. (2017), we combined muskrat and landcover data to account for these wetlands not being treated independently in anuran species counts. Additionally, Hay Bay North and Hay Bay South had bird data, but no anuran data. As a result, we used 26 and 24 wetlands in our statistical analysis for bird and anuran richness, respectively (Fig. 1; Supplementary Table 1).

Results

Bird Species Richness

Eighty-three bird species were observed across our study wetlands (Fig. 2). When considering all bird species, the model with muskrat density was best supported (ΔAICc = 0; Table 2), while the muskrat presence model (ΔAICc = 0.28) and connectedness to Lake Ontario model (openness; ΔAICc = 1.32) were equivalent to the muskrat density model (ΔAICc < 2, Table 2; Burnham et al. 2011). None of these models had a good fit to the data ($R^2 \leq 0.06$). Muskrat density (Estimate (± SE) = 0.67 (± 0.52), $p = 0.21$), muskrat presence (0.98 (± 0.97), $p = 0.32$), openness (0.80 (± 1.13), $p = 0.49$), and wetland type (drowned river mouth: 0.72 (± 0.95), $p = 0.46$; open coastal: 1.57 (± 0.99), $p = 0.13$) did not appear to be associated with all bird species richness (all $p > 0.1$, Table 3). Across all bird species richness models, the area of the wetland (log-transformed) and density of surrounding road cover were also not significant (Table 3).

Table 2

Model comparisons for all linear models relating bird and anuran species richness to muskrat (*Ondatra zibethicus*) activity and connectedness to Lake Ontario in 2013, listed in decreasing order of support (most supported model bolded). Bird species richness is estimated for all bird species and for only the bird species that nest in emergent wetland vegetation. Muskrat activity is estimated as muskrat density (houses/ha) and density reduced to presence. Connectedness is estimated as whether the wetland is directly connected to the lake (openness) or wetland type (open coastal, drowned river mouth, and barrier beach; Table 1). Wetland area (ha) and percentage of road cover are covariates; R^2 is adjusted for degrees of freedom.

Species Richness	Model	K	AICc	ΔAICc	Log Likelihood	R^2	F_{DF}
Birds ~	**Muskrat Density + log(Area) + % Road**	**5**	**116.28**	**0**	**-51.64**	**0.06**	**$1.49_{3,22}$**
	Muskrat Presence + log(Area) + % Road	5	117.00	0.28	-52.00	0.03	$1.25_{3,22}$
	Openness + log(Area) + % Road	5	117.60	1.32	-52.30	0.01	$1.06_{3,22}$
	Wetland Type + log(Area) + % Road	6	118.61	2.33	-51.10	0.05	$1.34_{4,21}$
Emergent Vegetation Nesters ~	**Muskrat Density + log(Area) + % Road**	**5**	**63.78**	**0**	**-25.39**	**0.22**	**$3.37_{3,22}$**
	Muskrat Presence + log(Area) + % Road	5	66.76	2.98	-26.88	0.13	$2.22_{3,22}$
	Openness + log(Area) + % Road	5	69.53	5.75	-28.27	0.03	$1.25_{3,22}$
	Wetland Type + log(Area) + % Road	6	71.96	8.18	-27.77	0.02	$1.13_{4,21}$
Anurans ~	**Openness + log(Area) + % Road**	**5**	**42.90**	**0**	**-14.78**	**0.57**	**$11.04_{3,20}$**
	Wetland Type + log(Area) + % Road	6	43.67	0.76	-13.36	0.60	$9.45_{4,19}$
	Muskrat Presence + log(Area) + % Road	5	44.08	1.18	-15.38	0.55	$10.19_{3,20}$
	Muskrat Density + log(Area) + % Road	5	44.10	1.20	-15.39	0.54	$10.17_{3,20}$

Table 3

Variable estimates (± SE) for all linear models relating bird species richness to muskrat (*Ondatra zibethicus*) activity and connectedness to Lake Ontario in 2013. Bird species richness is estimated for all bird species and only bird species that nest in emergent wetland vegetation. Muskrat activity is estimated as muskrat density (houses/ha) and density reduced to presence. Connectedness is estimated as whether the wetland is directly connected to the lake (Openness) or wetland type (OC - open coastal; DRM - drowned river mouth; and barrier beach, included here as the reference variable; Table 1). Wetland area (ha) and percentage of road cover are considered as covariates. Significant variables are bolded.

		All Birds				**Emergent Vegetation Nesters**			
		Muskrat Activity		Connectedness		Muskrat Activity		Connectedness	
Variable		Density	Presence	Openness	Type	Density	Presence	Openness	Type
(Intercept)		2.86(± 1.85) p = 0.14	2.42(± 2.04) p = 0.25	2.85(± 1.97) p = 0.16	2.37(± 1.91) p = 0.23	**1.47(± 0.67) p = 0.04**	1.21(± 0.78) p = 0.13	**1.92(± 0.78) p = 0.02**	1.54(± 0.78) p = 0.06
Density (houses/ha)		0.67(± 0.52) p = 0.21				**0.46(± 0.19) p = 0.02**			
Presence/ Absence			0.98(± 0.97) p = 0.32				0.62(± 0.37) p = 0.11		
Openness				0.80(± 1.13) p = 0.49				-0.26(± 0.45) p = 0.57	
Wetland Type	DRM				0.72(± 0.95) p = 0.46				0.008(± 0.39) p = 0.98
	OC				1.57(± 0.99) p = 0.13				0.38(± 0.40) p = 0.35
log(Area)		0.32(± 0.30) p = 0.29	0.39(± 0.32) p = 0.24	0.21(± 0.31) p = 0.51	0.24(± 0.30) p = 0.43	**0.25(± 0.11) p = 0.03**	**0.29(± 0.12) p = 0.03**	0.23(± 0.12) p = 0.08	0.21(± 0.12) p = 0.10
% Road		0.14(± 0.09) p = 0.14	0.13(± 0.10) p = 0.22	0.16(± 0.10) p = 0.11	0.20(± 0.10) p = 0.07	0.006(± 0.03) p = 0.85	-0.004(± 0.04) p = 0.91	0.01(± 0.04) p = 0.72	0.03(± 0.04) p = 0.47

We identified 18 species in our dataset as emergent vegetation nesters (Fig. 2; Supplementary Table 2). When we included only these species in the models, we found that the muskrat density model was the only well-supported model (Table 2), with the species richness index for emergent vegetation nesters increasing with muskrat density (houses/ha; 0.46 (± 0.19), p = 0.02; Fig. 3). We also found that wetland area was the only other variable that had an effect on emergent vegetation nester richness when muskrats were considered as an independent variable, but this effect was lost when connectedness to Lake Ontario was considered instead (Table 3).

Anuran Species Richness

Nine species of anurans were observed across our study wetlands (Fig. 2). The model with openness was best supported, however, all models were equivalent (Table 2). Both covariates were associated with anuran richness. We found that the percentage of road cover around wetlands had a strong negative effect overall on anuran species richness (Adjusted R^2 = 0.49, $F_{1, 22}$ = 23.4, $p < 0.0001$; Fig. 3). Additionally, wetland area had a positive effect across some models (muskrat presence (0.18 (± 0.09), p = 0.05) and wetland type (0.18 (± 0.08), p = 0.03)), but this effect was lost when muskrat density (0.16 (± 0.08), p = 0.06) or openness (0.14 (± 0.08), p = 0.09) were considered (Table 4). Muskrat density (-0.07 (± 0.14), p = 0.63), muskrat presence (0.13 (± 0.25), p = 0.62), openness (0.32 (± 0.28), p = 0.27), and wetland type (drowned river mouth: 0.01 (± 0.23), p = 0.96; open coastal: 0.45 (± 0.25), p = 0.09) did not have a significant effect on anuran species richness (all p > 0.1, Table 4).

Table 4
Variable estimates (± SE) for all linear models relating anuran species richness to muskrat (*Ondatra zibethicus*) activity and connectedness to Lake Ontario in 2013. Muskrat activity is estimated as muskrat density (houses/ha) and density reduced to presence. Connectedness is estimated as whether the wetland is directly connected to the lake (Openness) or wetland type (OC - open coastal; DRM - drowned river mouth; and barrier beach, included here as a reference variable; Table 1). Wetland area (ha) and percentage of road cover are considered as covariates. Significant variables are bolded.

		Muskrat Activity		**Connectedness**	
Variable		Density (houses/ha)	Presence/ Absence	Openness	Wetland Type
(Intercept)		**1.76(± 0.49) p = 0.002**	**1.60(± 0.54) p = 0.007**	**1.54(± 0.50) p = 0.006**	**1.42(± 0.48) p = 0.008**
Density (houses/ha)		-0.07(± 0.14) *p* = 0.63			
Presence/ Absence			0.13(± 0.25) *p* = 0.62		
Openness				0.32(± 0.28) *p* = 0.27	
Wetland Type	DRM				0.01(± 0.23) *p* = 0.96
	OC				0.45(± 0.25) *p* = 0.09
Area (ha)		0.16(± 0.08) *p* = 0.06	**0.18(± 0.09) p = 0.05**	0.14(± 0.08) *p* = 0.09	**0.18(± 0.08) p = 0.03**
% Road		**-0.08(± 0.03) p = 0.003**	**-0.09(± 0.03) p = 0.003**	**-0.08(± 0.02) p = 0.003**	**-0.07(± 0.03) p = 0.01**

We did not detect any significant correlations between pairs of predictor variables (Supplementary Table 3).

Discussion

Our study examined relationships between bird and anuran species richness and muskrat activity. Overall, our results indicate that some species are more strongly affected by muskrat activity than others. We did not find support for our hypothesis that muskrat activity increases species richness in coastal wetlands for anuran or bird species overall. However, when investigating this relationship for emergent vegetation nesters, we did find support for our hypothesis in that wetlands with higher densities of muskrat houses also had higher richness of these emergent vegetation nesters.

One explanation for the relationship between muskrats and emergent vegetation nesters may be the changes in interspersion that occur as a result of muskrat activity. Interspersion is the distribution of emergent vegetation in relation to open water within a wetland (Schummer et al. 2012; Hohman et al. 2021) and can also be interpreted as the density of water-vegetation edge (Rehm and Baldassarre 2007). Muskrats influence interspersion by removing vegetation, which they use for food or as a material for their houses, as well as by creating travel routes through their home range (Weller and Spatcher 1965; Kaminski and Prince 1981; Boutin and Birkenholz 1987). Increasing interspersion produces patchiness among vegetation stands, the edges of which can be used by birds for nesting and feeding (Alisauskas and Arnold 1994; Bogner and Baldassarre 2002). Increases in interspersion are related to increases in the abundance and richness of marsh-obligate bird species (Hohman et al. 2021), particularly in wetlands dominated by cattail and *Phragmites* (Schummer et al. 2012). Another explanation for the positive relationship between muskrats and emergent vegetation nesters is that some of these species (e.g., Trumpeter Swan [*Cygnus buccinator*], Mute Swan [*Cygnus olor*], Canada Goose [*Branta canadensis*], and Black Tern [*Chlidonias niger*]) will nest directly on top of old muskrat houses (Kiviat 1978; personal observations by Sadowski, Melvin, and Ward.). As such, they are deriving a direct benefit from the presence of muskrats in the wetland.

For emergent vegetation nesters, wetland size was also important in predicting mean species richness, with higher richness indices in larger wetlands. Likewise, other studies have shown that wetland size can significantly influence marsh bird richness (Riffell et al. 2001) and avian productivity (Tozer et al. 2010; Tozer 2016). Large wetlands may be important for area-sensitive species that require large amounts of habitat to maintain populations. Four of the emergent vegetation nesters from our study are considered area-sensitive in Ontario (American Bittern [*Botaurus lentiginosus*], Least Bittern [*Ixobrychus exilis*], American Coot [*Fulica americana*], and Black Tern; OMNR 2000); and an additional four species may also be area-sensitive in coastal wetlands on Lake Huron (Red-winged Blackbird [*Agelaius phoeniceus*], Sedge Wren [*Cistothorus stellaris*], Sora [*Porzana carolina*], and Virginia Rail [*Rallus limicola*]; Riffell et al. 2001). Interestingly, we only observed this relationship when accounting for muskrat activity within the wetland. When accounting for wetland connectedness rather than muskrat activity, wetland area was no longer significant in predicting the species richness of emergent vegetation nesters, indicating that the presence of muskrats within the ecosystem is important, regardless of the type of wetland waterbody.

Wetland area was also a significant predictor of anuran species richness, with larger wetlands having higher anuran richness index values. However, we only observed this relationship when also accounting for muskrat presence and wetland type in our models indicating that, regardless of wetland size, the presence of muskrats and the type of connection between the wetland and Lake Ontario are important in defining anuran habitat.

For anurans, the proportion of road cover within 2 km was a significant predictor of species richness in all of our models. Our findings are consistent with previous studies suggesting that anurans are sensitive to wetland size and to road density in the surrounding landscape (Findlay and Houlahan 1997; Findlay and Bourdages 2001; Eigenbrod et al. 2008). This is especially true for areas with high traffic density and large populations of anurans, where there are significant declines in amphibians (Fahrig et al. 1995; Ashley and Robinson 1996). Roads and urban environments are negatively associated with anuran presence and species richness (Knutson et al. 1999). Roads present barriers to anuran movement (Gibbs 1998) and are a source for amphibian mortality, particularly during seasonal migrations and in certain weather conditions (Fahrig and Rytwinski 2009; LeClair et al. 2021). Some of the coastal wetlands sampled in our analysis were located in the Greater Toronto Area, a region with some of the busiest roads in Canada. For example, two of the wetlands sampled, Second Marsh and McLaughlin Bay in Oshawa, are located less than 1 km from Highway 401, with over 100,000 vehicles passing through every day (Hellinga and Van Aerde 1994; Trenouth et al. 2015). This may have had a strong effect on our amphibian abundance and richness measures (Fahrig et al. 1995; Carr and Fahrig 2001).

Previous research has shown that wetlands connected to the Great Lakes have lower occupancies and richness of marsh-breeding birds than those inland (Tozer 2016; Hohman et al. 2021; Studholme et al. 2023) and connectivity to the lake improves habitat quality for anurans (Knutson et al. 1999). Studhome et al. (2023) determined that extinction rates were higher, and initial occupancy was lower for 38% of marsh-breeding birds in Great Lakes coastal wetlands compared to inland wetlands. In our study, we compared richness between different types of coastal wetlands and found that our variable representing the type of connection to Lake Ontario was not significant when modeling all bird richness, anuran richness, or emergent vegetation nester richness. This suggests that the differences in habitat quality between coastal and inland wetlands may be more pronounced than those between different types of coastal wetlands.

Wetland type in our analysis was based on wetland classification from Greenhorn et al. (2017). Open coastal (OC) wetlands are directly connected to Lake Ontario. However, while connected to Lake Ontario, all OC wetlands were sheltered (e.g., located in a bay or behind a sand spit). Sheltered OC wetlands that are shallow can support growth of vegetation, which further reduces effects of wave action (Keough et al. 1999; Albert et al. 2005). Furthermore, all OC wetlands within this study were located east of Presqu'ile Provincial Park (Fig. 1) and were less affected by urbanization due to relatively lower human density in this region. Road density and traffic intensity both decline as the distance from urban centers increases (Quinn 2013; Pulugurtha and Mathew 2021). This positively affects anuran populations as roads present a barrier to anuran movement (Gibbs 1998) and are a leading cause of anuran declines in urban areas (Fahrig et al. 1995; LeClair et al. 2021). Notably, while OC wetlands within this study had lower road density in the surrounding area than the DRM and BB wetlands, the OC wetlands also had higher percent forest cover (Greenhorn et al 2017). Previous studies in eastern Ontario found that the negative effect of road density on the landscape is similar in importance to the positive effect of forest cover (Eigenbrod et al. 2008). Anurans rely on forest cover as movement corridors (Gibbs 1998) and increased wetland-forest edges have been found to be positively associated with the abundance of anurans (Knutson et al. 1999). As such, in our study, the relationship between lower road density and increased forest cover of OC wetlands (Greenhorn et al. 2017) likely influenced our observed higher, although only marginally significantly so, index of anuran species richness in OC wetlands.

Muskrat abundance in the coastal marshes of Lake Ontario is low. For example, Greenhorn et al. (2017) estimated an average of 0.27 muskrat houses/ha. This is a much lower estimate than the densities of 2.05–3.6 houses/ha reported for cattail-dominated marshes previously at other sites in Canada (Proulx and Gilbert 1984; Messier and Virgl 1992). As such, it is possible that the muskrat densities in our study system were too low to detect broader effects on biodiversity when considering all bird species and anurans. Similarly, these groups may not be as strongly influenced by interspersion compared to emergent vegetation nesters. Our results may be similar to those from other studies investigating the effect of habitat and landscape variables on wetland bird richness in that species-specific models might have been more informative. For example, the spatial scale at which land cover influences occupancy of wetland breeding birds can be species-specific (Tozer et al 2020). Furthermore, the AICc values were much smaller when modeling species of emergent vegetation nesters compared to species richness of all birds, indicating better model fit with the data.

We did not account for the prevalence of invasive species, such as the common reed (*Phragmites australis australis*) and hybrid cattail *Typha* x *glauca* within this study. *P. australis australis* and *Typha* x *glauca* are fast growing macrophytes that monopolize resources and reduce habitat quality for a variety of species, including marsh birds (Schummer et al. 2012; Lishawa et al. 2020). All of the wetlands within our study are currently invaded by *Typha* x *glauca*, and many are also invaded with *P. australis australis.* Tozer and Mackenzie (2019) found that abundance and species richness of nine breeding marsh birds increased after control of *P. australis* in three Great Lakes wetland systems across Lake Huron and Lake Ontario. Additionally, Tozer (2016) found that occupancy of 15 marsh breeding birds declined as *P. australis australis* cover increased between 1996 and 2013 throughout the southern portion of the Great Lakes basin. Studholme et al. (2023) partially attributed the decline in marsh breeding birds to the greater abundance of *P. australis* within Great Lakes coastal wetlands compared to inland wetlands (Robichaud and Rooney 2022). Previous studies have established that the most significant effect muskrats have on their habitat, through their foraging and house construction behaviors, is the removal of emergent vegetation (Connors et al. 2000; Higgins and Mitsch 2001; Farrell et al. 2010). Muskrat foraging breaks up monocultural stands of emergent vegetation, allowing for diversification of wetland vegetation (van der Valk and Davis 1978; Hewitt and Miyanishi 1997; Batzer et al. 2006). This diversification is a likely driver of the strong positive relationship we found between birds that nest in emergent vegetation and muskrat density. Diversification of emergent vegetation and its structure may be especially important for marsh bird conservation in the coastal wetlands of Lake Ontario where emergent vegetation is particularly thick and dense.

Conclusions, implications, and recommendations

We found that muskrat activity was unrelated to species richness of anurans or all birds in the coastal wetlands of Lake Ontario. In contrast, we found that species richness of emergent vegetation nesters increased with increasing muskrat activity. This latter finding has implications for conservation of emergent marsh-nesting obligate bird species because many of these species are designated as species at risk or species of conservation concern in the region.

A possible operational hypothesis that puts our findings in greater context is that muskrat abundance has declined over the past several decades in Great Lakes coastal wetlands largely due to structural and compositional changes in vegetation disliked by muskrats (Sadowski and Bowman 2021). As the muskrats have declined, their ecosystem service of increasing and maintaining open water-vegetation interspersion through their activities has also declined and contributed, along with a number of other stressors, to the decline of wetland-dependent bird habitat quality (Tozer 2016). In places where muskrats remain, wetland-dependent bird habitat quality is higher due to greater open water-vegetation interspersion and other favorable vegetation characteristics created and maintained by the muskrats. Thus, the bird species that favor muskrat-maintained conditions do better where there are muskrats, as we have demonstrated with our finding of higher species richness of emergent vegetation nesters. Given that reductions in fluctuations of Great Lakes water levels appear to be the main driver of the vegetation changes disliked by muskrats, then conservation actions that revive more natural, widely-ranging water levels may favor vegetation structure and composition preferred by muskrats, which will potentially increase muskrat abundance, and in turn, increase populations of wetland-dependent birds.

Water level fluctuations in Lake Ontario have been reduced from natural conditions through regulation of the Lake Ontario-St. Lawrence River system (Desgranges et al. 2006), causing declines in wetland diversity (Keddy and Reznicek 1986; Kushlan 1989). Our study focused on data from 2013–2014; however, the International Joint Committee updated its outflow regulation plan for Lake Ontario in 2017. The updated regulation plan, called Plan 2014, aims to better reflect natural fluctuations in water levels (IJC 2016). This new regulation plan may positively influence the prevalence of muskrats in Lake Ontario and in turn increase overall species richness of various taxa, including wetland-dependent birds. Therefore, we support continued monitoring and research of the relationship between muskrat activity and its influence on birds and anurans in Great Lakes coastal wetlands. Specifically, we recommend repeating muskrat house counts and comparing those to bird richness following the implementation of Plan 2014.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

C. Sadowski collected muskrat data and J. Greenhorn summarized muskrat and habitat data. D. Tozer provided data from CWMP and GLMMP. All authors contributed to the study conception and design. Statistical analyses and the first draft of the manuscript were conducted by J.E. Baici, J.Bowman, T. Burgess, S.R. Kielar, K.D. Martin, L. Menelon, G.P. Melvin, S.L. Newar, R.N. Persad, K. Solmundson, and M. Ward and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data Availability

Our final dataset and R coding script are available on Dryad.

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Figures

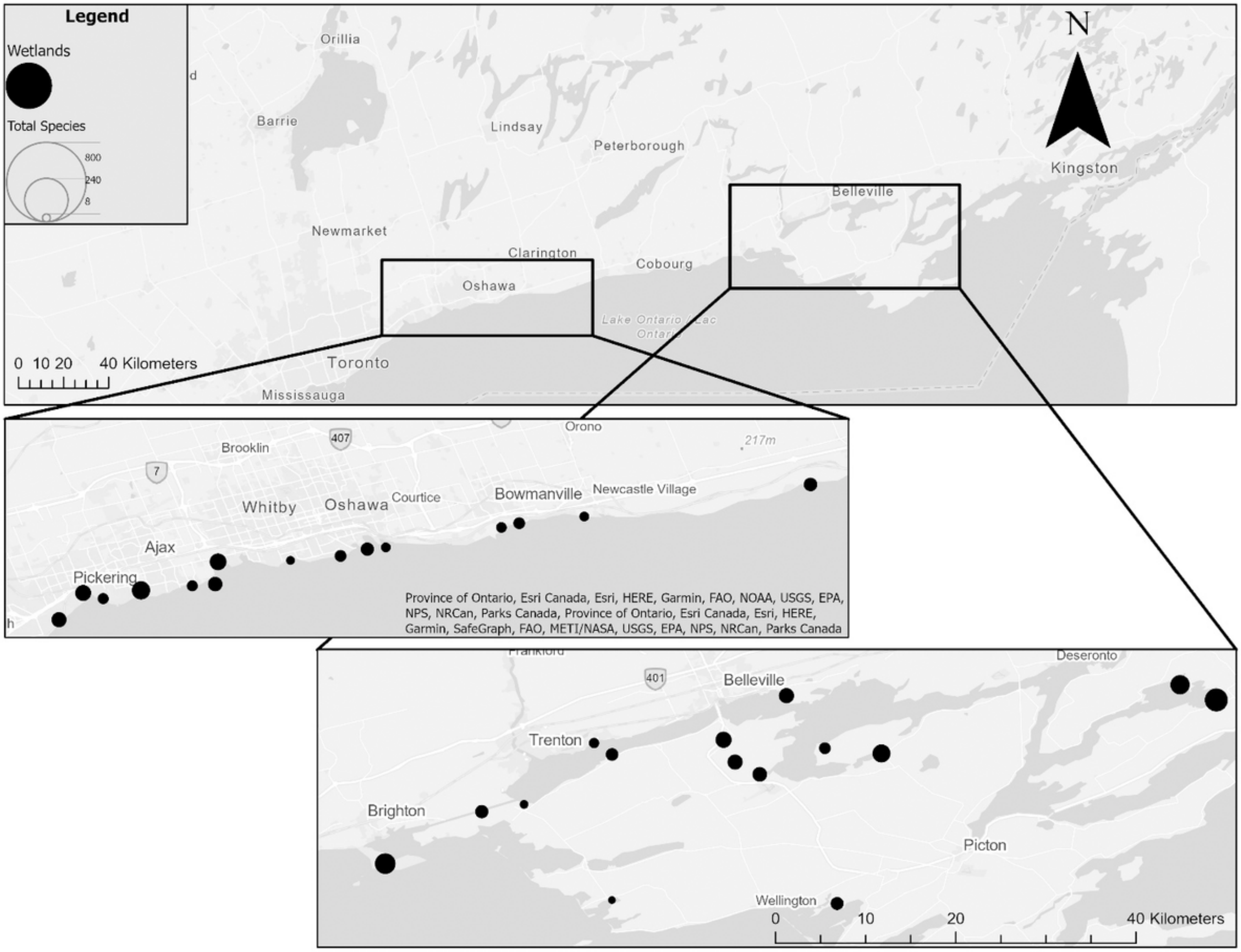

Figure 1

Locations of the 32 wetlands on the north shore of Lake Ontario which had muskrat house counts conducted in 2013-2014, presented in Greenhorn et al 2017. Circles are scaled to illustrate total richness of birds plus anurans recorded in 2013 from the Great Lakes Marsh Monitoring Program and the Great Lakes Coastal Wetland Monitoring Program.

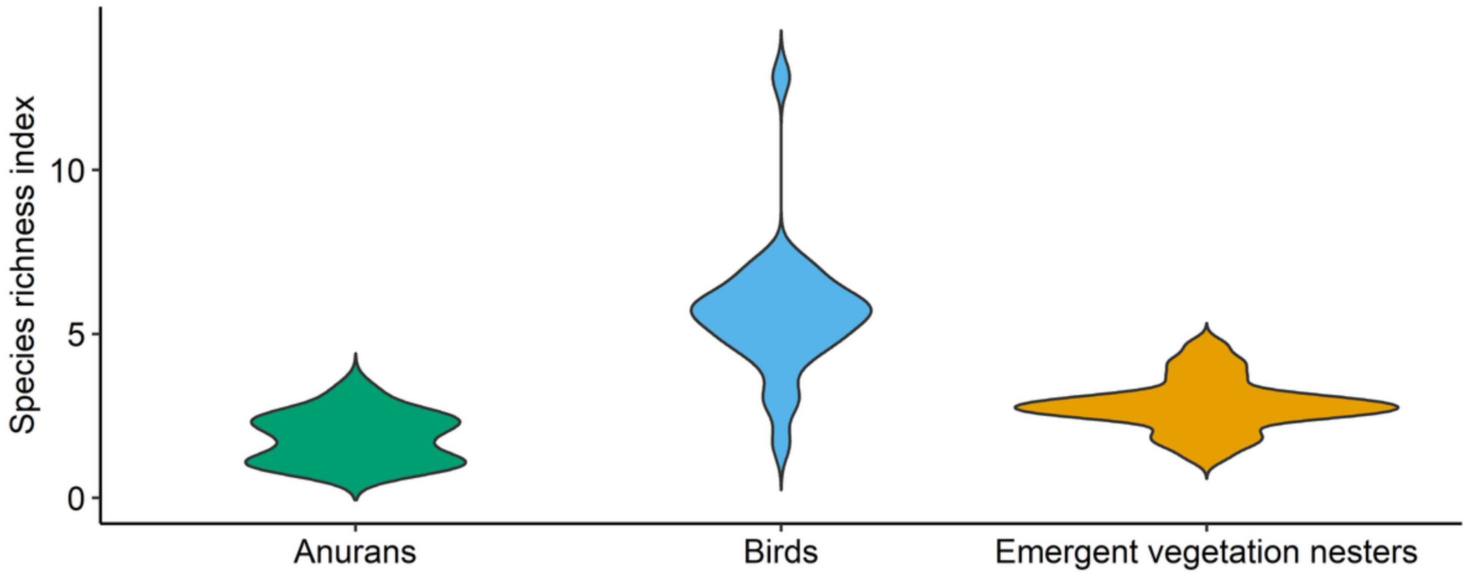

Figure 2

Frequency distribution of species richness indices for anurans (n = 24 wetlands), birds (n = 26 wetlands), and emergent vegetation nesters (n = 30 wetlands).

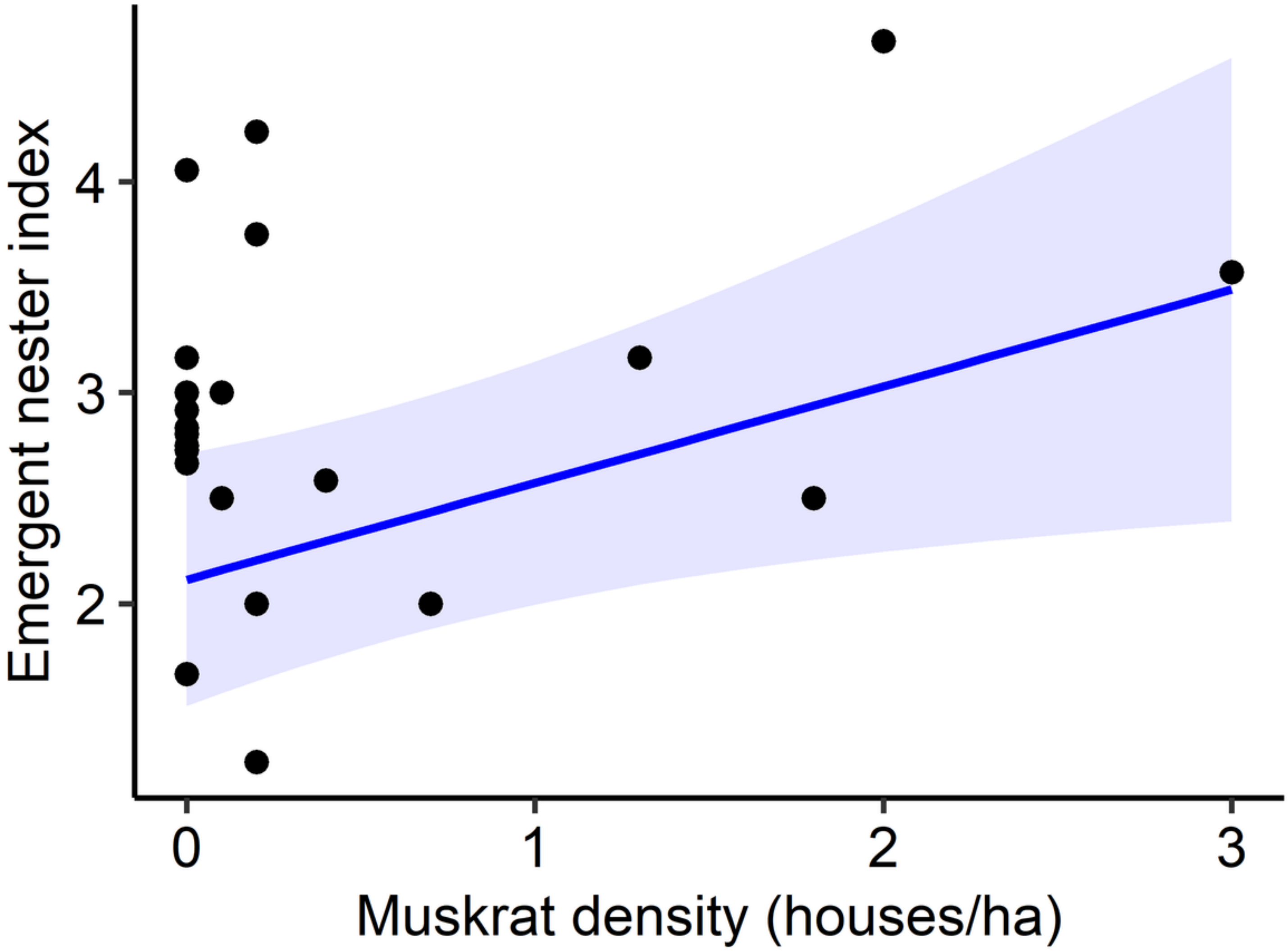

Figure 3

Emergent vegetation nester species richness index as a function of muskrat density. Shown are predicted values (line) based on the best model with 95% confidence intervals (shadows) and the raw data used to fit the model (points). Other variables in the model were held at their mean values.

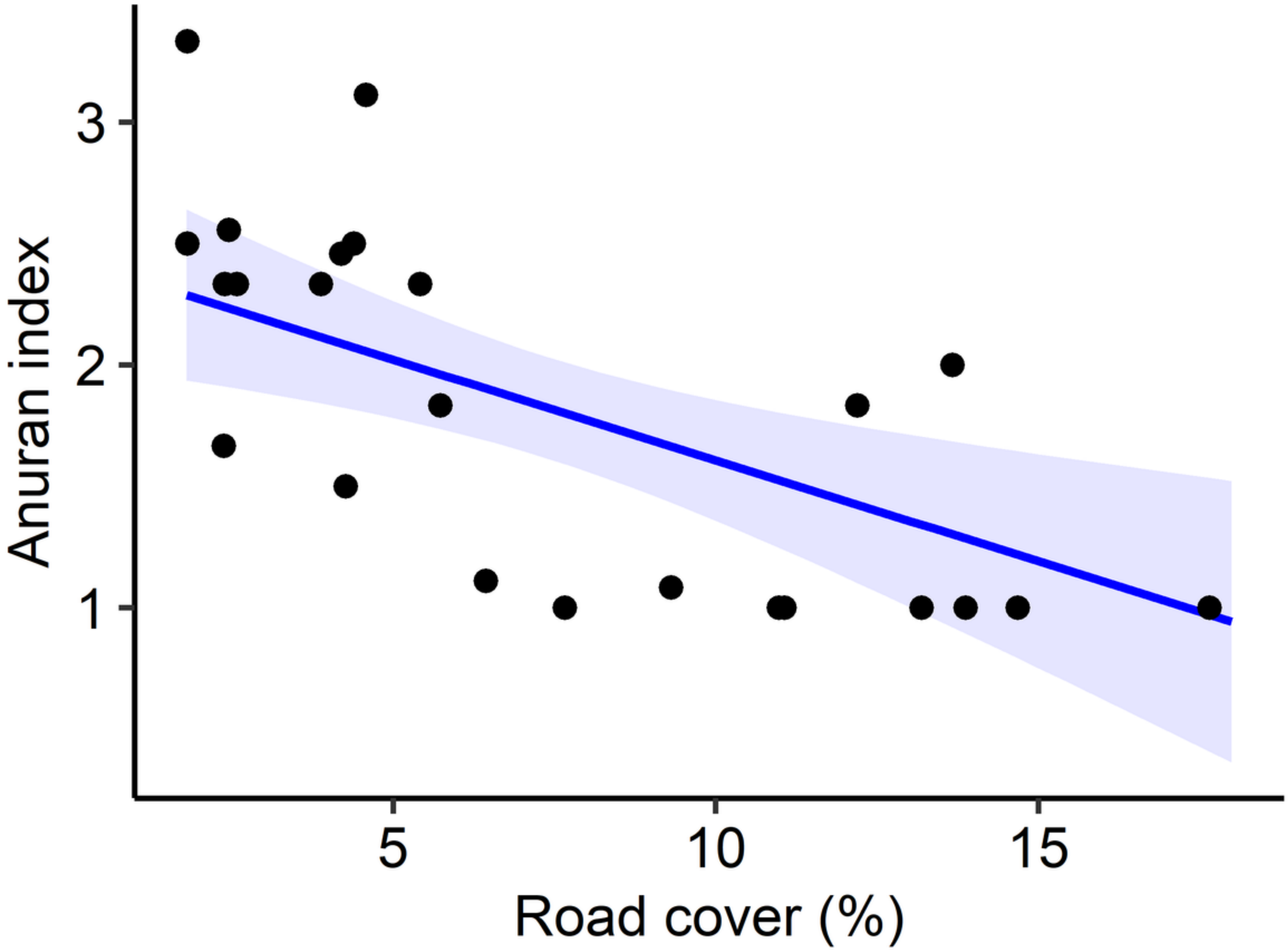

Figure 4

Anuran species richness index as a function of road cover. Shown are predicted values (line) based on the best model with 95% confidence intervals (shadows) and the raw data used to fit the model (points). Other variables in the model were held at their mean values.

Supplementary Files

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