Impacts of invasive hybrid cattail *Typha* x *glauca* and reduced marsh interspersion on muskrats (*Ondatra zibethicus*) in North America

A thesis submitted to the Committee on Graduate Studies

in partial fulfillment of the requirements for the degree of

Master of Science in the Faculty of Arts and Science

Trent University

Peterborough, Ontario, Canada

Environmental and Life Science M.Sc. Graduate Program

January 2024

Abstract

Impacts of invasive hybrid cattail *Typha* x *glauca* and reduced marsh interspersion on muskrats (*Ondatra zibethicus*) in North America

Gregory P. Melvin

Muskrat populations are declining across North America. In recent decades, hybrid cattail *Typha* x *glauca* has been invading wetlands in North America. This invasion is degrading wetland habitat, leading to reduced interspersion of water and vegetation. Muskrats are wetland-obligates and their populations are positively linked to marsh interspersion. Therefore, muskrat populations may be declining due to the invasion of *T.* x *glauca* and subsequent reduction in interspersion. To test this hypothesis, I first sampled marshes across south-central Ontario, comparing muskrat densities with the relative frequency of *T.* x *glauca* and the degree of interspersion. Second, I measured intensity of use by muskrats in a large wetland along a gradient of interspersion. My findings suggest that reduced interspersion may be contributing to muskrat population declines, but it is unclear to what degree *T.* x *glauca* is responsible. Further research is needed to understand the effects of wetland invasions on muskrat populations.

Keywords: *Ondatra zibethicus*, *Typha* x *glauca*, invasive species, wetlands, population declines, furbearers, interspersion, southern Ontario, North America

Acknowledgements

I would like to thank my advisor, Dr. Jeff Bowman, who gave me the freedom to run my own project and the guidance to make it a success. A very big thank you to Carrie Sadowski who dedicated a tremendous amount of time and energy to this project, as well as Janet Greenhorn who assisted with field work and aerial house counts. Thank you to Dr. Joanna Freeland and Dr. Robert Metcalfe of my graduate committee who contributed their expertise to this thesis.

Thank you to Shane White who spent a whole summer with me in the marsh conducting field work. Thank you to everyone else who helped me with field work: Mark Browning, Sasha Newar, Kirsten Solmundson, Rebekah Persad, Jenn Baici, and Ryan Holt.

Thank you to those who spent hours upon hours processing remote camera images: Shane White, Trevor MacLaurin, Tami Balmaceda, and Maddisyn Kowalik.

A very big thank you to Justin Barker and Geoff Andrews from the Trent MaDGIC office who spent countless hours troubleshooting spatial analysis issues for me.

Thank you to all who granted property access for field work: Peter Overgoor and the Osler family, Ontario Parks, Ducks Unlimited Canada, Central Lake Ontario Conservation Authority, Ganaraska Region Conservation Authority, and Toronto and Region Conservation Authority.

Thank you to those who generously provided funding for this project: Canada-Ontario Agreement on Great Lakes Water Quality and Ecosystem Health, Natural Sciences and

Engineering Research Council of Canada (NSERC), Ontario Ministry of Natural Resources and Forestry, and Trent University.

Finally, I would like to sincerely thank my family and friends who helped me through this journey. I would not be where I am today without your support.

Table of Contents

List of figures

List of tables

Chapter 1: General introduction

Muskrats: Ecology

Muskrats (*Ondatra zibethicus*) are semi-aquatic, mostly herbivorous rodents native to North America (Willner *et al.*, 1980; Kurta, 1995). They are the sole species of their genus but belong to the diverse family *Muridae* along with mice, squirrels, beavers, and porcupines (Kurta, 1995). While resembling their rodent relative the beaver (*Castor canadensis*) in appearance and habits, muskrats are more closely related to voles and lemmings, and thus, similarities with the beaver are more likely the result of convergent evolution. On average, they measure 45 - 55 cm in total length (Willner *et al.*, 1980) and range from 700 g to nearly 2 kg (Nowak & Paradiso, 1983). In general, body size is positively correlated with habitat suitability and resource availability (Boyce, 1978). The lifespan of wild muskrats is estimated to be three to four years (Kurta, 1995). Adaptations to aquatic habitats include partially webbed feet, waterproof fur, a rudder-like laterally-compressed tail, and the construction of houses and other structures using emergent vegetation or the excavation of bank dens (Boutin & Birkenholz, 1987; Willner *et al.*, 1980). In lakes and rivers with steep enough banks, muskrats excavate bank burrows. In marshes and other shallow-water habitats with more gradual banks, they construct houses (also “huts” or “lodges”) using surrounding emergent vegetation (Sather, 1958; Dozier, 1948; Kurta, 1995). Both dwellings have entrances underwater and are typically built for a family unit or several individuals (Kurta, 1995).

Muskrats occur in every Canadian province and territory and every state except Hawaii. Their native range also extends into northern Mexico (IUCN, 2016). Additionally, muskrats have been introduced to parts of Europe and Asia (Hoffman, 1958, as cited in Danell, 1966) and South America (Jaksic *et al.*, 2002), and resident populations have since been established (Boutin & Birkenholz, 1987; Jaksic *et al.*, 2002). Globally, the species is generally bound by the Tropic of Cancer in the south except for its relatively small range in southern Argentina and Chile. To the north, muskrats can be found beyond the Arctic Circle (IUCN, 2016). The muskrat's wide range can be attributed in part to its flexible habitat requirements. Evidently, it is tolerant of a broad range of climatic conditions, from frigid winters and extreme seasonality in the north to warm year-round temperatures in Mexico's Baja California. Its only basic requirements are a permanent source of water, the ability to excavate a bank den or build a house from surrounding vegetation, and suitable vegetation for consumption (Boutin & Birkenholz, 1987). Therefore, muskrats may inhabit lakes, ponds, rivers, creeks, and wetlands, as well as engineered waterways such as canals, stormwater reservoirs, and ditches (Butler *et al.*, 1885; Willner et *al.* 1980; Boutin & Birkenholz, 1987). Moreover, they are tolerant of saline water and can thus be found in estuaries and coastal wetlands (Boutin & Birkenholz, 1987). However, they avoid large, open bodies of water with greater wind and wave action (Errington, 1963; Ervin, 2011; Larreur *et al.*, 2020) and prefer slow-moving or still water (Soper, 1942; Kurta, 1995; Brietzke, 2015) that is relatively shallow (Kurta, 1995; Larreur *et al.*, 2020).

Muskrats remain active year-round (Danell, 1996) and may conduct their activity at any time of day (Willner *et al.*, 1980; Kurta, 1995), though many report mostly nocturnal activity (Butler, 1885; Chatterton, 1944; Dozier, 1948; Boutin & Birkenholz, 1987; Marinelli & Messier, 1993). In the north, where water bodies freeze in winter, muskrats forage beneath the ice (Jelinski, 1989; Sadowski & Bowman, 2021). However, in shallower depths or during periods of extreme cold, the water surrounding a muskrat's house or burrow may freeze completely, forcing the occupant to forage above-ground (Errington, 1939; Errington *et al.*, 1963). Throughout most of their range, the onset of breeding is correlated to air temperature and appears to be limited to the ice-free period (Olsen, 1959). Consequently, there is a negative correlation between winter length and number of litters produced, but this is compensated by a poleward increase in the average number of young per litter (Boutin & Birkenholz, 1987). Litter size typically ranges from 4-8 young (Willner *et al.*, 1980). Where ice formation does not occur, muskrats may breed year-round. Still, it is rare to see more than three litters per year (Willner *et al.*, 1980; Boutin & Birkenholz, 1987), although up to six litters have been observed in Louisiana (O'Neil, 1949). Females may reach sexual maturity as early as 6 – 8 weeks (O'Neil & Linscombe, 1976) but usually begin breeding during the spring following their birth (Willner *et al.*, 1980; Kurta, 1995). Gestation typically lasts 30 days (Errington, 1937; Boutin & Birkenholz, 1987; Kurta *et al.*, 1995), after which females immediately re-enter estrus (Olsen, 1959). Females wean their young after four weeks (Willner *et* al., 1980). Muskrats exhibit a mostly monogamous mating system (Sather, 1958; Caley, 1987; Marinelli & Messier, 1993; Kurta, 1995) but pairing with different males throughout the season has been observed (Errington, 1963).

Habitat preferences of muskrats coincide with the occurence of aquatic macrophytes, especially emergent growth. They eat primarily the nutrient-dense parts of aquatic plants such as roots, rhizomes, and bulbs (Danell, 1977; Willner *et al.*, 1980; Boutin & Birkenholz, 1987; Campbell & MacArthur, 1994; Kurta, 1995). They have a strong preference for cattail (*Typha* sp.) (Takos, 1947; Bellrose, 1950; Proulx & Gilbert, 1983; Lacki *et al.*, 1990; Kurta, 1995), though they are known to eat a wide variety of plants depending on local availability (Boutin & Birkenholz, 1987). These include emergent plants such as bulrush, horsetail, burreed, wild rice, arrowhead, water-arum, and various grasses, sedges, and rushes. They may also consume floating plants such as pondweeds, water lilies, and duckweeds. More rarely, they consume submerged plants such as water milfoils and aquatic buttercups (Takos, 1947; Bellrose, 1950; Sather, 1958; Jelinksi, 1989; Lacki *et al.*, 1990). However, submerged plants generally do not meet their protein requirements (Jelinksi, 1989). They may also feed on nearby crops when available (Errington, 1939; Dozier, 1950; Errington *et al.*, 1963). While muskrats are highly adapted to a herbivorous diet (Boutin & Birkenholz, 1987; Campbell & MacArthur, 1994), they are not strict herbivores. Muskrats have been observed preying on mussels (Butler, 1885; Willner *et al*., 1980; Hersey *et al*., 2013), crayfish (Bellrose, 1950; Adams & Rosamond, 2022), fish (Butler, 1885; Errington, 1939; Sather, 1958), frogs (Errington, 1939; Sather, 1958), and turtles (Willner *et al*., 1980; Kurta, 1995) when vegetation is in short supply. They may also scavenge on a variety of animal foods, including other muskrats (Butler, 1885; Errington, 1939). The muskrat can be an important or supplementary food source to a wide variety of predators. Mink are widely regarded as top predators of the muskrat (Errington, 1954; Sather, 1958; Proulx *et al*., 1987; Kurta, 1995). Depending on the region, they may also be hunted by raccoons (Kurta, 1995; Kadlec *et al.*, 2007), foxes (Danell, 1978; Wagnon & Serfass, 2017), raptors (Willner, 1980; Dunstan & Harper, 1975; Turner *et al.*, 2020), otters (Wilson, 1954; Brietzke, 2015; Turner *et al.*, 2020), other mustelids (Danell, 1978, Brietzke, 2015), coyotes (Sather, 1958; Ahlers *et al.*, 2021, Melvin, pers. obs.), bears, wolves (Brietzke *et al.*, 2015), snapping turtles (Butler, 1885; Kurta, 1995), and even large fish (Butler, 1885; Kurta, 1995). In the southern United States, they are also hunted by alligators, feral pigs, and snakes (Chatterton, 1944).

Muskrats: Population declines, management, and conservation

Once a ubiquitous and abundant wetland species, muskrat populations have been declining across North America for up to 50 years (Benoit & Askins, 1999; Roberts & Crimmins, 2010; Gregory *et al.*, 2019; Ahlers & Heske, 2017; Ward & Gorelick, 2018; Sadowski & Bowman, 2021). This trend was first perceived from harvest data which shows steep, decade-long declines in muskrat harvest in many parts of the United States and Canada (Ahlers & Heske, 2017; Roberts & Crimmins, 2010). At its peak in the mid-twentieth century, muskrat pelt sales reached over 5 million per year in Canada and nearly 20 million in the United States (Obbard *et al.*, 1987). Roberts & Crimmins (2010) and Ahlers & Heske (2017) conducted analyses that controlled for the effect of pelt prices on harvest declines in both countries and both concluded that harvest declines likely indicate population declines. The number of muskrat trappers has indeed declined over the decades in at least several regions (Brietzke, 2015; Ahlers *et al.*, 2016; Gregory *et al.*, 2019), yet numerous trappers have reported lower harvests over this period (Benoit & Askins, 1999; Roberts & Crimmins, 2010; Brietzke, 2015; Ward & Gorelick, 2018; Gregory *et al.*, 2019), and these claims have been echoed by other anecdotal reports of declines (Roberts & Crimmins, 2010; Brietzke, 2015; Sadowski & Bowman, 2021). Though widespread and long-term population monitoring is still scant, some studies have corroborated the downward trend in muskrat populations with empirical data. For example, Sadowski & Bowman (2021) replicated historical muskrat house counts and showed over 90 % declines in muskrat populations in southern Ontario at Point Pelee National Park and Matchedash Bay from the 1970s and 1980s, respectively, through 2019. Ward & Gorelick (2018) reported declines of roughly 75% in the Peace-Athabasca Delta in Alberta from 1970 to 2016. Benoit and Askins (1999) reported declines of 78% and 100% in marshes on two rivers in Connecticut between 1970 and 1990, where densities were as high as 5.8 houses/ha in late 1960 (Smith & Jordan, 1976, as cited in Benoit & Askins, 1999). Finally, Gregory *et al.* (2019) reported low densities of both muskrats (1 – 5/ha) and houses (< 0.12/ha) in Prince Edward Island marshes, with more than a five-fold decrease in houses at one marsh since 1960. Notably, these observed declines have occurred over sufficient time scales to rule out the possibility of normal population cycles, which may occur every 4-14 years depending on the region (Elton & Nicholson, 1942; O'Neil, 1949; Butler, 1962; Danell, 1978).

Despite their economic, cultural, and ecological importance, muskrats have not generally been a concern for conservation until recently. Muskrats were the most widely harvested furbearers throughout the twentieth century (Obbard *et al.*, 1987) and still make up 28% of fur exports as of 2015 (Fur Institute of Canada, 2015). They are an important source of food, clothing, and income for First Nation communities (Brietzke, 2015; Straka *et al.*, 2018), and they are recognized by the Anishinaabe as symbols of courage and humility for their role in the creation of the earth (MacGregor, 2013). Furthermore, muskrats have been deemed ecosystem engineers (Toner *et al.*, 2010; Mott *et al.*, 2013; Kua *et al.*, 2020), keystone species (Danell, 1996; Nummi *et al.*, 2006), and indicator species (Kua *et al.*, 2020; Ward *et al.*, 2021) for their important and unique role in marsh ecosystems. For example, muskrat herbivory increases connectivity and open water within wetlands (Weller & Spatcher, 1965; Danell, 1977; Kua *et al.*, 2020) which may benefit plant communities (Nyman *et al.*, 1993; Danell, 1996; Hewitt & Miyanishi; 1997; Kua *et al*., 2020), waterfowl (Weller & Spatcher, 1965; Danell, 1979; Kaminski & Prince, 1981), marsh birds (Weller & Spatcher, 1965; Rehm & Baldassarre, 2007), and invertebrates (Wilcox & Meeker, 1992; Higgins & Mitsch, 2000). Their houses are used by a plethora of vertebrate species for nesting, basking, and shelter (Kiviat, 1978). And, through herbivory, muskrats control the growth of dominant plants (Danell, 1996; Kadlec *et al.*, 2007), thereby maintaining high levels of species diversity (Danell, 1996; Kua *et al.*, 2020). Taken for granted by many, muskrats clearly have measurable and intrinsic value in North America. Given their historical abundance and ecological importance, a continental-scale decline in muskrat populations is concerning and worthy of investigation.

Muskrats: Potential causes of decline

Whether there is a universal cause or multiple factors driving declines, and what those drivers may be, is still largely unknown. Habitat destruction by humans is a major cause of species extinctions (Fahrig, 1997; Brooks *et al.*, 2002; Gonçalves-Souza *et al.*, 2020), but may not be the primary cause of muskrat declines for at least two reasons. First, the rate of wetland conversion in North America since 1980 has been relatively low (Davidson, 2014) and muskrat populations have continued to decline since then (Benoit & Askins, 1999; Brietzke, 2015; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Gregory *et al.*, 2019; Sadowski & Bowman, 2021). Second, several studies reporting localized declines do not associate these declines with wetland loss (Greenhorn *et al.*, 2017; Gregory *et al.*, 2019; Sadowski & Bowman, 2021). Muskrats do not appear to be adversely affected by several well-known environmental toxins such as lead, mercury, and polychlorinated biphenyls (PCBs) (Ganoe *et al.*, 2020) and continue to be found in habitats with generally poor water quality such as agricultural ditches (Ahlers *et al.*, 2010; Miller, 2018; Adams & Rosamond, 2022) and tailings ponds (d'Entremont, 2014). Muskrats are susceptible to a wide variety of diseases (Miller, 2018; Ganoe *et al.*, 2020), but these are generally localized and triggered by stressors in the environment. Furthermore, density dependence should prevent diseases from leading to a sustained decline (Errington, 1963). Abundance of American mink (*Neogale vison*), largely regarded as the muskrat's top predator in North America (Errington, 1954; Sather, 1958;

Proulx *et al*., 1987; Kurta, 1995), is closely tied to muskrat abundance (Bulmer, 1974; Viljugrein *et al.*, 2001; Gorman, 2007). Unsurprisingly, mink have been showing similar harvest declines in various parts of North America in recent decades (Gorman *et al.*, 2007; Ahlers *et al.*, 2021). While more research is needed, it is likely that mink are experiencing similar population declines, and are thus unlikely to be driving muskrat declines. I know of only one muskrat predator, the coyote (*Canis latrans*), which has appreciably increased in range and abundance over the last fifty years in North America (Hody & Kays, 2018). Notably, muskrat harvest in Prince Edward Island drastically declined in the mid-1980s following the introduction and rapid increase of coyotes, and many trappers believe this has led to population declines (Gregory *et al.*, 2019). However, it is unlikely that this has led to a considerable increase in muskrat predation in other parts of the continent, as coyotes tend to prefer other foods (Jensen *et al.*, 2022). In general, muskrat populations are highly resilient toward short-term die-offs (Chatterton, 1944; Kroll & Meeks, 2020; Straka *et al.*, 2018; Sadowski & Bowman, 2021) due to their high fecundity (Errington, 1963; Boutin & Birkenholz, 1987; Sadowski & Bowman, 2021) and their ability to disperse across large distances (Errington & Errington, 1937; Errington, 1963; Ahlers *et al.*, 2021) thereby recolonizing depleted populations. This suggests that the declines are widespread, and whatever has caused the declines is having a sustained negative effect on muskrat populations.

Two main hypotheses explaining widespread muskrat declines have recently garnered the most attention: direct impacts of water level management (Toner *et* al, 2010; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018), and widespread changes in marsh habitat structure and composition, especially due to invasive *Typha* (Greenhorn *et al.*, 2017; Sadowski & Bowman, 2021). Reduced winter water levels caused by fall water level drawdowns have been shown to suppress muskrat populations in upper St. Lawrence River marshes (Toner *et al.*, 2010). Declines in marsh water levels resulting from fall drawdowns may reduce fall and winter habitat suitability, as muskrats require a minimum depth of unfrozen water to effectively forage beneath the ice (Errington, 1939). Muskrats with existing houses may experience “freeze-outs” which occur when water freezes to the substrate, thereby preventing them from foraging underwater and accessing their houses (Errington, 1939; Ganoe *et al.*, 2021). Subject to these conditions, muskrats may experience increased predation, disease, and intra-specific strife (Chatterton, 1944; Errington, 1951; Danell, 1978), all of which may increase mortality (Errington, 1954). Muskrat populations upstream in Lake Ontario coastal marshes subject to the same water level management regime may also be suppressed by drawdowns, as densities were found to be lower in marshes directly connected to Lake Ontario compared to those isolated by a barrier beach (Greenhorn *et al.*, 2017). Water level management has also been directly linked to the regional-scale decline of muskrat populations in the Peace-Athabasca Delta over nearly a half-century (Ward & Gorelick, 2018). Damming the Peace River for power generation, in combination with increased water usage by industry and nearby communities, have contributed to progressively lower water output in the delta (Straka *et al.*, 2018). This has led to reduced spring flooding which has decreased overall water levels, spillover, and connectivity within the delta, thereby reducing critical habitat for muskrats (Straka *et al.*, 2018).

While muskrats may be directly impacted by water level management, manipulating water levels may also alter marsh habitat structure and composition, which may have confounding negative consequences on muskrat populations. For example, stabilizing water levels promotes the growth of invasive macrophytes (Herrick & Wolf, 2005), especially hybrid cattail *Typha* x *glauca* (Shay *et al.*, 1999; Boers *et al.*, 2007; Boers & Zedler, 2008; Wilcox & Bateman, 2018). Sadowski & Bowman (2021) suggest that the expansion of dense emergent vegetation, primarily *T.* x *glauca*, and subsequent loss of open water habitat in recent decades may be responsible for the precipitous muskrat declines at Point Pelee National Park and Matchedash Bay. *Typha* x *glauca*, a hybrid of native *T. latifolia* and introduced *T. angustifolia*, has become widespread and common in many parts of North America in recent decades (Galatowitsch *et al.*, 1999; Pieper *et al.*, 2022; Tangen *et al.*, 2022; Stewart *et al.*, 2023). Due to its highly competitive nature (Bansal *et al.*, 2019), *T.* x *glauca* is now the dominant taxon in many wetlands in North America (Freeland *et al.*, 2013; Larreur *et al.*, 2020; Pieper *et al.*, 2020; Stewart *et al.*, 2023; Tangen *et al.*, 2022). This is generally problematic, as *T.* x *glauca* is associated with a host of negative consequences in wetland habitats, including the reduction of biodiversity (Boers *et al.*, 2007; Farrer & Goldberg, 2009; Tuchman *et al.*, 2009; Lishawa *et al.*, 2015), open water habitat (Wilcox *et al.*, 2005; Harris & Marshall, 1963; Markle *et al.*, 2018), interspersion of water and emergent plants (Wilcox *et al.*, 2008; Schummer *et al.*, 2012; Hohman *et al.*, 2021), and structural complexity (Wilcox *et al.*, 2008). Muskrats require open water travel routes and are typically most abundant when there is a high degree of interspersion of water and emergent vegetation (Weller & Spatcher, 1965; Proulx & Gilbert, 1983). It has been suggested that while the previous water-level management plan for Lake Ontario and St. Lawrence River water levels clearly has a negative impact on muskrat abundance (Toner *et al.*, 2010; Greenhorn *et al.*, 2017), a more likely explanation for population declines is the resulting changes in wetland structure and composition (Sadowski & Bowman, 2021). These changes are not limited to the Great Lakes region, nor are they exclusively triggered by extended periods of stabilized water levels (Stewart *et al.*, 2023; Tangen *et al.*, 2022). Furthermore, *T.* x *glauca* may flourish in both disturbed and undisturbed habitats (Lishawa *et al.*, 2010; Freeland *et al.*, 2013). This suggests that *T.* x *glauca* is likely to continue expanding its range and altering wetlands throughout North America. Indeed, *T.* x *glauca* has already been observed in most provinces and states (Hall, 2018; Tangen *et al.*, 2022; Stewart *et al.*, 2023), with relatively recent expansions into coastal BC (Stewart *et al.*, 2023) and the Prairie Pothole Region (Tangen *et al.*, 2022). Moreover, the timeframe of increasing *Typha* invasions generally coincides with the continental decline in muskrat populations (Sadowski & Bowman, 2021). There is currently no research examining the relationship between *Typha* invasions and muskrat populations. Therefore, I believe this is an interesting avenue for research.

Study objectives

I set out to test the hypotheses that *T*. x *glauca* invasions and resulting reductions in interspersion are contributing to widespread muskrat population declines in North America. I designed two studies to test these hypotheses: the first at a regional scale across multiple wetlands in south-central Ontario, and the second at a fine scale within one of these wetlands. This research will help determine the impacts of a prominent wetland invader on muskrats and provide managers with a clearer picture of what is causing widespread muskrat population declines in North America.

References

Adams, S. B., & Rosamond, R. L. (2022). Direct observation of muskrat Feeding on crayfish. *Southeastern Naturalist*, *21*(3).

Ahlers, A. A., & Heske, E. J. (2017). Empirical evidence for declines in muskrat populations across the United States. *Journal of Wildlife Management*, *81*(8), 1408–1416. https://doi.org/10.1002/jwmg.21328

Ahlers, A. A., Heske, E. J., Schooley, R. L., & Mitchell, M. A. (2010). Home ranges and space use of muskrats Ondatra zibethicus in restricted linear habitats. *Wildlife Biology*, *16*(4), 400–408. https://doi.org/10.2981/10-044

Bansal, S., Lishawa, S. C., Newman, S., Tangen, B. A., Wilcox, D., Albert, D., Anteau, M. J., Chimney, M. J., Cressey, R. L., DeKeyser, E., Elgersma, K. J., Finkelstein, S. A., Freeland, J., Grosshans, R., Klug, P. E., Larkin, D. J., Lawrence, B. A., Linz, G., Marburger, J., Noe, G., Otto, C., Reo, N., Richards, J., Richardson, C., Rodgers, L., Schrank, A., Svedarsky, D., Travis, S., Tuchman, N., & Windham-Myers, L. (2019). *Typha* (cattail) invasion in North American wetlands: Biology, regional problems, impacts, ecosystem services, and management. *Wetlands, 39*, 645–684. https://doi.org/10.1007/s13157-019-01174-7

Bellrose, F. C. (1950). The Relationship of Muskrat Populations to Various Marsh and Aquatic Plants. *The Journal of Wildlife Management*, 14(3), 299–315.

Benoit, L. K., & Askins, R. A. (1999). Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *The Society of Wetland Scientists*, *19*(1), 194–208.

Boers, A. M., & Zedler, J. B. (2008). Stabilized water levels and *Typha* invasiveness. *Wetlands*, *28*(3), 676–685. https://doi.org/10.1672/07-223.1

Boers, A. M., Veltman, R. L. D., & Zedler, J. B. (2007). *Typha* x *glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering*, *29*(3), 232–244. https://doi.org/10.1016/j.ecoleng.2006.04.011

Boutin, S., & Birkenholz, D. E. (1987). Muskrat and round-tailed muskrat. In Novak, M., Baker, J.A., Obbard, M. E., & Malloch, B. (Eds.), *Wild Furbearer Management and Conservation in North America*, 314–325. Ontario Ministry of Natural Resources.

Boyce, M. S. (1978). Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. *Oecologia*, *19*, 1–19.

Brietzke, C. (2015). Muskrat ecology in the Mackenzie Delta: Insights from local knowledge and ecological field surveys. *Arctic*, *68*(4), 527–531. https://doi.org/10.14430/arctic4538

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Bulmer, M. G. (1974). A statistical analysis of the 10-year cycle in Canada. *British Ecological Society*, *43*(3), 701–718.

Butler, A. W. (1885). Observations on the muskrat. *The American Naturalist*, *19*(11), 1044–1055. https://doi.org/10.1086/274091

Butler, L. (1962). Periodicities in the annual muskrat population figures for the province of Saskatchewan. *Canadian Journal of Zoology*, *40*(7), 1277–1286. https://doi.org/10.1139/z62-104

Hall, S. (2008). *Typha* x *glauca* (hybrid cattail). CABI Digital Library. https://doi.org/10.1079/cabicompendium.107745

Caley, M. J. (1987). Dispersal and Inbreeding avoidance in muskrats. *Animal Behaviour, 35*(4): 1225-1233.

Campbell, K. L., & MacArthur, R. A. (1994). Digestibility and assimilation of natural forages by muskrat. *The Journal of Wildlife Management*, *58*(4), 633–641.

Chatterton, H. J. (1944). The muskrat fur industry of Louisiana. *Journal of Geography*, *44*, 185-195

d'Entremont, M. (2014). The Presence of muskrats (*Ondatra zibethicus*) in a highly contaminated watershed near Yellowknife, Northwest Territories. *Northwestern Naturalist*, *95*(2), 113–115. https://doi.org/10.1898/nwn13-14.1

Danell, K. (1977). Short-term plant Successions following the colonization of a northern Swedish Lake. *British Ecological Society*, *14*(3), 933–947.

Danell, K. (1978). Population dynamics of the muskrat in a shallow Swedish Lake. *Journal of Animal Ecology*, *47*(3), 697–709.

Danell, K. (1979). Reduction of aquatic vegetation following the colonization of a Northern Swedish Lake by the muskrat, *Ondatra zibethica*. *Oecologia*, *106*, 101–106.

Danell, K. (1996). Introductions of aquatic rodents: Lessons of the muskrat *Ondatra zibethicus* invasion. *Wildlife Biology*, *2*(3), 213–220. https://doi.org/10.2981/wlb.1996.021

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*(10), 934–941. https://doi.org/10.1071/MF14173

Dozier, H. L. (1948). Estimating muskrat populations by house counts. *Thirteenth North American Wildlife Conference*, 372-392.

Dunstan, T. C., & Harper, J. F. (1975). Food habits of bald eagles in north-central Minnesota. *The Journal of Wildlife Management*, *39*(1), 140–143. https://www.jstor.org/stable/3808554

Elton, C., & Nicholson, M. (1942). Fluctuations in numbers of the muskrat (*Ondatra zibethica*) in Canada. *British Ecological Society*, *11*(1), 96–126.

Errington, P. L. (1939). Reaction of muskrat populations to drought. *Ecology*, *20*(2), 168–186.

Errington, P. L. (1951). Concerning fluctuations in populations of the prolific and widely distributed muskrat. *The American Naturalist*, *85*(824), 273–292. https://doi.org/10.1086/281680

Errington, P. L. (1954). The special responsiveness of minks to epizootics in muskrat populations. *Ecological Monographs*, *24*(4), 377–393.

Errington, P. L. (1963). Muskrat populations. The Iowa State University Press, Ames, Iowa, USA.

Errington, P. L., & Errington, C. S. (1937). Experimental tagging of young muskrats for purposes of study. *The Journal of Wildlife Management*, *1*(3/4), 49-41. https://doi.org/10.2307/3795761

Ervin, M. D. (2011). Population characteristics and habitat selection of muskrats (*Ondatra zibethicus*) in response to water level management at the Summerberry Marsh Complex, The Pas (M.Sc. Thesis). Iowa State University, Iowa, USA.

Fahrig, L. (1997). Relative effects of habitat loss and fragmentation on population extinction. *The Journal of Wildlife Management*, *61*(3), 603–610.

Freeland, J., Ciotir, C., & Kirk, H. (2013). Regional differences in the abundance of native, introduced, and hybrid Typha spp. In northeastern North America influence wetland invasions. *Biological Invasions*, *15*(12), 2651–2665. https://doi.org/10.1007/s10530-013-0481-4

Fur Institute of Canada. (2015). Canada's fur trade: Facts and figures. http://fur.ca/fur-trade/canadas-fur-trade-fact-figures/. Accessed April 2023.

Galatowitsch, S. M., Anderson, N. O., Ascher, P. D., & Hall, A. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*(4), 733–755.

Ganoe, L. S., Brown, J. D., Yabsley, M. J., Lovallo, M. J., & Walter, W. D. (2020). A review of pathogens, diseases, and contaminants of muskrats (*Ondatra zibethicus*) in North America. *Frontiers in Veterinary Science*, *7*(May), 1–13. https://doi.org/10.3389/fvets.2020.00233

Ganoe, L. S., Lovallo, M. J., Brown, J. D., & Walter, W. D. (2021). Ecology of an isolated muskrat population during regional population declines. *Northeastern Naturalist*, *28*(1), 49–64. https://doi.org/10.1656/045.028.0104

Gonçalves-Souza, D., Verburg, P. H., & Dobrovolski, R. (2020). Habitat loss, extinction predictability and conservation efforts in the terrestrial ecoregions. *Biological Conservation*, *246*(May), 108579. https://doi.org/10.1016/j.biocon.2020.108579

Gorman, R. 2007. Spatio-temporal patterns of mink and muskrat in Canada during a quarter century (M.Sc. Thesis). Trent University, Peterborough, Ontario.

Greenhorn, J. E., Sadowski, C., Holden, J., & Bowman, J. (2017). Coastal wetlands connected to Lake Ontario have reduced muskrat (*Ondatra zibethicus*) abundance. *Wetlands*, *37*(2), 339–349. https://doi.org/10.1007/s13157-016-0874-0

Gregory, G. J., Dibblee, R., Daoust, P.-Y., & Van Den Heuvel, M. R. (2019). Declines in muskrat (*Ondatra zibethicus*) population density in Prince Edward Island, Canada. *Canadian Wildlife Biology and Management*, *8*(2), 46–60.

Herrick, B. M., & Wolf, A. T. (2005). Invasive plant species in diked vs. undiked great lakes wetlands. *Journal of Great Lakes Research*, *31*(3), 277–287. https://doi.org/10.1016/S0380-1330(05)70259-8

Higgins, C., & Mitsch, W. J. (2000). The role of muskrats (*Ondatra zibethicus*) as ecosystem engineers in created freshwater marshes. *Biomass*, 81–86.

Hody, J. W., & Kays, R. (2018). Mapping the expansion of coyotes (Canis latrans) across North and central America. *Zookeys*, *2018*(759), 81–97. https://doi.org/10.3897/ZOOKEYS.759.15149

International Union for Conservation of Nature [IUCN]. 2016. *Ondatra zibethicus*. The IUCN Red List of Threatened Species. Version 2022-2.

Jaksic, F. M., Iriarte, J. A., Jiménez, J. E., & Martínez, D. R. (2002). Invaders without frontiers: Cross-border invasions of exotic mammals. *Biological Invasions*, *4*(1–2), 157–173. https://doi.org/10.1023/A:1020576709964

Jelinski, D. E. (1989). Seasonal differences in habitat use and fat reserves in an arctic muskrat population. *Canadian Journal of Zoology*, *67*(2), 305–313. https://doi.org/10.1139/z89-045

Jensen, A. J., Marneweck, C. J., Kilgo, J. C., & Jachowski, D. S. (2022). Coyote diet in North America: geographic and ecological patterns during range expansion. *Mammal Review*, *52*(4), 480–496. https://doi.org/10.1111/mam.12299

Kadlec, R. H., Pries, J., & Mustard, H. (2007). Muskrats (*Ondatra zibethicus*) in treatment wetlands. *Ecological Engineering*, *29*(2), 143–153. https://doi.org/10.1016/j.ecoleng.2006.06.008

Kirk, H., Connolly, C., & Freeland, J. R. (2011). Molecular genetic data reveal hybridization between *Typha angustifolia* and *Typha latifolia* across a broad spatial scale in eastern North America. *Aquatic Botany*, *95*(3), 189–193. https://doi.org/10.1016/j.aquabot.2011.05.007

Kiviat, E. (1978). Vertebrate use of muskrat lodges and burrows. *Estuaries*, *1*(3), 196–200. https://doi.org/10.2307/1351464

Kroll, R. W., & Meeks, R. L. (2020). Muskrat population recovery following habitat re-establishment near southwestern Lake Erie. *Wildlife Society Bulletin*, *13*(4), 483–486.

Kua, Z. X., Stella, J. C., & Farrell, J. M. (2020). Local disturbance by muskrat, an ecosystem engineer, enhances plant diversity in regionally-altered wetlands. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3256

Kurta, A. Mammals of the Great Lakes Region. 3rd Ed. The University of Michigan Press, Ann Arbor, Michigan, USA.

Lacki, M. J., Peneston, W. T., Adams, K. B., Vogt, F. D., & Houppert, J. C. (1990). Summer foraging patterns and diet selection of muskrats inhabiting a fen wetland. *Canadian Journal of Zoology*, *68*(6), 1163–1167. https://doi.org/10.1139/z90-172

Larreur, M. R., Windels, S. K., Olson, B. T., & Ahlers, A. A. (2020). Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. *Landscape Ecology*, *35*(1), 59–68. https://doi.org/10.1007/s10980-019-00925-5

Lishawa, S. C., Lawrence, B. A., Albert, D. A., & Tuchman, N. C. (2015). Biomass harvest of invasive *Typha* promotes plant diversity in a Great Lakes coastal wetland. *Restoration Ecology*, *23*(3), 228–237. https://doi.org/10.1111/rec.12167

Macarthur, R. A. (1980). Daily and seasonal activity patterns of the muskrat *Ondatra zibethicus* as revealed by radiotelemetry. *Ecography*, *3*(1), 1–9. https://doi.org/10.1111/j.1600-0587.1980.tb00702.x

MacGregor, D. (2013). Teachings from the muskrat. http://muskratmagazine.com/teachings-from-the-muskrat/. Accessed April 2023.

Miller, J. E. (2018). Muskrats. *Wildlife Damage Management Technical Series, 14*. https://digitalcommons.unl.edu/nwrcwdmts/14

Mott, C. L., Bloomquist, C. K., & Nielsen, C. K. (2013). Within-lodge interactions between two ecosystem engineers, beavers (Castor canadensis) and muskrats (Ondatra zibethicus). *Behaviour*, *150*(11), 1325–1344. https://doi.org/10.1163/1568539X-00003097

Nowak, R. M., & Paradiso, J. L. 1983. Walker's Mammals of the World. Volume 2. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Nummi, P., Väänänen, V. M., & Malinen, J. (2006). Alien grazing: Indirect effects of muskrats on invertebrates. *Biological Invasions*, *8*(5), 993–999. https://doi.org/10.1007/s10530-005-1197-x

O'Neil, T. 1949. The muskrat in the Louisiana coastal marshes. Louisiana Department of Wildlife and Fish., New Orleans. p. 49.

O'Neil, T. & Linscombe, G. (1976). The fur animals, the alligator, and the fur industry in Louisiana. *Louisiana Wildlife and Fish Commission*, *Wildlife Education Bulletin*, *106*.

Obbard, M. E., Jones, J. G., Newman, R., Booth, A., Satterthwaite, A. J., & Linscombe, G. (1987). *Furbearer Harvests in North America*. *January 1987.*

Pieper, S. J., Freeland, J., & Dorken, M. (2022). Patterns of pollen dispersal and pollen capture in the hybridizing cattails, *Typha latifolia* and T. *angustifolia*. *Botany*. https://doi.org/10.1139/cjb-2021-0166

Proulx, G., & Gilbert, F. F. (1983). The ecology of the muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario. *Canadian Field-Naturalist*, *97*(4), 377–390.

Proulx, G., McDonnell, J. A., & Gilbert, F. F. (1987). Effect of water level fluctuations on muskrat, *Ondatra zibethicus*, predation by mink, Mustela vison. *Canadian Field-Naturalist*, *101*, 90-92.

Rehm, E. M., & Baldassarre, G. A. (2007). The influence of interspersion on marsh bird abundance in New York. *Wilson Journal of Ornithology*, *119*(4), 648–654. https://doi.org/10.1676/06-060.1

Roberts, N. M., & Crimmins, S. M. (2010). Do trends in muskrat harvest indicate widespread population declines? *Northeastern Naturalist*, *17*(2), 229–238. https://doi.org/10.1656/045.017.0206

Sadowski, C., & Bowman, J. (2021). Historical surveys reveal a long-term decline in muskrat populations. *Ecology and Evolution*, *11*(12), 7557–7568. https://doi.org/10.1002/ece3.7588

Sather, J. H. (1958). Biology of the Great Plains Muskrat in Nebraska. *Wildlife Monographs*, *2*, 1–35.

Shay, J. M., de Geus, P. M. J., & Kapinga, M. R. M. (1999). Changes in shoreline vegetation over a 50-year period in the Delta Marsh, Manitoba in response to water levels. *Wetlands*, *19*(2), 413–425.

Soper, D. (1942). Mammals of Wood Buffalo Park, Northern Alberta and District of Mackenzie. *Academy of Management Review*, *31*(2), 386–408.

Stewart, D., Hood, W. G., & Martin, T. G. (2023). Undetected but Widespread: the Cryptic Invasion of Non-Native Cattail (*Typha*) in a Pacific Northwest Estuary. *Estuaries and Coasts*, *46*(3), 802–817. https://doi.org/10.1007/s12237-023-01171-4

Straka, J. R., Antoine, A., Bruno, R., Campbell, D., Campbell, R., Campbell, R., Cardina, J., Gibot, G., Gray, Q. Z., Irwin, S., Kindopp, R., Ladouceur, R., Ladouceur, W., Lankshear, J., Maclean, B., Macmillan, S., Marcel, F., Marten, G., Marten, L., McKinnon, J., Patterson, L. D., Voyageur, M., Whiteknife, G., Wiltzen, L. & Giguère,

N. (2018). We used to say rats fell from the sky after a flood: Temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta. *Arctic*, *71*(2), 218–228. https://doi.org/10.14430/arctic4714

Takos, M. J. (1947). A Semi-Quantitative Study of Muskrat Food Habits. *The Journal of Wildlife Management*, *11*(4), 331–339.

Tangen, B. A., Bansal, S., Freeland, J. R., Travis, S. E., Wasko, J. D., mcgonigle, T. P., Goldsborough, L. G., Gow, K., Marburger, J. E., & Meier, J. A. (2022). Distributions of native and invasive Typha (cattail) throughout the Prairie Pothole Region of North America. *Wetlands Ecology and Management*, *30*(1), 1–17. https://doi.org/10.1007/s11273-021-09823-7

Toner, J., Farrell, J. M., & Mead, J. V. (2010). Muskrat abundance responses to water level regulation within freshwater coastal wetlands. *Wetlands*, *30*(2), 211–219. https://doi.org/10.1007/s13157-010-0034-x

Turner, C. K., Lantz, T. C., & Fisher, J. T. (2020). Muskrat distributions in a changing Arctic delta are explained by patch composition and configuration. *Arctic Science*, *6*(2), 77–94. https://doi.org/10.1139/as-2018-0017

Viljugrein, H., Lingjærde, O. C., Stenseth, N. C., & Boyce, M. S. (2001). Spatio-temporal patterns of mink and muskrat in Canada during a quarter century. *Journal of Animal Ecology*, *70*(4), 671–682. https://doi.org/10.1046/j.1365-2656.2001.00526.x

Wagnon, C. J., & Serfass, T. L. (2017). Use of camera traps provides insight into the feeding ecology of Red Foxes (*Vulpes vulpes*). *Canadian Field-Naturalist*, *131*(1), 19–22. https://doi.org/10.22621/cfn.v131i1.1950

Ward, E. M., & Gorelick, S. M. (2018). Drying drives decline in muskrat population in the Peace-Athabasca Delta, Canada. *Environmental Research Letters*, *13*(12), 124026. https://doi.org/10.1088/1748-9326/aaf0ec

Ward, E. M., Solari, K. A., Varudkar, A., Gorelick, S. M., & Hadly, E. A. (2021). Muskrats as a bellwether of a drying delta. *Communications Biology*, *4*(1). https://doi.org/10.1038/s42003-021-02288-7

Weller, M. W., & Spatcher, C. S. (1965). Role of habitat in the distribution and abundance of marsh birds. *Special Report No. 43*, 4-31.

Wilcox, D. A., & Bateman, J. A. (2018). Photointerpretation analysis of plant communities in Lake Ontario wetlands following 65 years of lake-level regulation. *Journal of Great Lakes Research*, *44*(6), 1306–1313. https://doi.org/10.1016/j.jglr.2018.08.007

Wilcox, D. A., & Meeker, J. E. (1992). Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. *Wetlands*, *12*(3), 192–203. Https://doi.org/10.1007/BF03160609

Willner, B. G. R., Feldhamer, G. A., Zucker, E. E., & Chapman, J. A. (1980). *Ondatra zibethicus*. *The American Society of Mammologists*, *141*, 1–8.

Chapter 2: Impact of *Typha* x *glauca* invasions and interspersion on muskrat populations in southern Ontario

Abstract

Muskrat (*Ondatra zibethicus*) populations are declining in North America. The exact cause or causes of these widespread declines are largely unknown. Following a similar timeframe, wetlands have been experiencing an invasion of cattail (*Typha*) in large parts of the continent. Specifically, *T.* x *glauca*, a hybrid of native *T. latifolia* and *T. angustifolia*, has been increasing in range and abundance. The hybrid is associated with many negative impacts on wetland ecosystems, including reduced biodiversity, open water habitat, and the interspersion of water and vegetation, the latter of which is an important habitat feature for muskrats. We sought to determine the impact of these wetland invasions on muskrat populations. We sampled 39 *Typha*-dominated marshes across south-central Ontario to test the hypotheses that muskrats are declining in North America due to: (1) the increased relative frequency of *T.* x *glauca* in marshes, and (2) reduced marsh interspersion, which is associated with *T.* x *glauca* invasions. At all sites, we estimated muskrat population density using house counts as a proxy, sampled *Typha* communities in the field to determine the relative frequency of *T.* x *glauca*, and measured interspersion using remote sensing techniques. We found that muskrat population density was positively correlated with marsh interspersion, but not correlated with the relative frequency of *T.* x *glauca*. However, most sites were highly dominated by *T.* x *glauca*, limiting our inference. Our findings suggest that changing wetland structure may be contributing to muskrat population declines in North America, but more research is needed to determine the impacts of *T.* x *glauca* invasions on muskrat population declines.

Keywords: *Ondatra zibethicus*, *Typha* x *glauca*, interspersion, invasive species, wetlands, Lake Ontario

Introduction

Increasing evidence is pointing to pronounced, widespread declines in North American muskrat populations (Benoit & Askins, 1999; Roberts & Crimmins, 2010; Brietzke, 2015; Ahlers & Heske, 2017; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Gregory, 2019; Sadowski & Bowman, 2021). Muskrats are important furbearers in Canada and the United States (Willner *et al.*, 1980; Boutin & Birkenholz, 1987), with millions of pelts being sold each year and annual sales peaking at over $100 million (CAD) in the mid-1900s (Boutin & Birkenholz, 1987). They are also highly valued by many First Nations, providing food, clothing, and income and serving a pivotal role in the Anishinaabe story of creation (MacGregor, 2013; Brietzke, 2015; Straka *et al*., 2018). Furthermore, muskrats are widely considered to be ecosystem engineers (Higgins & Mitch, 2000; Mott *et al.*, 2013; Kua *et al.*, 2020) and keystone species (Straka *et al.*, 2018; Danell, 1996) in wetlands, disproportionately influencing their habitats through intense herbivory and the construction of houses and bank dens. In doing so, they create and maintain habitat for many wetland species (Weller & Spatcher, 1965; Danell, 1977; Hewitt & Miyanishi, 1997; Kua *et al*., 2020). A widespread decline in this historically prolific rodent is surprising, and given their overall importance, more research is needed to determine the underlying cause.

Muskrat abundance may fluctuate widely and follow distinct cycles of four to fourteen years (Elton & Nicholson, 1942; O'Neil, 1949; Butler, 1962; Danell, 1978). However, many observed declines in recent decades are of a magnitude and duration not previously seen (Benoit & Askins, 1999; Ward & Gorelick, 2018; Gregory, 2019;

Sadowski & Bowman, 2021; Brietzke, 2015). Populations are usually quick to rebound from short-term die-offs (Chatterton, 1944; Errington, 1951), as low population density often stimulates breeding (Errington, 1951), and muskrats are highly fecund (Errington, 1963; Boutin & Birkenholz, 1987; Sadowski & Bowman, 2021). Therefore, the widespread and sustained declines are likely the result of some persistent environmental stressor. The loss of wetland habitat may be leading to declines in certain muskrat populations (e.g. Ward & Gorelick, 2018), but the loss of wetlands in North America since 1980 has not been sufficient to explain observed muskrats declines since that time (Davidson, 2014). However, the structure and composition of many North American wetlands are changing, and this may have negative implications for muskrats.

Reported long-term declines in muskrat populations are mostly associated with marshes (Benoit & Askins, 1999; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Gregory, 2019; Sadowski & Bowman, 2021). Marshes are important habitats for muskrats as they provide shallow, still water that generally supports large quantities of emergent vegetation on which muskrats primarily feed (Errington, 1963; Boutin & Birkenholz, 1987; Kadlec *et al.*, 2007). Cattail (*Typha*) is a highly prominent component of marsh habitats in North America (Smith, 2000). It is strongly associated with muskrats for both feeding (Takos, 1947; Bellrose, 1950; Lacki *et al.*, 1990; Kurta, 1995) and house-building (Bellrose & Brown, 1941; Messier *et al.*, 1990; Clark, 1994). As a result, marshes have historically supported large numbers of muskrats (Dozier, 1950; Errington, 1963; Bishop, 1979; Proulx & Gilbert, 1983). Broadleaf cattail (*T. latifolia*) is native to North America and is found in marshes across the United States and Canada (Smith, 2000).

Narrowleaf cattail (*T. angustifolia*), likely native to Eurasia (Ciotir *et al.*, 2013), has coexisted in North America for over a century. The range of *T. angustifolia* has been steadily expanding westward from the east coast (Galatowich, 1999; Shih & Finkelstein, 2008; Tangen *et al.*, 2022) and it is widely considered an invasive species (Frieswyck *et al.*, 2007; Vaccaro *et al.*, 2009; Schummer *et al.*, 2012; Stewart *et al.*, 2023); however, this claim may not be warranted, as these studies fail to properly differentiate *T. angustifolia* from hybrids. Due to range and niche overlap, hybridization between *T. latifolia* and *T. angustifolia* is widespread and common (Galatowitsch *et al.*, 1999; Pieper *et al.*, 2022; Tangen *et al.*, 2022; Stewart *et al.*, 2023). The resulting hybrid is known as *T.* x *glauca* (Smith, 2000), though back-crossed and advanced-generation hybrids also exist (Pieper *et al*., 2017). Its range has generally expanded concurrently with that of *T. angustifolia* where *T. latifolia* also exists (Galatowitsch, 1999; Smith, 2000). Today, it can be found in a large portion of the continent from Quebec to Hawaii and from Alaska to Florida (Hall, 2008). *Typha* x *glauca* is considered an aggressive invader, outcompeting many wetland plants, including both parental species (Shay & Shay, 1986; Smith, 1967; Boers & Zedler, 2008; Freeland *et al.*, 2013). *Typha* x *glauca* is now the dominant taxon in many Great Lakes coastal wetlands (Woo & Zedler, 2002; Tuchman *et al.*, 2009; Travis *et al.*, 2011; Pieper *et al.*, 2020) and wetlands across the Prairie Pothole region in Canada and the United States (Tangen *et al.*, 2022). The invasion of *T.* x *glauca* has been cryptic, as hybrids closely resemble both parental species (Kuehn & White, 1999). Consequently, the prevalence of *T.* x *glauca* in North American wetlands is likely underestimated. The impact of this invasion on wetlands and muskrats remains poorly understood. However, invasions by *T.* x *glauca* are associated with a reduction in wetland habitat quality (Boers *et al.*, 2007; Lishawa *et al.*, 2010; Lawrence *et al.*, 2016; Markle *et al.*, 2018; Wilcox & Bateman, 2018), which may have negative effects on muskrat populations.

A catalyst to the invasion of *T.* x *glauca* in North America is water level management (Shay *et al.*, 1999; Wilcox *et al.*, 2008; Farrell *et al.*, 2010; Wilcox & Bateman, 2018). Specifically, *Typha* is highly productive when water levels are stabilized (Wilcox *et al.*, 1985; Shay *et al.*, 1999; Boers *et al.*, 2007; Boers & Zedler, 2008). A well-documented example of such an invasion followed the construction of the St. Lawrence Seaway and the implementation of a decades-long water management regime enacted by the International Joint Commission (IJC). Beginning in 1963, the IJC enacted Plan 1958D that would regulate water levels in Lake Ontario and the upper St. Lawrence River. Naturally occurring seasonal fluctuations in water levels were dampened via fall drawdowns and water retention, thereby stabilizing water levels and creating optimal conditions for hydroelectric power generation and other interests (Farrell *et al.*, 2010). After decades of operating under Plan 1958D, concerns mounted over expanding cattail stands and the resulting loss of wetland biodiversity (IJC, 2014). Today, despite abundant cattail stands, muskrat population densities in Lake Ontario coastal wetlands have likely declined considerably (Greenhorn *et al*., 2017). Though it has been suggested that fall drawdowns under Plan 1958D are responsible for reduced muskrat populations in Lake Ontario coastal wetlands (Toner *et al.*, 2010), others have suggested that the resulting changes in wetland vegetation due to the overall stabilization of water levels could be to blame (Greenhorn *et al.*, 2017; Sadowski & Bowman, 2021).

Muskrats are known to be found in areas with high levels of marsh interspersion – that is, a roughly equal ratio of water and emergent growth (Weller & Spatcher, 1965; Weller, 1988; Proulx & Gilbert, 1983), otherwise known as hemi-marsh (Weller & Spatcher, 1965; Kaminski & Prince, 1981) – which likely provides optimal forage, cover, and mobility (Brinson *et al.*, 1995). Invasions by *T.* x *glauca* typically lead to reduced marsh interspersion and open water habitat (Harris & Marshall, 1963; Wilcox *et al.*, 2005; Wilcox *et al.*, 2008; Schummer *et al.*, 2012; Markle *et al*., 2018; Smith *et al.*, 2021). As the highly aggressive *T.* x *glauca* progressively invades wetlands across the continent, it is possible that muskrat populations are responding negatively to the degradation of marsh habitat caused by these invasions, such as reduced marsh interspersion. Studies have yet to examine the effects of *Typha* invasions, namely *T.* x *glauca*, and resulting habitat changes on muskrat populations. We conducted a comprehensive, regional-scale study to determine whether muskrat populations in southern Ontario are indeed linked to the invasion of *T.* x *glauca*. We hypothesized that muskrat populations are declining in southern Ontario due to the invasion and resulting loss of interspersion caused by this hybrid cattail. We predicted that: (1) muskrat population density would be negatively correlated with the frequency of *T.* x *glauca* relative to parental *Typha* spp. across sites, and (2) muskrat population density would be positively correlated with interspersion across sites. Our study will provide managers of wildlife, wetlands, and water levels new insights to help guide policy development surrounding a culturally and economically important furbearer.

Methods

Site selection

We selected 39 marshes in south central Ontario for a broad-scale test of our hypothesis (Figure 2.1). We targeted marshes that were *Typha*-dominated, at least 10 ha in size, and relatively close to Peterborough, Ontario. At each site, we estimated the relative frequency of *Typha* taxa, the degree of marsh interspersion, and the population density of muskrats. Sites were located in the Great Lakes-St. Lawrence Lowlands between Toronto (43.64679, -79.36840) and Napanee, Ontario (44.24673, -76.95552) and included both inland and coastal marshes. Most of these marshes experience some degree of water level management throughout the year. We considered all sites to be inhabitable by muskrats based on the region and the high abundance of *Typha*. We initially conducted a visual assessment of *Typha* dominance using public mapping tools (e.g. Google Maps) and later confirmed habitat classes by conducting image classifications in ArcGIS Pro 2.9 (ESRI, 2021) with recent, high-resolution imagery. Many of these marshes are part of larger wetland complexes containing bog, fen, or swamp habitat, but we limited our sampling to marshes only. Other prominent vegetation in these marshes include water lily (family *Nymphaeceae*), wild rice (*Zizania* spp.), water milfoil (*Myriophyllum* sp.), common duckweed (*Lemna minor*) and European frogbit (*Hydrocharis morsus-ranae*).

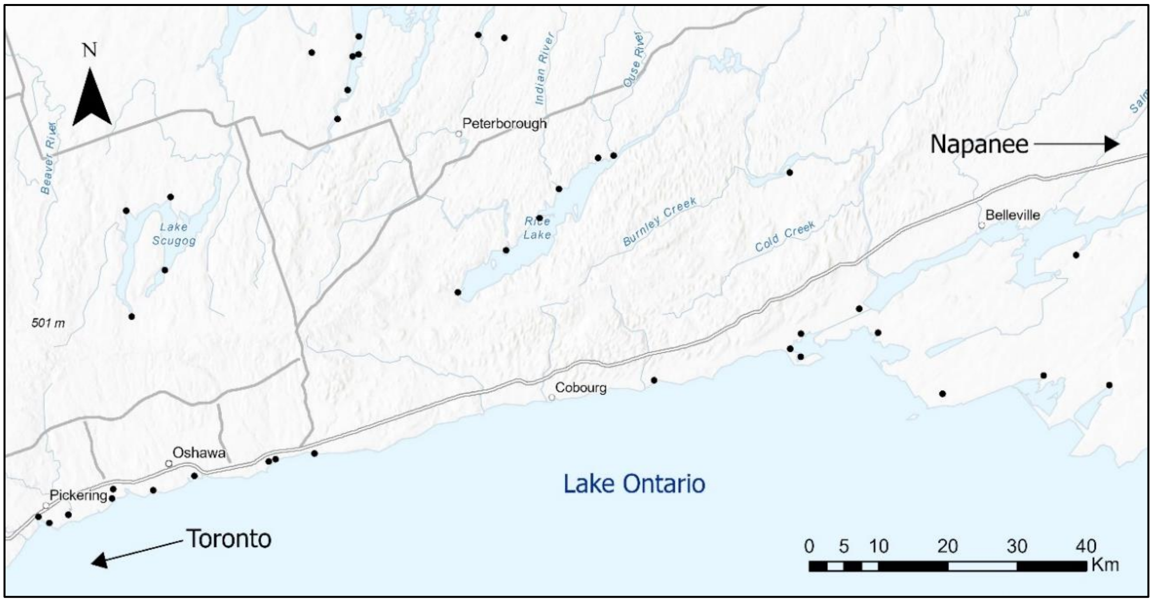

Figure 2.1. Study area with points representing all marshes sampled.

Cattail phenotype distribution

Field methods

We manually delineated 3 – 7 transects for *Typha* sampling *a priori* in ArcGIS Pro using recent aerial imagery as a guide. We employed roughly equal spacing of transects in a manner that was spatially representative of each site (Figure 2.2). For smaller sites (< 50 ha), transects were typically spread along the entire navigable cattail-water edge of the marsh. At larger sites, particularly those with multiple channels, transects typically spanned a large, accessible portion of the marsh. In most cases, more transects were sampled at larger sites to better represent the larger area. Transects began at the water's edge and moved toward the interior of the *Typha* stand in a roughly perpendicular line to approximate a depth gradient. This transect configuration was designed to approximate a depth gradient and avoid sample bias, as evidence has suggested that *T. latifolia* prefers shallower depths while *T. angustifolia* prefers deeper water (McDonald, 1955; Grace & Wetzel, 1981; Grace & Wetzel, 1982; Travis *et al.*, 2010), though more recent evidence suggests that *Typha* taxa are not segregated by depth in the Peterborough, Ontario region (McKenzie-Gopsill *et al.*, 2012; Zapfe & Freeland, 2015) or in the broader region of eastern North America (Pieper *et al.*, 2018). Apart from these guidelines, *Typha* sampling was effectively random. Where possible, we sampled three ramets along each transect approximately three meters apart, with the first ramet being sampled at the water's edge. Transects were accessed by canoe or motor craft or occasionally on foot by multiple teams. Most sampling occurred from June 15 to August 4, 2021; however, due to time constraints, a small number of sites and transects could only be sampled in summer 2022. When arriving at the start of a transect, surveyors sampled the nearest flowering ramet (rather than sampling the nearest ramet with leaves only, to ensure the ramet would flower over the summer). The surveyor then walked approximately three meters along the transect until they encountered another flowering ramet within reach, and repeated this with a third ramet at the end of the transect. If no flowering ramets were present at a given position along the transect, the nearest ramet was flagged with the hope that it would be flowering on the following visit. Occasionally, the third and/or second ramet along the transect had not flowered by the final visit. In these cases, the sampler diverged from the transect in a perpendicular direction up to 2m until a flowering ramet could be sampled. If a flowering ramet could not be found within 2m of the transect on the final visit for a given position, no sample was collected for that position. In a few rare cases, none of the ramets along the original transect flowered by the final visit, in which case we reassigned the transect to the nearest location with flowering ramets. Furthermore, in the rare occasion that a transect was devoid of *Typha* entirely, the transect was reassigned to a new location that included sufficient *Typha* for sampling. Logistical factors also prompted us to relocate or omit transects in certain cases, such as limited accessibility due to low water levels, inclement weather leading to reduced sample integrity, and limited sampling time. In all cases, we attempted to relocate transects to nearby locations and/or maintain a roughly equal spread of transects, keeping our sampling regime representative of the site.

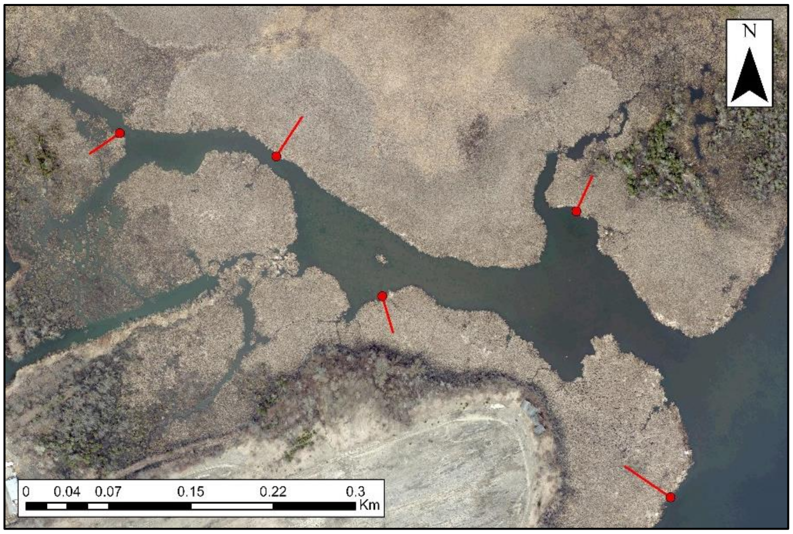

Figure 2.2. Typical transect configuration with points indicating starting locations (transects oversized to show direction).

Sample collection

While genetically pure ramets of *T. latifolia* and *T. angustifolia* can typically be distinguished in the field, there is overlap in the morphology of *T.* x *glauca* and its parental species (Tangen *et al.*, 2022; Figure 2.3). For this reason, we collected samples to be used for more reliable identification at the microscopic level. From each ramet, we collected a sprinkling of pollen (when present) in a glassine envelope, a portion of the pistillate spike in a paper bag, and two of the youngest and most intact leaf tips in a coin envelope. Pollen envelopes were sealed with tape and kept chilled in a cooler in the field and later kept in a refrigerator at a standard temperature (~ 3°C). Spike and leaf samples were kept at ambient temperature and stored in a dry room with silica bead packets to accelerate drying and prevent mold formation. Pollen is only shed for a limited time each growing season (Selbo & Snow, 2004; Ball & Freeland, 2013) making pollen collection at all sites and transects impossible. Therefore, we began sampling as soon as we observed signs of flowering in 2021 to ensure the maximum amount of pollen could be sampled. If we arrived at a transect and pollen shedding had not yet occurred from the ramet to be sampled, we marked the ramet with flagging tape and returned to the site later with the intention of collecting pollen on the next visit. However, most pollen had already shed by the second visit as we first prioritized visiting sites that had not yet been sampled, though we were still able to collect pistillate spikes for identification as well as leaf samples for additional validation. In addition to collecting samples, we measured median leaf width and spike gap for a large proportion of samples, and measured water depth at each location by inserting a pole into the water until we encountered firm resistance (i.e. depth measurements may have included soft, wet organic material). We attempted to measure depth as close to the sampled ramet as possible. In the presence of solid floating cattail mats, we punctured the mat wherever possible and measured depth as normal.

Figure 2.3. Typical *Typha* phenotypes observed in study area. From left to right: *T. latifolia* with wider leaves and no gap between spikes, *T. angustifolia* with narrower leaves and distinct gap between spikes, *T. x glauca* showing intermediate leaf width and variable spike gap length.

Sample identification

Typha in northeastern North America can be identified as either *T. latifolia, T. angustifolia,* or hybrid *T.* x *glauca* by the identification of alleles at microsatellite loci

(Snow *et al.*, 2010; Kirk *et al.*, 2011; Ball & Freeland, 2013). While we collected leaf tissue samples from nearly all ramets to be used in future DNA extraction, we identified ramets based on the morphological phenotype observed in pollen and spike samples using a key to *Typhaceae* by Smith (2000). This key uses pollen cluster configuration as a diagnostic character when differentiating the three taxa found in Canada. This has been shown to be highly reliable for differentiating *T. latifolia*, whose pollen exclusively forms tetrads (Smith, 2000; Finkelstein, 2003; Selbo & Snow, 2004). *T. angustifolia* and *T*. x *glauca* both produce monads, though *T.* x *glauca* may also produce dyads, triads, and tetrads (Smith, 2000; Finkelstein, 2003). Therefore, a sufficient number of monads is required to confidently identify a sample as *T. angustifolia* or *T.* x *glauca* (Finkelstein, 2003). Furthermore*,* the limited flowering period for staminate (male) flowers prevented us from sampling pollen from all ramets. Pistillate spikes, on the other hand, were present at the beginning of our sampling period, or soon after, at all transects and sites and remained viable for sampling throughout the spring and summer, allowing us to collect pistillate spikes from nearly all sampled ramets. The floral structures within them are recommended by Smith (2000) as “generally essential for accurate identification of *Typha* species and their hybrids”. Specifically, *T. latifolia* lacks bracteoles completely, while *T. angustifolia* has dark bracteoles that are wider than adjacent stigmas, and *T.* x *glauca* has lighter-coloured bracteoles that are narrower than adjacent stigmas (Smith, 2000; Figure 2.4). It should be noted that this key was developed only for identifying pure parental species and F1 hybrids; the morphological characteristics of pollen and pistillate spikes for introgressed and advanced-generation hybrids is currently unknown. For simplicity, we assumed that the characteristics used to distinguish *T.* x *glauca* apply to introgressed and advanced-generation hybrids; as such, we use the term *T.* x *glauca* to refer to all hybrid classes between *T. latifolia* and *T. angustifolia*. We processed all samples of pollen and pistillate spikes. Pollen samples were emptied onto a slide and viewed at 400x magnification using a compound microscope. For pistillate spikes, a bunch of flowers was removed and placed in a Petrie dish and viewed at 20 – 40 X magnification using a dissecting microscope. Finally, of the 664 ramets sampled along transects, we calculated the percentage of samples identified as *T.* x *glauca* (*T.* x *glauca* relative frequency) at each site. We assessed the accuracy of pistillate spike phenotype identification by comparing the number of pistillate spikes identified as each putative taxon to the number of corresponding pollen samples identified as the same taxon, assuming the latter represented the true phenotype. Each of the pollen and spike samples were identified independently to avoid bias. We also compared the spike gap and median leaf width among taxa to determine whether relative differences among putative taxa were congruent with Smith (2000). We used both transect and opportunistic cattail samples to conduct comparisons of identification methods and morphology.

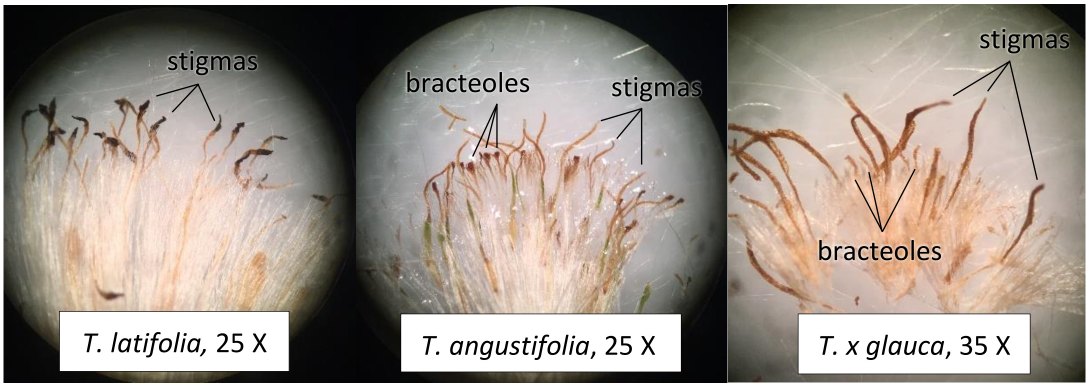

Figure 2.4. Pistillate flowers under magnification showing possible pistillate phenotypes of the three cattail (*Typha*) taxa occurring in Canada, as outlined in Smith (2000).

Land cover classification and interspersion

Imagery used

We conducted land cover classifications for all sites to estimate marsh interspersion and to ensure that sample cells to be used for muskrat house counts met criteria for suitable muskrat habitat. Sites were initially delineated by drawing polygons around contiguous or near-contiguous patches of cattail-dominated marsh and adjacent water features. We classified land cover types across sites using the Classification Wizard in ArcGIS Pro and recent high-resolution aerial imagery. We primarily used imagery from the South-Central Ontario Orthophotography Project 2018 (SCOOP 2018) collected by Land Information Ontario (2019). This imagery has a spatial resolution of 16 cm and is comprised of four bands (red, green, blue, and near-infrared). Imagery was acquired in clear, leaf-off, mostly ice-free conditions in early to mid-spring 2018. This was the latest available imagery with optimal resolution and conditions for conducting land cover classifications for our purposes, particularly for distinguishing water from non-water features. Though we also collected high-resolution imagery in 2021 and 2022 to use for muskrat house counts, this was collected in winter when snow cover would generally make it difficult to differentiate land cover types. Since SCOOP 2018 predated the study by two years, more recent imagery accessible in public mapping tools (e.g. Google Earth Pro) was used to identify any major wetland changes (e.g. shifting or expanding of cattail stands). Most sites remained largely static in vegetation structure and composition with the exception of Cranberry Marsh and Oshawa Second Marsh. For these sites, we used winter imagery collected in 2021 (see “Muskrat house counts” below) for land cover classifications. This imagery was obtained in low snow cover conditions where the emergent vegetation-water edge could easily be delineated and snow and ice in the marsh generally represented water in ice-free conditions, confirmed using ancillary imagery (e.g. Google Earth Pro).

Image classification

We used an object-based image classification approach which groups neighboring pixels into objects based on spatial and spectral relationships, thus producing more contextual and ecologically relevant classifications, particularly for wetlands (Grenier et al., 2008; Figure 2.5); this type of image classification is regarded as superior to traditional pixel-based classifications at higher resolutions (Luymes & Chow-Fraser, 2021). Before classifying, we produced a mosaic image for each site (for Cranberry and Oshawa Second Marsh, we also resampled the imagery to match the spatial resolution of SCOOP 2018). We then segmented all mosaics using the Segment Mean Shift tool in ArcGIS Pro. This tool allows the user to input three main parameters related to segmented image detail. We used the maximum spatial and spectral detail values (20 and 20) for nearly all sites, which clearly distinguished all or most landcover types that could be distinguished with the human eye at a scale of roughly 1:100. Due to higher levels of within-class spectral variation observed in our winter imagery, we used the minimum spectral detail (1) for Cranberry and Oshawa Second Marsh; this allowed for more blending of contiguous features in the resulting segmented image despite differences in spectral values. Finally, we used a minimum segment size of 30 pixels for all sites, meaning that no object smaller than 30 pixels, or 0.768 m^2 in our case, would be detected. This minimum threshold reduced the amount of speckle (i.e. classification of small, irrelevant features) caused by shadows, sheen, and other ‘false’ objects in the marsh. We do not believe this led to any significant loss of habitat features in our final classifications.

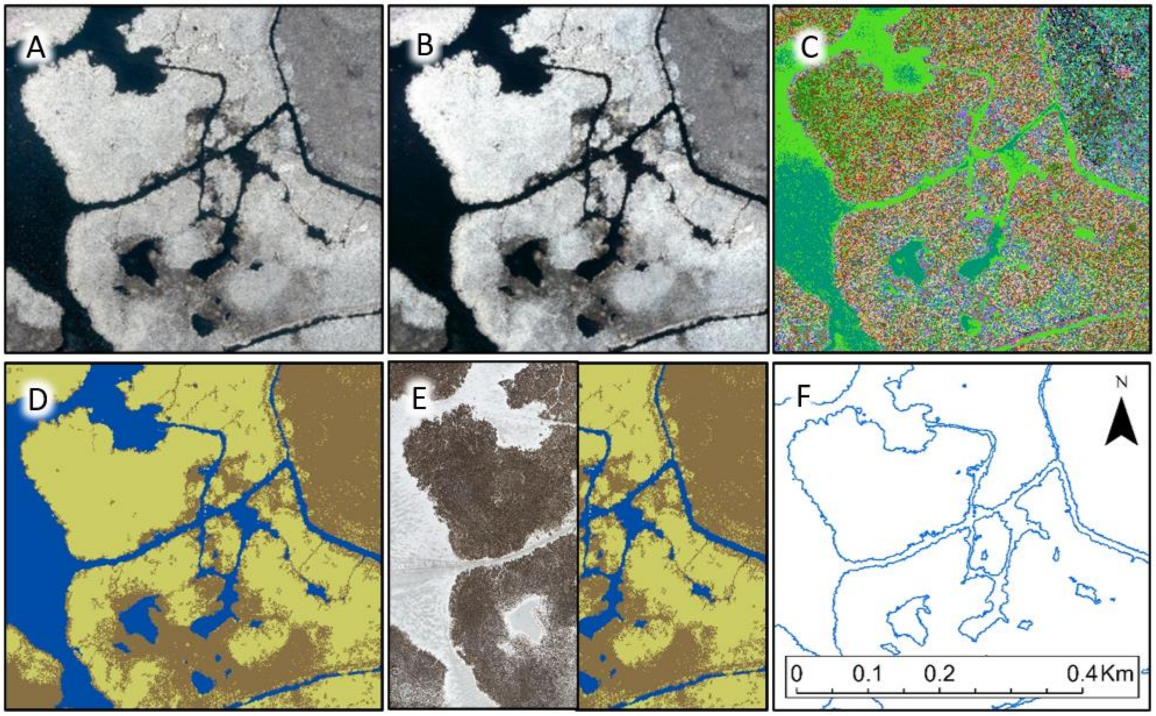

Figure 2.5. Unsupervised object-based classification of SCOOP 2018 imagery and resulting vegetation-water edges using Classification Wizard in ArcGIS Pro. Segment Mean Shift was used on mosaic of SCOOP 2018 imagery tiles (A) to produce a segmented image (B). The segmented image was used with SCOOP 2018 mosaic to produce a classified raster with a user-identified number of classes (C). Classes were then merged and assigned a class of interest (D; blue = *Water*, yellow = *Cattail*, brown = *Other*). The classified raster was converted to polygons representing each class. Polygon edges were edited to more closely approximate recent changes in marsh structure, using more recent imagery as a guide (E). *Water* polygons were converted to polylines to represent vegetation-water edges used to measure interspersion (F).

Due to a paucity of training data required for supervised classifications, we used an unsupervised classification approach where the classifier (i.e. computer) automatically differentiates a user-defined number of classes based on the spectral value of RGB pixels and the size and shape of segmented objects, and the user then identifies and merges each computer-generated class into one of their relevant classes of interest. We changed the maximum number of classes to 40 in most cases, allowing for a high level of differentiation between classes, as is common practice in unsupervised classification, except for a few highly heterogeneous sites where a maximum of 50 or 60 classes was more appropriate. We ultimately classified land cover types into three broad classes: cattail-dominated emergent vegetation, water, and all other land cover types, hereafter *Cattail*, *Water*, and *Other*. We defined *Cattail* as cattail having the greatest areal coverage of any plant species or type for a given area at a minimum of 50 %. It is also important to note that, depending on depth, water may be covered by submerged, floating, and/or emergent plants throughout the growing season. We reclassified any obvious misclassifications within the wizard (e.g., tree shadows classified as *Water*, pasture classified as *Cattail*, water classified as *Cattail*, etc.). We then converted these final rasters to polygons for ease of spatial processing.

Polygon editing

We further reclassified polygons corresponding to areas and/or objects that were still clearly misclassified. We then refined and improved the accuracy of classified polygons in several ways. For example, due to the high resolution of our imagery and high degree of computer-generated differentiation among classes (i.e. up to 60 initial classes), we ended up with a certain amount of speckle at all sites. This was mostly caused by shadows from trees, cattail, and other vegetation. Despite the high degree of initial class differentiation, there was still a considerable amount of spectral overlap between some of these features and other classes of interest. For example, certain groups of cattail shadows shared similar spectral values with parts of water bodies or buildings, such that identifying these shadows as *Cattail* would then lead to *Cattail* speckle appearing within that water body or building. We first tried to minimize the amount of speckle directly in the classification wizard. We prioritized the accurate classification of water features and wetland vegetation within the marsh to ensure that water edges would be accurately measured in calculating interspersion. If false water features appeared in the surrounding forest or developed areas, we could more easily identify and reclassify these objects in the reclassification step. Once the marsh appeared to be classified as closely as possible to what we perceived in the imagery with as little speckle as possible, we proceeded to reclassify any incorrectly classified objects in the surrounding area. To reduce the amount of remaining speckle in the marsh which was primarily caused by small shadows from cattail or other emergent vegetation being classified as *Other*, we reclassified all *Other* polygons under 5 m^2 to *Cattail*; this had no perceptible effect on the representation of actual objects in the *Other* class. Finally, to account for the few localized differences in marsh structure from 2018 to 2021/2022, we expanded or pared down existing polygons as necessary to account for the expansion or disappearance of marsh vegetation, respectively, and we digitized any new vegetation stands and manually classified them using our best judgement. Finally, since small (< $5m^2$) water features were sometimes misclassified as *Other* depending on the site, we reclassified all *Water* polygons < 5 m^2 to Other to have a standard minimum water feature size across sites.

Accuracy assessment

Upon completion of polygon edits, we conducted an accuracy assessment using over 1100 ground-truth points. *Cattail* and *Other* ground-truth points were collected across various discernable land cover classes at two heterogeneous sites (n = 76), as well as at predetermined cattail sampling locations at all sites (n = 229), and at arbitrary locations while conducting other field work at select sites (n = 256). GPS locations of ground-truth points were collected with a Garmin handheld GPS unit or iPhone SE 1st generation with an accuracy of ≤ 5 m. Some ground-truth points were not accessed directly but examined from the water's edge; these points were moved approximately 5 m inland from the water's edge prior to the accuracy assessment. Since water features are virtually unmistakable on SCOOP 2018, *Water* ground-truth points were not collected in the field. Rather, accuracy assessment points were identified using SCOOP 2018 imagery (n = 457), which allowed us to select small, inaccessible pools and rivulets leading to a more robust accuracy assessment. Furthermore, due to a lower sample of *Other* ground-truth points compared to *Cattail*, we identified additional unambiguous *Other* points using SCOOP 2018 imagery (e.g. forest, pasture, buildings) (n = 166). Ground-truth points remained hidden while conducting classifications and subsequent editing to avoid bias. We set a target overall accuracy of 80 % for our final classification and computed accuracy using a confusion matrix. Overall accuracy of final image classifications across sites was 87.7 % with a kappa coefficient of 81.4 %.

Habitat suitability

A grid of 1-ha sample cells was overlaid onto all site mosaics in ArcGIS Pro and clipped to original site boundary polygons. Cells were deemed suitable muskrat habitat and thus potentially sampled if the cell contained ≤ 80 % water, ≤ 80 % land, and ≥ 25 % cattail-dominated vegetation, replicating Greenhorn *et al.* (2017). Cattail dominance was defined as *Typha* spp. having the greatest areal coverage of any wetland plant species or type at a minimum of 50 %. Cells that did not fit these criteria were eliminated from the larger grid. To reduce the odds of sampling more than one distinct muskrat population per site, we further limited sample cells for each site to the largest group of contiguous suitable grid cells, and those no farther than one grid cell in distance (i.e. a maximum diagonal distance of 141 m) which is well within the dispersal abilities of muskrats (Errington, 1939; Errington & Errington, 1937; Miller, 2018) and within the home range of many individuals (MacArthur, 1980; Ahlers *et al.*, 2021).

Interspersion

Rather than the traditional definition of marsh interspersion as simply the ratio of emergent vegetation to water (Kaminski & Prince, 1981; Proulx & Gilbert, 1983), we measured interspersion as water edge density, in meters per hectare, as done by Rehm & Baldassarre (2007). Along with a reduction of open water relative to emergent plants, cattail invasions are linked with a reduction in emergent-water edge (Wilcox *et al.*, 2008). Edge density is likely an important metric for muskrat habitat suitability, and perhaps more so than the ratio of emergent vegetation to water. Muskrat activity in marshes is typically concentrated along these edges (Ervin, 2011; Sadowski & Bowman, 2021), and muskrats are less likely to be found in deep open water (Larreur *et al.*, 2020) or close to upland habitat (Ervin, 2011). Therefore, a given area may have an equal ratio of water and emergent vegetation but support fewer muskrats than an area of equal proportions but with higher edge density. Furthermore, vegetation-water edges are important habitat for other wetland vertebrates (Weller & Spatcher, 1965; Danell, 1979; Baltz *et al.*, 1993; Chabot *et al.*, 2014). We thus measured interspersion by converting final Water polygons to lines (i.e. polygon edges) and calculating the average length of these edges per suitable 1-ha cell at each site.

Muskrat house counts

Imagery collection

We used muskrat house counts as a proxy for muskrat population density as used in previous studies (Dozier, 1948; Proulx & Gilbert, 1984; Toner *et al*., 2010; Greenhorn et al., 2017; Straka *et* al., 2018; Sadowski & Bowman, 2021). We conducted counts using high-resolution aerial imagery collected in the winters of 2021 and 2022. Imagery used for primary house counts was collected in March 2021 for inland sites and February 2022 for coastal sites. Additionally, we collected imagery for a subset of coastal sites in 2021 for an inter-annual comparison of house counts. During winter in northern marshes, muskrat house numbers are typically static and represent the previous year's construction efforts (Errington, 1961; Boutin & Birkenholz, 1987; Danell, 1978); therefore, houses may be counted at any point during a given winter to reflect the preceding year's population level. We collected imagery for 36 of our 39 sites from a de Havilland Canada DHC-2T Turbo Beaver aircraft. Flights were conducted between 0900 and 1600 over several days each year in mostly clear conditions when possible. The target spatial resolution for these sites was 7.5 cm per pixel. This resolution typically results in aerial muskrat house counts that are not significantly different than muskrat house counts conducted on the ground at similar times (Ontario Ministry of Natural Resources and Forestry [OMNRF], unpublished). We used a Nikon D800 digital SLR camera with a factory resolution of 38 megapixels paired with a Nikon AF-S Nikkor 50mm f/1.8G lens in 2021 and a Nikon AF-S Nikkor 50mm f/1.4D lens in 2022. The camera was floor-mounted to a de Havilland Canada DHC-2T Turbo Beaver aircraft. We flew at a target speed of approximately 90 knots, taking photos every two seconds using the camera's interval timer shooting mode to achieve 75% photo overlap. We flew parallel flight lines spaced 276 m apart to achieve 50% sidelap at a target altitude of 765 m (2510 ft) above-ground-level to achieve our target image resolution. The camera was connected to a Garmin Aera 550 GPS unit equipped with a booster antenna to automatically geotag each photo. Raw photos were stitched into single, georeferenced mosaics for each site by droneMetrics (Ottawa, ON) using SimActive Correlator3D. Due to a spatial offset of up to 75 m, we further georeferenced each mosaic in ArcGIS Pro using SCOOP 2018 as a reference, which was considered accurate to within 0.45 m at 95%. The remaining three sites (Frenchman's Bay, Hydro Marsh, and Duffin's Creek) were flown by a private company (Airborne Sensing; Toronto, Ontario) at a target resolution of 5cm to replicate methods used in 2014 by the OMNRF at these sites (unpublished). This imagery was collected using a Vexcel Ultramap UCX photogrammetric camera system with 100.5 mm focal length on a SOMAG GSM3000 gyro-stabilized mount. The camera system was mounted to a Piper Aztec PA-27 twin turbo aircraft. Aircraft speed and image capture intervals were set to achieve 60% image overlap. Parallel flight lines were flown at 30% image sidelap at a target altitude of 730 m (2395 ft) above-ground-level to achieve our target image resolution. Images were geotagged using a Trimble Applanix IMU Type 57 and mosaics were produced using Inpho 4.6.2 OrthoVista.

Aerial house counts

Suitable cells within each site were each labelled with a sequential number. We then randomly selected ten cells to sample at each site using a random number generator. Three sites were limited to less than ten suitable cells, in which case we sampled all cells. Occupied or ‘active’ houses can be difficult to discern from inactive houses, and to a lesser extent, feeding structures (‘feeders’), when conducting aerial counts (Dozier, 1948; Boutin & Birkenholz, 1987; Sadowski & Bowman, 2021). However, feeders are often too small to be detected when there is snow cover (Dozier, 1948), and houses that have not been occupied since the previous winter generally break down throughout the year (Nicholson & Davis, 1957; Sather, 1958; Danell, 1978; Kurta, 1995) and should thus be less conspicuous than recently constructed or actively maintained houses which typically have a symmetrical, dome-like appearance (Butler, 1885; Dozier, 1948) with a resulting rounded shadow (Cline *et al.*, 2021). Therefore, we primarily searched sample cells for circular or elliptical structures with a raised appearance. Furthermore, a ring of roughly cleared vegetation around such a structure is typically diagnostic of a muskrat house (Dozier, 1948; Danell, 1977; Proulx & Gilbert, 1984). We also used the following attributes as additional indications of muskrat houses based on personal observations: a diameter of approximately 0.5 – 2.5 m (larger structures more likely to be beaver lodges), contrasting colour and/or texture to adjacent vegetation, connection via one or more rivulets to a larger water body (if within vegetation stand), and absence from SCOOP 2018 imagery suggesting that the structure was more recently constructed. Cells were systematically scanned at a scale that maximized magnification while minimizing image pixelation for optimum house detection (approximately 1:210, on average). Based on how closely suspected houses adhered to these criteria, we assigned one of three levels of confidence when marking houses, with “High” signifying ≥ 90% confidence, “Medium” signifying ≥ 50% confidence, and “Low” signifying < 50% confidence. However, we omitted low-confidence structures in calculating final house densities, as these possessed few of the characteristics of active houses. As such, “house density” and “houses” will hereafter refer to only high- and medium-confidence structures, collectively.

Ground-truthing

A subset of sites and sample cells were surveyed in the field in winter 2021 and 2022 to collect data on ‘true’ house counts. Sample cells varied in cattail stand density, extent of open water, and cattail-water interspersion to provide robust validation of sample cells with varying levels of house detectability. Two surveyors covered the entirety of each cell on foot by walking straight lines in a sweeping motion across the cell with a buffer of no more than 15 m on either side, within which the observer was able to spot a house. In addition to the house indicators outlined above, surveyors were able to observe some of the more cryptic structures on the ground. Furthermore, structures could be measured and their condition assessed. Structures were included in the total house count and considered recent (built or maintained in the previous fall) if they fit the general appearance of a muskrat house, were of reasonable quality (i.e. dome-shaped or otherwise upright and structurally sound) and had a minimum height of 40 cm from the surface of the ice as suggested by Dozier (1948) and used by others (Greenhorn *et al*., 2017). A prerequisite for an active house that can be measured in the field is a minimum water depth beneath the ice, typically 10 - 15 cm (Bellrose & Brown, 1941; Proulx & Gilbert, 1984, Clark, 1994) to allow for muskrat movement. However, we did not measure water depth at all structures due to time constraints. House occupancy in winter conditions can only be truly confirmed by excavating the structure and finding muskrats or fresh sign (Dozier, 1948). There is some promise of detecting house occupancy by measuring the internal temperature of the house, which can be up to 20^{o}C warmer than the ambient temperature (Kurta, 1995), using thermal imagery (Cline, 2021), or possibly by using a simple thermometer, though this latter method has not yet been tested to our knowledge. Cells that were surveyed on the ground were later sampled using the corresponding imagery to validate the accuracy of aerial counts, with ground counts considered true house counts for each cell.

Figure 2.6. Aerial view at 7.16 cm spatial resolution (left) and ground view (right) of same muskrat house. House was 54 cm tall from top of house to surface of ice.

Data analysis

Muskrat house density was modelled using linear regression models. Our dependent variable for all models was the average number of houses per hectare. Predictors used in models included relative frequency of *T.* x *glauca* (% of transect samples; “%glauca”), interspersion (water edge density in meters per hectare; “interspersion”), average proportion of open water per hectare (“%water”), and site type (inland or coastal marsh; “type”). We tested for correlations between variables using Pearson correlation. Highly correlated variables were not used in the same model. We used a paired t-test to test for a difference between pistillate spike phenotype and pollen phenotype identification methods, and ANOVAS to test for differences in morphological characteristics (i.e. spike gap and median leaf width) among taxa. Finally, we used ANOVAs to test for significant differences in depth at sampled ramets among the three taxa and among the three transect positions sampled to determine whether cattail sampling may have been biased for a certain depth.

Results

Muskrat house density

Aerial and ground counts of houses were identical for 14 of 18 sampled cells (78%) where both methods were used. On average, aerial counts were slightly lower than ground counts, but were not significantly different (two-tailed t-test, t = -0.94, p = 0.36). Mean house density across sites was 0.22 (± 0.036 SE). Houses were found at 32 of 39 sites (82%). At these sites, house densities ranged from 0.1 to 0.9 houses/ha. We found no correlation between house density and frequency of *T*. x *glauca* relative to parental *Typha* spp. (r = -0.05, p = 0.78), but we found a significant, positive correlation between house density and interspersion (r = 0.51, p < 0.001) as well as the proportion of open water per hectare (r = 0.46, p < 0.005; Figure 2.7). House density was lower at inland sites (x̅ = 0.17 ± 0.029 SE) compared to coastal sites (x̅ = 0.26 ± 0.065 SE), but this difference was not significant (two-tailed t-test; t = 2.06, p = 0.20).

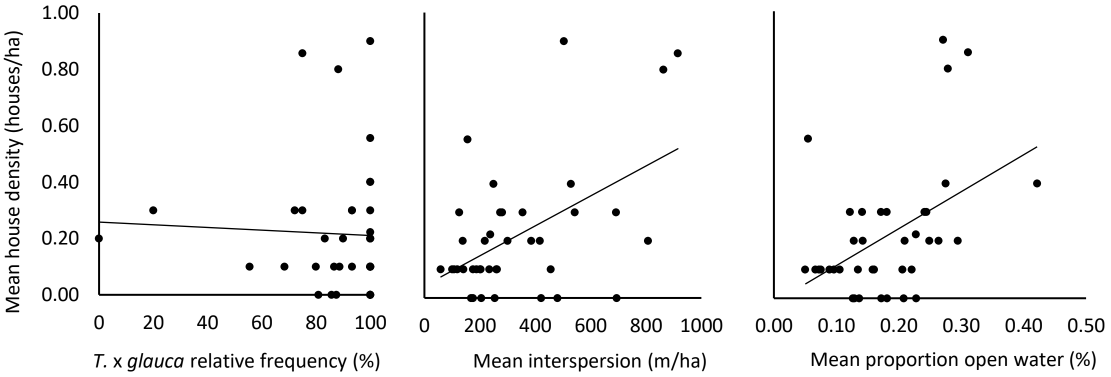

Figure 2.7. Mean muskrat house density in relation to three habitat variables across 39 marshes in south-central Ontario, with linear trendlines.

Cattail distribution

We found no significant difference between identification methods on ramet identification (paired t-test, $t = 2$, $p = 0.18$; Table 2.1). Therefore, to maintain consistency, we based our ramet identifications entirely on pistillate bracteole phenotypes, except in the rare cases where only pollen was collected, whereby we identified ramets based on pollen morphology. Spike gap was significantly different among taxa (ANOVA, $F = 170.30$, df = 2, 460, $p < 0.0001$) and was greatest for *T. angustifolia*, followed by *T.* x *glauca* and *T. latifolia*, respectively (Table 2.1). Median leaf width was significantly different among taxa (ANOVA, $F = 271.98$, df = 2, 460, $p < 0.0001$) and was greatest for *T. latifolia*, followed by *T.* x *glauca* and *T. angustifolia*, respectively (Table 2.1). We found all three cattail taxa across our study area (Figure 2.8). *Typha* x *glauca* had the greatest site occupancy (97.4 %) and relative frequency (88.7 %) of the three taxa across sites, while *T. latifolia* had the lowest site occupancy (7.7 %) and relative frequency (1.2 %) across sites. We found no significant difference in water depth at sampled ramets among taxa (95% CI; *T. latifolia* $\bar{x} = 108.29 \pm 7.53$; *T. angustifolia* $\bar{x} = 79.85 \pm 13.79$; *T.* x *glauca* $\bar{x} = 83.75$ cm $\pm$ 4.43) and transect positions varied significantly in depth, on average (ANOVA, $F = 4.40$, df = 2, 635, $p = 0.013$).

Table 2.1. Comparison of *Typha* identification methods and morphological traits for each putative taxon including both transect and opportunistic samples. Taxa were identified using Smith (2000). For identification method comparison (left), only ramets where both pollen and pistillate spikes were sampled are presented (n = 263). For morphological measurement comparisons (right), only ramets where both traits were measured are included (n = 463).

	Corresponding samples from ramet					
Putative taxon	Pollen	Pistillate spike	% Match	n	Spike gap (mm) ± SE	Median leaf width (mm) ± SE
T. latifolia	13	12	92.3	23	1.0 ± 0.4	18.5 ± 0.5
T. angustifolia	16	16	100.0	51	38.3 ± 2.1	7.2 ± 0.2
T. x *glauca*	234	233	99.6	389	11.3 ± 0.5	11.2 ± 0.1
Total	263	261	99.2	463		

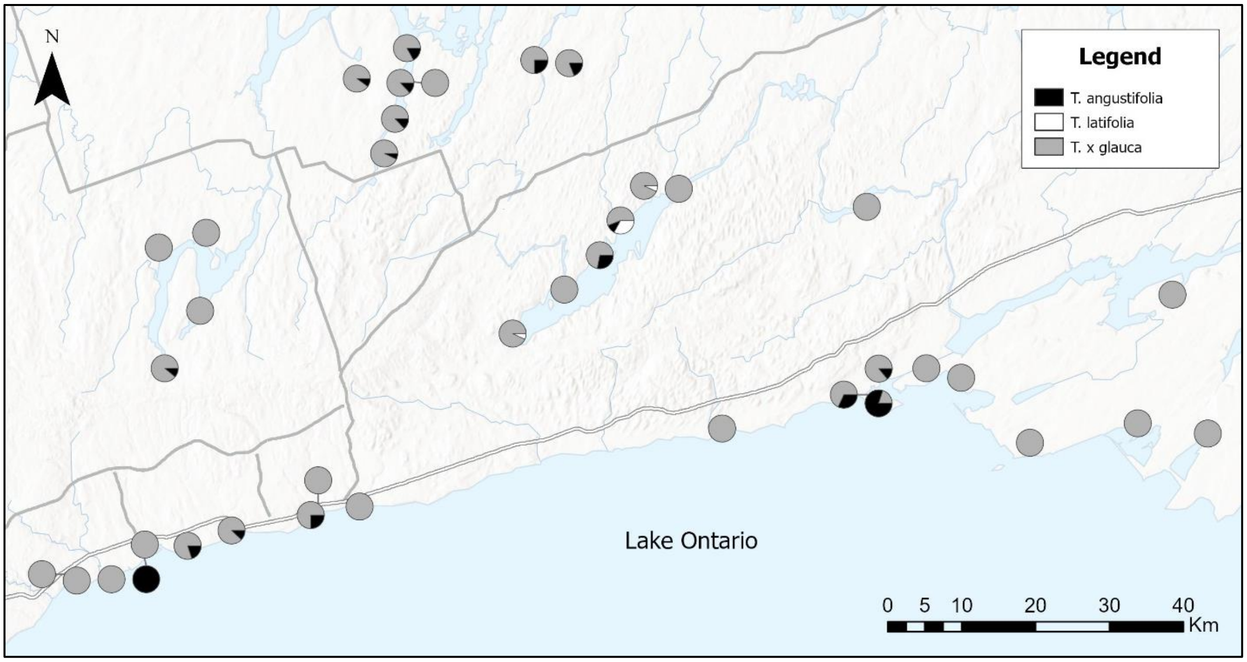

Figure 2.8. Relative frequency of *T. latifolia*, *T. angustifolia*, and hybrids (*T.* x *glauca*) sampled across 39 marshes in south-central Ontario (n = 664 ramets). Ramets were identified based on pistillate bracteole and pollen cluster phenotypes outlined in Smith (2000).

Interspersion

We found a negative, nearly significant correlation between interspersion and relative frequency of *T.* x *glauca* (r = -0.31, p = 0.054) and a significant, positive correlation between interspersion and proportion of open water per hectare (r = 0.70, p < 0.001; Figure 2.9). Proportion of open water ranged from 5 – 42 % across sites while proportion of cattail-dominated marsh ranged from 43 – 78 %.

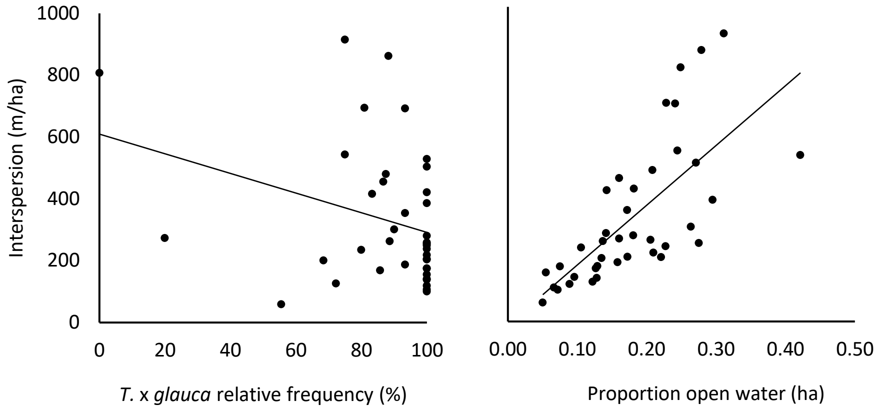

Figure 2.9. Interspersion as measured by vegetation-water edge density in relation to *T. x glauca* relative frequency and proportion of open water across 39 marshes in south-central Ontario, with linear trendlines.

Linear models

Interspersion and proportion of open water were strongly correlated (r = 0.70, p < 0.001), so we ran two separate models. We square-root-transformed house density to improve the distribution. *Typha* x *glauca* relative frequency was not a significant predictor of muskrat house density in either model, nor was site type. Interspersion was a significant predictor of house density, as was the proportion of open water per hectare (Table 2.2). The model containing proportion of open water per hectare was more highly supported than the model containing interspersion (Table 2.3).

Table 2.2. Summary of the strength and direction of the relationship between three predictor variables and the square-root-transformed average muskrat house density at 39 marshes in south central Ontario, as determined from two linear models. Bold type indicates significant p-values where $\alpha = 0.05$.

Model	Variable	Estimate	Std. Error	t-value	p-value
Model 1	%glauca	$4.684e^{-2}$	$1.906e^{-1}$	0.246	0.807
	interspersion	$4.636e^{-4}$	$1.852e^{-4}$	2.504	**0.017**
	type	$9.551e^{-2}$	$7.709e^{-2}$	1.239	0.224
Model 2	%glauca	-0.0760	0.178	-0.427	0.672
	%water	1.297	0.469	2.763	**0.009**
	type	0.097	0.076	1.280	0.209

Table 2.3. Two linear models of muskrat house density in decreasing order of support. Bold type indicates significant p-values where $\alpha = 0.05$.

Model	Std. error$_{res}$	R^2_{adj}	F-statistic	df	p-value
Model 2	0.234	0.136	2.995	3, 35	**0.044**
Model 1	0.238	0.108	2.526	3, 35	0.073

Discussion

Contrary to our prediction, we found no correlation between muskrat house density and abundance of *T.* x *glauca* relative to parental *Typha* spp. Most sites were highly dominated by hybrid *T.* x *glauca*, while native *T. latifolia* was rare. Interspersion, as measured by vegetation-water edge density, was a good predictor of muskrat house density, with higher interspersion being associated with higher house densities across sites. The proportion of open water was also a good predictor of house density, and our model containing open water outperformed the model containing interspersion. Despite our assumption that *T.* x *glauca* would be associated with reduced interspersion, we did not observe a significant correlation between these variables.

The prevalence of *T*. x *glauca* in Great Lakes coastal wetlands, especially Lake Ontario, is well-documented (Woo & Zedler, 2002; Boers *et al.*, 2007; Wilcox *et al.*, 2007; Tuchman *et al.*, 2009; Kirk *et al.*, 2011; Freeland *et al.*, 2013; Pieper *et al.*, 2020), but we now present the most comprehensive inventory of *Typha* in the Great Lakes Region north of Lake Ontario. Our study suggests that native *T. latifolia* is the rarest of the three taxa in south central Ontario wetlands, especially coastal Lake Ontario wetlands, while *T. angustifolia* is more abundant and *T.* x *glauca* is generally dominant. The dominance of *T.* x *glauca* and relative rarity of *T. latifolia* is generally consistent with other studies of Lake Ontario coastal marshes (Wilcox *et al*., 2008; Wilcox *et al.*, 2017; Wilcox & Bateman, 2018). However, given the higher relative frequencies of *T. latifolia* found near Peterborough, Ontario in recent studies, albeit through mostly targeted sampling (McKenzie-Gopsill *et al.*, 2012; Ball & Freeland, 2013; Freeland *et al.*, 2013), we anticipated a higher prevalence of *T. latifolia* and thus a wider range of *T.* x *glauca* relative frequency, particularly at inland sites which have not experienced the same water level stabilization as Lake Ontario. On the other hand, the considerably higher frequency of *T. angustifolia* relative to *T. latifolia* contradicts recent findings in the region (McKenzie-Gopsill *et al.*, 2012; Ball & Freeland, 2013; Freeland *et al.*, 2013). Aside from differences in the sampling regime, a key difference between these studies and ours is that they included comparatively few wetlands that occurred on larger water bodies such as lakes and rivers. As such, they likely encountered shallower depths overall, and likely few, if any, floating mats. Studies show that *T. angustifolia* and *T.* x *glauca* can both expand via floating mats (Wilcox *et al.*, 2005; Wilcox *et al.*, 2008; Larreur *et al.*, 2020). However, all putative *T. latifolia* ramets sampled on transects in this study also occurred on floating mats. Furthermore, we were successful in sampling a range of water depths along transects and we did not find any statistical differences in water depth at sampled ramets among the three taxa. Therefore, differences in relative frequency of taxa in our study are likely to reflect true relative abundance. Cranberry Marsh in Whitby, Ontario was the only marsh sampled that was devoid of *T.* x *glauca* on transects and was instead fully dominated by *T. angustifolia*. However, this site had the lowest sample size (n = 2 transects, 6 ramets) and *T.* x *glauca* was discovered off-transect. The high degree of observed *T.* x *glauca* dominance and minimal variation across sites (95% CI; $\bar{x}$ = 88% ± 6.74) may limit our understanding of the relationship between *T.* x *glauca* and muskrat populations. Therefore, we cannot reject the hypothesis that *T.* x *glauca* invasions are leading to muskrat declines in southern

Ontario. Furthermore, it is possible that the invasion of *T.* x *glauca*, and downstream effects on habitat quality that may not be well understood, have already led to muskrat population declines in this region and that populations have since levelled off.

Our comparison of ramet identification methods suggests that using pistillate spikes alone is effective for identifying cattail phenotypes. We preferred this method of identification as the differences among taxa outlined in Smith (2000) were more obvious in our pistillate spike samples than in our pollen samples. Specifically, we observed considerable overlap in phenotypes among pollen samples from putative *T. angustifolia* and *T.* x *glauca* ramets, particularly with low pollen grain counts, as experienced by Finkelstein (2003). Nevertheless, the high level of agreement between these two methods likely indicates that we correctly identified most observed phenotypes for both sample types. Furthermore, relative differences in mean spike gaps and median leaf widths for each putative taxon also agree with Smith (2000), adding further support to our correct identification of *Typha* ramets. Though it remains unclear which phenotypes may be exhibited by introgressed and advanced-generation hybrids, it can likely be assumed that advanced-generation hybrids possess pollen and pistillate spike phenotypes more similar to those of F1 hybrids. On the other hand, it is possible that an F1 hybrid backcrossed with *T. angustifolia* may exhibit a phenotype more similar to *T. angustifolia*. However, if this is the case, then we have likely underestimated the abundance of hybrids across sites as opposed to overestimating the abundance of progenitors, and thus, our finding that nearly all sites in our study area are dominated by invasive hybrid cattail would not change. Some evidence also suggests that most hybrids of *T. latifolia* and *T. angustifolia* in the Great Lakes Region exist as F1 hybrids (Travis *et al.*, 2010; Freeland *et al.*, 2013). Genotyping leaf tissue from the ramets sampled in our study will eventually provide more certainty in our assessment of relative frequency of cattail taxa.

Our finding that muskrat house density was positively correlated with both vegetation-water edge density and proportion of open water (from 5 - 42%) is consistent with the idea that muskrat populations are most productive where there is a high degree of marsh interspersion. We also found a negative correlation between house density and proportion of cattail-dominated marsh as it diverged from hemi-marsh conditions (from 43 – 78 % cover), which further supports this idea. The relatively low proportion of open water and high proportion of cattail cover at our sites suggests that hemi-marsh habitat is likely rare in this region. Vegetation-water edge density, as we measured it, included all water edges regardless of the adjacent feature class. However, these largely represented the interface with emergent vegetation (e.g. *Typha*). Only a small fraction of these edges represented the interface with other dominant vegetation classes which may still serve a similar purpose for muskrats, and a negligible proportion represented the interface of less relevant features such as bare soil or shoreline infrastructure. The strong correlation between the proportion of open water and edge density also suggests that edge density may be a good proxy for interspersion and supports the idea that emergent-water edges, in addition to hemi-marsh, are important habitat features for muskrats.

Though *T*. x *glauca* is often associated with reduced marsh interspersion (Harris & Marshall, 1963; Wilcox *et al.*, 2008; Schummer *et al.*, 2012; Markle *et al*., 2018; Smith *et al.*, 2021), we did not observe a significant correlation between these variables. Similar to the lack of correlation with house density, this may be due to the limited variation in relative frequency of *T.* x *glauca* across sites. However, the site with the greatest interspersion (Westside Beach Marsh, Bowmanville, Ontario) was dominated by *T.* x *glauca* and was devoid of *T. latifolia*, and the site with the lowest levels of interspersion (Indian River Marsh, Keene, Ontario) had among the lowest proportions of *T.* x *glauca* and among the highest proportions of *T. latifolia*. Nevertheless, greater variation in the relative frequency of *T.* x *glauca* may be needed to illicit a significant correlation with interspersion. Interspersion is also influenced by factors other than cattail community composition. Other invasive macrophytes, such as *Phragmites australis*, have also been associated with reduced interspersion (Markle *et al.*, 2018). More broadly, any land features included in our sample cells would have resulted in reduced interspersion for a given cell, thereby reducing the overall interspersion for that site, though our cell selection criteria ensured that the vast majority of our sample cells were dominated by marsh habitat. Nevertheless, limiting sample cells to exclusively cattail-dominated marsh and water, and sampling sites with a greater variety in cattail community composition, may lead to a stronger and more significant correlation between interspersion and relative frequency of *T.* x *glauca* that is more reflective of trends observed in other studies.

Along with house counts in Lake Ontario coastal marshes, we present the first comprehensive muskrat population survey for marshes north of Lake Ontario. Mean house density observed in our study is considerably lower than the density observed at Luther Marsh, a *Typha*-dominated marsh in southern Ontario, from 1979 – 1980 (Proulx & Gilbert, 1984), as well as other marshes in Canada and the United States prior to 1980 (Benoit & Askins, 1999; Ward & Gorelick, 2018). These findings add to the growing body of evidence of widespread muskrat population declines. The mean house density in coastal marshes in this study is very similar to mean house density found by Greenhorn *et al.* (2017) who surveyed many of the same sites. With evidence pointing to low house densities in marshes connected to Lake Ontario (Toner *et al.*, 2010; Greenhorn *et al.*, 2020), we expected house densities at inland sites to be higher than at coastal sites, but this was not the case. Average site depth at the cattail-water edge in summer was more than twice as deep at inland sites than at coastal sites (inland $\overline{x}$ = 105 cm, coastal $\overline{x}$ = 48 cm). While muskrat houses are generally only built within a limited range of water depths (Proulx & Gilbert, 1983; Toner *et al.*, 2010), summer water depth was not found to be a useful predictor of winter house counts where water levels are managed (Toner *et al.*, 2010). For this reason, we did not use summer water depths to model house density.

Inland and coastal marsh imagery used for house counts was collected in 2021 and 2022, respectively. Therefore, the difference in site type may also be subject to the random effect of year. To verify whether sample year influenced house counts across sites, we arbitrarily selected a small number of sites where we collected imagery and conducted house counts for both years. One inland site (Osler Marsh) had no change, one coastal site (Port Darlington Marsh, directly connected to Lake Ontario) showed a marginal increase, but another coastal site (Westside Beach, intermittently connected to Lake Ontario) showed a dramatic increase in houses from 2021 to 2022 (0.14 to 0.86 houses/ha). House-building typically occurs in the fall (Dozier, 1948; Westworth, 1974) when muskrats may be more sensitive to climatic conditions such as lower air and water temperatures coupled with a lack of ice and snow cover for insulation (MacArthur, 1980). However, mean monthly temperatures in November and December were comparable in 2020 and 2021 (Government of Canada, 2023a, 2023b). Snow cover at the time of imagery acquisition was lower in 2021 than in 2022, though this is most likely due to imagery being acquired later in the winter (March) in 2021, rather than reflecting differences in precipitation between years. Finally, since house counts did not decrease at any site with increasing snow coverage, it is unlikely that houses became hidden by additional snow coverage in 2022. Westside Beach Marsh appears to have experienced an unusual drop in water levels (0.64 m) from October 2020 to May 2021, likely resulting from a breach of the barrier beach over the winter (CLOCA, 2023), though winter water levels were not recorded. This would likely account for lower observed house counts at Westside Beach Marsh in winter 2021. We were unable to obtain water level data for Port Darlington and Osler Marsh. However, water levels in Lake Ontario were above average in January 2021 and did not experience any drastic declines in the fall (IJC, 2023), making changes in house densities due to changes in water levels unlikely at Port Darlington Marsh from 2021 to 2022. Though house counts were only replicated at these three sites and we could not obtain precise water level data for all sites included in this study, we believe that annual population fluctuations of the magnitude observed at Westside Beach are likely indicative of abrupt changes in local site conditions, such as reductions in water levels, as observed by others (Chatterton, 1944; Errington, 1951; Danell, 1978), and that our house counts over two years still represent relative differences in populations across sites.

Fall drawdowns effected by Plan 1958D have been shown to negatively affect muskrat populations in upper St. Lawrence River wetlands by reducing winter water levels, thereby reducing habitat suitability (Toner *et al.*, 2010). This may also be the case in Lake Ontario wetlands where muskrat densities were found to be higher in wetlands which were isolated from the effects of lake level regulation (Greenhorn *et al.*, 2017). Reduced water levels in late fall and winter are also likely to cause “freeze-outs” for muskrats with existing houses, where water freezes down to the substrate and underwater feeding is no longer possible (Ganoe *et al.*, 2021a), which may lead to significant mortality (Errington, 1954), and thus, reduced population sizes (Bellrose, 1950). However, despite the recent implementation of Plan 2014 which more closely mimics the natural water level regime of Lake Ontario (IJC, 2014), muskrat house density does not appear to have increased from 2014 (Greenhorn *et al.*, 2017). While more extensive investigations of muskrat abundance in coastal Lake Ontario and upper St. Lawrence River wetlands are currently underway (OMNRF, unpublished), this suggests that the direct impact of water level management may not be the only factor leading to reduced muskrat densities in coastal Lake Ontario marshes. The greater fluctuations and slightly higher upper limits for Lake Ontario water levels that are now seen under Plan 2014 are also predicted to suppress cattail populations and regenerate healthy marsh ecosystems that have been lost due to Plan 1958D (IJC, 2014). This will likely take time, as succession in Great Lakes coastal wetlands has historically spanned many years (Wilcox *et al.*, 2004). If this management plan is successful, coastal wetlands may see the return of native biodiversity and structural complexity, which would likely benefit many species, including muskrats. However, given the aggressive nature of *T.* x *glauca* (Bansal *et al.*, 2019), its general tolerance of variable water levels and fluctuations (Shay & Shay, 1986; Boers *et al.*, 2007; Boers & Zedler, 2008; Lishawa *et al.*, 2010), the persistence of high nutrient concentrations promoting growth (Woo & Zedler, 2002; Elgersma *et al.*, 2017), and the difficulty of localized control efforts (Boers *et al.*, 2007; Elgersma *et al.*, 2017; Wilcox *et al.*, 2017), it has been suggested that large-scale *T.* x *glauca* invasions cannot easily be undone (Farrer & Goldberg, 2014; Meeker *et al.*, 2023; Stewart *et al.*, 2023). We recommend continued monitoring of plant assemblages and muskrats in Lake Ontario coastal wetlands to determine the success of Plan 2014 in suppressing cattail invasions and its potential for increasing muskrat populations.

Aside from the loss of interspersion and open water habitat observed in wetlands in Lake Ontario and other parts of eastern North America, there may be other impacts on wetlands and muskrat populations in recent decades that are still poorly understood which may be associated with the invasion of *T.* x *glauca*. For example, cattail stands occasionally form floating mats (Bansal *et al.*, 2019). The formation of these floating cattail mats is widespread and seemingly common (Bishop *et al.*, 1979;

Hogg & Wein, 1987; Hewitt & Miyanishi, 1997; Ervin, 2011; Larreur *et al.*, 2020; Johnson *et al.*, 2021; this study). Notably, most sites in our study area were dominated by floating mats at the water's edge. Muskrats have been found to avoid floating cattail mats over rooted stands (Bishop *et al.*, 1979; Kadlec *et al.*, 2007; Ervin *et al.*, 2011). We found similar results, as mean house density was lower at sites dominated by floating mats ($\bar{x}$ = 0.19 ± 0.04 SE) than by rooted stands (0.27 ± 0.09 SE), though this was not significant ($p = 0.21$). There are several plausible reasons for the avoidance of floating mats. First, contrary to rooted stands, floating mats may expand into water that is too deep for house-building. We found that mean site depth, as measured by mean water depth at sampled ramets, was significantly deeper at sites dominated by floating mats ($\bar{x}$ = 97 cm, $p < 0.001$) and nearly two-fold greater than mean water depth at active muskrat houses observed by Proulx & Gilbert (1984; $\bar{x}$ = 54 cm). Since cattail mats float, water above the mats is often shallow or non-existent (Melvin, pers. obs.); this, in combination with high stand density, may deter muskrats from navigating these stands. Moreover, the area below these mats is often thick with organic material (Hogg & Wein, 1988) and may thus also impede travel. Floating mats may limit winter foraging opportunities as rhizomes and stems may become frozen in the ice layer, thus reducing food availability. Finally, terrestrial predators that may otherwise avoid swimming through rooted cattail stands are known to travel through marshes on floating mats (Hewitt & Miyanishi, 1997; Melvin, pers. obs.). It has been suggested that mat formation may be an adaptation to fluctuating water levels (Herdendorf, 1987). Mat formation allows cattails to occupy areas with less suitable substrate (Larreur *et al.*, 2020) and can act as a dispersal mechanism when mats break and colonize new areas (Bansal *et al.*, 2019). Additionally, cattail mats appear to be especially difficult to control (Krusi & Wein, 1988; Sojda & Solberg, 1993), and, ironically, the mechanical treatment of *T.* x *glauca* may promote mat formation (Johnson *et al.*, 2021). It is unclear whether cattail mat formation has been accelerating and whether it is catalyzed by the invasion of *T.* x *glauca*. However, the resilience of floating cattail mats and their adaptability to water level changes may limit the efficacy of Plan 2014 in reversing cattail invasions. The prevalence of floating cattail mats in North America, their impact on wetlands, and their potential role in muskrat population declines may be an interesting avenue for study.

Conclusion

Our study provides further evidence that muskrats are most abundant in marshes with a high degree of interspersion, supporting our hypothesis that muskrat populations are declining in southern Ontario due to reduced interspersion. Moreover, our results support the idea that vegetation-water edges are important habitat for muskrats, and we provide methods to measure this edge density using remote sensing. Due to the lack of variation in *T.* x *glauca* relative frequency in our study area, we cannot confidently reject the hypothesis that muskrat populations are declining in direct response to the invasion of *T.* x *glauca*. Including more sites with lower *T.* x *glauca* and greater *T. latifolia* abundance would allow for a more robust test of this hypothesis. While there is currently no evidence to suggest that *T.* x *glauca* plants are inherently harmful to muskrats, the overwhelming dominance of *T.* x *glauca* at our study wetlands is concerning given its aggressive tendencies and resistance to control measures. The negative effects of *T*. x *glauca* on species richness and habitat structure in Great Lakes coastal wetlands are well-documented, but more research is needed to determine whether the invasion of *T.* x *glauca* is contributing to widespread muskrat population declines and to what extent other factors are at play. We recommend regular monitoring of muskrat populations throughout their native range, an investigation of the impacts of floating cattail mats on muskrats, and continued research into effective cattail control methods. Clearly, there is a complex and dynamic relationship among muskrats, water levels, and marsh vegetation, and isolating these elements for empirical testing of hypotheses can be difficult. However, given optimal water levels and healthy emergent plant communities, it seems likely that muskrat populations will swiftly rebound.

References

Ahlers, A. A., & Heske, E. J. (2017). Empirical evidence for declines in muskrat populations across the United States. *Journal of Wildlife Management*, *81*(8), 1408–1416. https://doi.org/10.1002/jwmg.21328

Ahlers, A. A., Lyons, T. P., & Heske, E. J. (2021). Population dynamics of muskrats (Ondatra *zibethicus*) and American mink (*Neovison vison*): Investigating contemporary patterns in a classic predator–prey system. *Canadian Journal of Zoology*, *99*(8), 681–688. https://doi.org/10.1139/cjz-2020-0296

Ball, D., & Freeland, J. R. (2013). Synchronous flowering times and asymmetrical hybridization in *Typha latifolia* and *T. angustifolia* in northeastern North America. *Aquatic Botany*, *104*, 224–227. https://doi.org/10.1016/j.aquabot.2012.08.006

Baltz, D. M., Rakocinski, C., & Fleeger, J. W. (1993). Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes*, *36*(2), 109–126. https://doi.org/10.1007/BF00002790

Bansal, S., Lishawa, S. C., Newman, S., Tangen, B. A., Wilcox, D., Albert, D., Anteau, M. J., Chimney, M. J., Cressey, R. L., DeKeyser, E., Elgersma, K. J., Finkelstein, S. A., Freeland, J., Grosshans, R., Klug, P. E., Larkin, D. J., Lawrence, B. A., Linz, G., Marburger, J., Noe, G., Otto, C., Reo, N., Richards, J., Richardson, C., Rodgers, L., Schrank, A., Svedarsky, D., Travis, S., Tuchman, N., & Windham-Myers, L. (2019). *Typha* (cattail) invasion in North American wetlands: Biology, regional problems, impacts, ecosystem services, and management. *Wetlands, 39*, 645–684. https://doi.org/10.1007/s13157-019-01174-7

Bellrose, F. C., & Brown, L. G. (1941). The Effect of Fluctuating Water Levels on the Muskrat Population of the Illinois River Valley. *The Journal of Wildlife Management*, *5*(2), 206. https://doi.org/10.2307/3795587

Bellrose, F. C. (1950). The Relationship of Muskrat Populations to Various Marsh and Aquatic Plants. *The Journal of Wildlife Management*, *14*(3), 299–315.

Benoit, L. K., & Askins, R. A. (1999). Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *The Society of Wetland Scientists*, *19*(1), 194–208.

Bishop, R. A., Andrews, R. D., & Bridges, R. J. (1979). Marsh management and its relationship to vegetation, waterfowl and muskrats. *Proceedings - Iowa Academy of Science*, *86*(2), 50–56.

Boers, A. M., & Zedler, J. B. (2008). Stabilized water levels and *Typha* invasiveness. *Wetlands*, *28*(3), 676–685. https://doi.org/10.1672/07-223.1

Boers, A. M., Veltman, R. L. D., & Zedler, J. B. (2007). Typha x glauca dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering*, *29*(3), 232–244. https://doi.org/10.1016/j.ecoleng.2006.04.011

Boutin, S., & Birkenholz, D. E. (1987). Muskrat and round-tailed muskrat. In Novak, M., Baker, J.A., Obbard, M. E., & Malloch, B. (Eds.), *Wild Furbearer Management and Conservation in North America*, 314–325. Ontario Ministry of Natural Resources.

Brietzke, C. (2015). Muskrat ecology in the Mackenzie Delta: Insights from local knowledge and ecological field surveys. *Arctic*, *68*(4), 527–531. https://doi.org/10.14430/arctic4538

Brinson, M. M., Rheinhardt, R. D., Hauer, F. R., Lee, L. C., Nutter, W. L., Smith, R. D., Whigham, D., Rheinhardt, R. D., Smith, R. D., & Whigham, D. (1995). A guidebook for application of hydrogeomorphic assessments to riverine wetlands. *Wetlands Research Program Technical Report WRP-DE-11*, *December 1995*, 219. http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA308365

Butler, A. W. (1885). Observations on the muskrat. *The American Naturalist*, *19*(11), 1044–1055. https://doi.org/10.1086/274091

Butler, L. (1962). Periodicities in the annual muskrat population figures for the province of Saskatchewan. *Canadian Journal of Zoology*, *40*(7), 1277–1286. https://doi.org/10.1139/z62-104

Chabot, D., Carignan, V., & Bird, D. M. (2014). Measuring habitat quality for least bitterns in a created wetland with use of a small unmanned aircraft. *Wetlands*, *34*(3), 527–533. https://doi.org/10.1007/s13157-014-0518-1

Chatterton, H. J. (1944). The muskrat fur industry of Louisiana. *Journal of Geography*.

Ciotir, C., Kirk, H., Row, J. R., & Freeland, J. R. (2013). Intercontinental dispersal of *Typha angustifolia* and *T. latifolia* between Europe and North America has implications for *Typha* invasions. *Biological Invasions*, *15*(6), 1377–1390. https://doi.org/10.1007/s10530-012-0377-8

Clamen, M., & Macfarlane, D. (2018). Plan 2014: The historical evolution of Lake Ontario–St. Lawrence River regulation. *Canadian Water Resources Journal*, *43*(4), 416–431. https://doi.org/10.1080/07011784.2018.1475263

Clark, W. R. (1994). Habitat selection by muskrats in experimental marshes undergoing succession. In *Canadian Journal of Zoology, 72*(4). https://doi.org/10.1139/z94-091

Cline, E. E., Gehring, T. M., & Etter, D. R. (2021). Evaluating unoccupied aerial vehicles for estimating relative abundance of muskrats. *Wildlife Society Bulletin*, *October 2021*, 1–11. https://doi.org/10.1002/wsb.1306

Danell, K. (1977). Short-term plant successions following the colonization of a northern Swedish Lake. *British Ecological Society*, *14*(3), 933–947.

Danell, K. (1978). Population dynamics of the muskrat in a shallow Swedish lake. *Journal of Animal Ecology*, *47*(3), 697–709.

Danell, K. (1979). Reduction of aquatic vegetation following the colonization of a Northern Swedish Lake by the muskrat, *Ondatra zibethica*. *Oecologia*, *106*, 101–106.

Danell, K. (1996). Introductions of aquatic rodents: Lessons of the muskrat *Ondatra zibethicus* invasion. *Wildlife Biology*, *2*(3), 213–220. https://doi.org/10.2981/wlb.1996.021

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*(10), 934–941. https://doi.org/10.1071/MF14173

Dozier, H. L. (1948). Estimating muskrat populations by house counts. *Thirteenth North American Wildlife Conference*, 372-392.

Dozier, H. L. (1950). Muskrat trapping on the Montezuma National Wildlife Refuge, New York. *The Journal of Wildlife Management*, *14*(4), 403–412.

Elgersma, K. J., Martina, J. P., Goldberg, D. E., & Currie, W. S. (2017). Effectiveness of cattail (Typha spp.) management techniques depends on exogenous nitrogen inputs. *Elementa*, *5*. https://doi.org/10.1525/elementa.147

Elton, C., & Nicholson, M. (1942). Fluctuations in numbers of the muskrat (*Ondatra zibethica*) in Canada. *British Ecological Society*, *11*(1), 96–126.

Environmental Systems Research Institute [ESRI]. 2021. ArcGIS Pro Desktop: Version 2.9. Environmental Systems Research Institute, Redlands, California.

Errington, P. L. (1939). Reaction of muskrat populations to drought. *Ecology*, *20*(2), 168–186.

Errington, P. L. (1951). Concerning fluctuations in populations of the prolific and widely distributed muskrat. *The American Naturalist*, *85*(824), 273–292. https://doi.org/10.1086/281680

Errington, P. L. (1954). The special responsiveness of minks to epizootics in muskrat populations. *Ecological Monographs*, *24*(4), 377–393.

Errington, P. L. (1963). Muskrat populations. The Iowa State University Press, Ames, Iowa, USA.

Errington, P. L., & Errington, C. S. (1937). Experimental tagging of young muskrats for purposes of study. *The Journal of Wildlife Management*, *1*(3/4), 49. https://doi.org/10.2307/3795761

Ervin, M. D. (2011). Population characteristics and habitat selection of muskrats (*Ondatra zibethicus*) in response to water level management at the Summerberry Marsh Complex, The Pas (M.Sc. Thesis). Iowa State University, Iowa, USA.

Farrell, J. M., Murry, B. A., Leopold, D. J., Halpern, A., Rippke, M. B., Godwin, K. S., & Hafner, S. D. (2010). Water-level regulation and coastal wetland vegetation in the upper St. Lawrence River: Inferences from historical aerial imagery, seed banks, and *Typha* dynamics. *Hydrobiologia*, *647*(1), 127–144. https://doi.org/10.1007/s10750-009-0035-z

Farrer, E. C., & Goldberg, D. E. (2014). Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. *Aquatic Botany*, *116*, 35–43. https://doi.org/10.1016/j.aquabot.2014.01.002

Finkelstein, S. A. (2003). Identifying pollen grains of *Typha latifolia*, *Typha angustifolia*, and *Typha* x *glauca*. *Canadian Journal of Botany*, *81*(9), 985–990. https://doi.org/10.1139/b03-084

Freeland, J., Ciotir, C., & Kirk, H. (2013). Regional differences in the abundance of native, introduced, and hybrid Typha spp. in northeastern North America influence wetland invasions. *Biological Invasions*, *15*(12), 2651–2665. https://doi.org/10.1007/s10530-013-0481-4

Frieswyk, C. B., Johnston, C. A., & Zedler, J. B. (2007). Identifying and characterizing dominant plants as an indicator of community condition. *Journal of Great Lakes*

Research, *33*(SPEC. ISS. 3), 125–135. https://doi.org/10.3394/0380-1330(2007)33[125:IACDPA]2.0.CO;2

Galatowitsch, S. M., Anderson, N. O., Ascher, P. D., & Hall, A. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*(4), 733–755.

Ganoe, L. S., Lovallo, M. J., Brown, J. D., & Walter, W. D. (2021a). Ecology of an isolated muskrat population during regional population declines. *Northeastern Naturalist*, *28*(1), 49–64. https://doi.org/10.1656/045.028.0104

Government of Canada, 2023a. Daily data report for December 2020 (Peterborough A). https://climate.weather.gc.ca/. Retrieved on July 7, 2023.

Government of Canada, 2023b. Daily data report for December 2021 (Peterborough A). https://climate.weather.gc.ca/. Retrieved on July 7, 2023.

Grace, J. B., & Wetzel, R. G. (1981). Habitat partitioning and competitive displacement in cattails (*Typha*): Experimental field studies. *The American Naturalist*, *118*(4), 463–474. https://doi.org/10.1086/283841

Grace, J. B., & Wetzel, R. G. (1982). Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany*, *60*(1), 46–57. https://doi.org/10.1139/b82-007

Greenhorn, J. E., Sadowski, C., Holden, J., & Bowman, J. (2017). Coastal wetlands connected to Lake Ontario have reduced muskrat (*Ondatra zibethicus*) abundance. *Wetlands*, *37*(2), 339–349. https://doi.org/10.1007/s13157-016-0874-0

Gregory, G. J., Dibblee, R., Daoust, P.-Y., & Van Den Heuvel, M. R. (2019). Declines in muskrat (*Ondatra zibethicus*) population density in Prince Edward Island, Canada. *Canadian Wildlife Biology and Management*, *8*(2), 46–60.

Grenier, M., Labrecque, S., Benoit, M., & Allard, M. (2008). Accuracy assessment method for wetland object-based classification. *GEOBIA 2008 - Pixels, Objects, Intelligence*, 6. http://www.isprs.org/proceedings/XXXVIII/4-C1/Sessions/Session1/6589_Y_Gao_Proc_pap.pdf

Hall, S. (2008). *Typha* x *glauca* (hybrid cattail). CABI Digital Library. https://doi.org/10.1079/cabicompendium.107745

Harris, S. W., & Marshall, W. H. (1963). Ecology of water-level manipulations on a northern marsh. *Ecology*, *44*(2), 331–343.

Herdendorf, C. E. (1987). The ecology of the coastal marshes of western Lake Erie - A community profile. *U.S. Fish and Wildlife Service Biological Report, 85*(7.9).

Hewitt, N., & Miyanishi, K. (1997). The role of mammals in maintaining plant species richness in a floating Typha marsh in southern Ontario. *Biodiversity and Conservation*, *6*(8), 1085–1102. https://doi.org/10.1023/A:1018380000881

Higgins, C., & Mitsch, W. J. (2000). The role of muskrats (*Ondatra zibethicus*) as ecosystem engineers in created freshwater marshes. *Biomass*, 81–86.

Hogg, E., & Wein, R. W. (1988). The contribution of *Typha* components to floating mat buoyancy. *Ecology*, *69*(4), 1025–1031.

International Joint Commission [IJC]. (2023). Lake Ontario: Daily mean levels. https://ijc.org/en/loslrb/watershed/water-levels. Accessed June 2023.

International Joint Commission [IJC]. (2014). Lake Ontario St. Lawrence River Plan 2014: Protecting against extreme water levels, restoring wetlands and preparing for climate change. https://ijc.org/sites/default/files/IJC_LOSR_EN_Web.pdf

Johnson, O. F., Panda, A., Lishawa, S. C., & Lawrence, B. A. (2021). Repeated large-scale mechanical treatment of invasive Typha under increasing water levels promotes floating mat formation and wetland methane emissions. *Science of the Total Environment*, *790*, 147920. https://doi.org/10.1016/j.scitotenv.2021.147920

Kadlec, R. H., Pries, J., & Mustard, H. (2007). Muskrats (*Ondatra zibethicus*) in treatment wetlands. *Ecological Engineering*, *29*(2), 143–153. https://doi.org/10.1016/j.ecoleng.2006.06.008

Kaminski, R. M., & Prince, H. H. (1981). Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. *The Wildlife Society*, *45*(1), 1–15.

Krusi, B. O., & Wein, R. W. (1988). Experimental studies on the resiliency of floating *Typha* mats in a freshwater marsh. *Ecology*, *76*(1), 60–72.

Kua, Z. X., Stella, J. C., & Farrell, J. M. (2020). Local disturbance by muskrat, an ecosystem engineer, enhances plant diversity in regionally-altered wetlands. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3256

Kuehn, M., & White, B. N. (1999). Morphological analysis of genetically identified cattails *Typha latifolia*, *Typha angustifolia*, and *Typha* x *glauca*. *Canadian Journal of Botany*, *77*(6), 906–912. https://doi.org/10.1139/b99-037

Kirk, H., Connolly, C., & Freeland, J. R. (2011). Molecular genetic data reveal hybridization between Typha angustifolia and Typha latifolia across a broad spatial scale in eastern North America. *Aquatic Botany*, *95*(3), 189–193. https://doi.org/10.1016/j.aquabot.2011.05.007

Kurta, A. Mammals of the Great Lakes Region. 3rd Ed. The University of Michigan Press, Ann Arbor, Michigan, USA.

Lacki, M. J., Peneston, W. T., Adams, K. B., Vogt, F. D., & Houppert, J. C. (1990). Summer foraging patterns and diet selection of muskrats inhabiting a fen wetland. *Canadian Journal of Zoology*, *68*(6), 1163–1167. https://doi.org/10.1139/z90-172

Land Information Ontario. (2019). South Central Ontario Orthophotography Project. Ontario: Ministry of Natural Resources, Spring 2018 & 2019.

Larkin, D. J., Freyman, M. J., Lishawa, S. C., Geddes, P., & Tuchman, N. C. (2012). Mechanisms of dominance by the invasive hybrid cattail *Typha* x *glauca*. *Biological Invasions*, *14*(1), 65–77. https://doi.org/10.1007/s10530-011-0059-y

Larreur, M. R., Windels, S. K., Olson, B. T., & Ahlers, A. A. (2020). Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. *Landscape Ecology*, *35*(1), 59–68. https://doi.org/10.1007/s10980-019-00925-5

Lawrence, B. A., Lishawa, S. C., Rodriguez, Y., & Tuchman, N. C. (2016). Herbicide management of invasive cattail (Typha × glauca) increases porewater nutrient concentrations. *Wetlands Ecology and Management*, *24*(4), 457–467. https://doi.org/10.1007/s11273-015-9471-x

Lishawa, S. C., Albert, D. A., & Tuchman, N. C. (2010). Water level decline promotes *Typha* x glauca establishment and vegetation change in Great Lakes coastal wetlands. *Wetlands*, *30*(6), 1085–1096. https://doi.org/10.1007/s13157-010-0113-z

Luymes, N., & Chow-Fraser, P. (2021). Detection of potential vernal pools on the Canadian Shield (Ontario) using object-based image analysis in combination with machine learning. *Canadian Journal of Remote Sensing*, *47*(4), 519–534. https://doi.org/10.1080/07038992.2021.1900717

MacArthur, R. A. (1980). Daily and seasonal activity patterns of the muskrat Ondatra zibethicus as revealed by radiotelemetry. *Ecography*, *3*(1), 1–9. https://doi.org/10.1111/j.1600-0587.1980.tb00702.x

MacGregor, D. 2013. Teachings from the muskrat. http://muskratmagazine.com/teachings-from-the-muskrat/. Accessed April 2023.

Markle, C. E., Chow-Fraser, G., & Chow-Fraser, P. (2018). Long-term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. *PLoS ONE*, *13*(2), 1–15. https://doi.org/10.1371/journal.pone.0192134

McDonald, M. E. (1955). Cause and effects of a die-off of emergent vegetation. *The Journal of Wildlife Management*, *19*(1), 24–35.

McKenzie-Gopsill, A., Kirk, H., Van Drunen, W., Freeland, J. R., & Dorken, M. E. (2012). No evidence for niche segregation in a North American cattail (*Typha*) species complex. *Ecology and Evolution*, *2*(5), 952–961. https://doi.org/10.1002/ece3.225

Meeker, J. E., Wilcox, D. A., Johnson, S. E., & Tillison, N. (2023). Tracking vegetation transitions due to invasion of cattail (*Typha*) in Lake Superior coastal peatlands. *Wetlands*, *43*(2). https://doi.org/10.1007/s13157-023-01664-9

Messier, F., Virgl, J. A., & Marinelli, L. (1990). A test of the ideal free distribution model. *Ecology*, 380–385.

Mott, C. L., Bloomquist, C. K., & Nielsen, C. K. (2013). Within-lodge interactions between two ecosystem engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). *Behaviour*, *150*(11), 1325–1344. https://doi.org/10.1163/1568539X-00003097

Nicholson, W. & Davis, D. (1957). The duration of life of muskrat houses. *Ecology*, *38*(1), 161–163.

Ontario Ministry of Natural Resources and Forestry [OMNRF]. n.d. Unpublished.

Central Lake Ontario Conservation Authority [CLOCA]. 2023. Westside Beach water levels, 2005 – 2022. Unpublished.

Phaneuf, R. (1979). Indian reserve band rights: Enforcement on the St. Lawrence River. *Canadian Water Resources Journal*, *4*(3), 30–34. https://doi.org/10.4296/cwrj0403030

Pieper, S. J., Nicholls, A. A., Freeland, J. R., & Dorken, M. E. (2017). Asymmetric hybridization in cattails (*Typha* spp.) and its implications for the evolutionary maintenance of native *Typha latifolia*. *Journal of Heredity*, *108*(5), 479–487. https://doi.org/10.1093/jhered/esx036

Pieper, S. J., Freeland, J. R., & Dorken, M. E. (2018). Coexistence of *Typha latifolia*, *T. angustifolia* (*Typhaceae*) and their invasive hybrid is not explained by niche partitioning across water depths. *Aquatic Botany*, *144*(November 2017), 46–53. https://doi.org/10.1016/j.aquabot.2017.11.001

Pieper, S., Dorken, M., & Freeland, J. (2020). Genetic structure in hybrids and progenitors provides insight into processes underlying an invasive cattail (*Typha* x *glauca*) hybrid zone. *Heredity*, *124*(6), 714–725. https://doi.org/10.1038/s41437-020-0307-y

Pieper, S. J., Freeland, J., & Dorken, M. (2022). Patterns of pollen dispersal and pollen capture in the hybridizing cattails, *Typha latifolia* and *T. angustifolia*. *Botany*. https://doi.org/10.1139/cjb-2021-0166

Proulx, G., & Gilbert, F. F. (1983). The ecology of the muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario. *Canadian Field-Naturalist*, *97*(4), 377–390.

Proulx, G., & Gilbert, F. F. (1984). Estimating muskrat population trends by house counts. *The Journal of Wildlife Management*, *48*(3), 917–922.

Proulx, G., McDonnell, J. A., & Gilbert, F. F. (1987). Effect of water level fluctuations on muskrat, *Ondatra zibethicus*, predation by mink, *Mustela vison*. *Canadian Field-Naturalist*, *101*, 90-92.

Rehm, E. M., & Baldassarre, G. A. (2007). The influence of interspersion on marsh bird abundance in New York. *Wilson Journal of Ornithology*, *119*(4), 648–654. https://doi.org/10.1676/06-060.1

Roberts, N. M., & Crimmins, S. M. (2010). Do trends in muskrat harvest indicate widespread population declines? *Northeastern Naturalist*, *17*(2), 229–238. https://doi.org/10.1656/045.017.0206

Sadowski, C., & Bowman, J. (2021). Historical surveys reveal a long-term decline in muskrat populations. *Ecology and Evolution*, *11*(12), 7557–7568. https://doi.org/10.1002/ece3.7588

Sather, J. H. (1958). Biology of the Great Plains Muskrat in Nebraska. *Wildlife Monographs*, *2*, 1–35.

Schummer, M. L., Palframan, J., McNaughton, E., Barney, T., & Petrie, S. A. (2012). Comparisons of bird, aquatic macroinvertebrate, and plant communities among dredged ponds and natural wetland habitats at Long Point, Lake Erie, Ontario. *Wetlands*, *32*(5), 945–953. https://doi.org/10.1007/s13157-012-0328-2

Selbo, S. M., & Snow, A. A. (2004). The potential for hybridization between Typha angustifolia and Typha latifolia in a constructed wetland. *Aquatic Botany*, *78*(4), 361–369. https://doi.org/10.1016/j.aquabot.2004.01.003

Shay, J. M., & Shay, C. T. (1986). Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. *Canadian Journal of Botany*, *64*(2), 443–454. https://doi.org/10.1139/b86-059

Shay, J. M., de Geus, P. M. J., & Kapinga, M. R. M. (1999). Changes in shoreline vegetation over a 50-year period in the Delta Marsh, Manitoba in response to water levels. *Wetlands*, *19*(2), 413–425.

Shih, J. G., & Finkelstein, S. A. (2008). Range dynamics and invasive tendencies in *Typha latifolia* and *Typha angustifolia* in eastern North America derived from herbarium and pollen records. *Wetlands*, *28*(1), 1–16. http://www.ncdc.noaa.gov/paleo/

Smith, I. M., Fiorino, G. E., Grabas, G. P., & Wilcox, D. A. (2021). Wetland vegetation response to record-high Lake Ontario water levels. *Journal of Great Lakes Research*, *47*(1), 160–167. https://doi.org/10.1016/j.jglr.2020.10.013

Smith, S. G. (1967). Experimental and Natural Hybrids in North American *Typha* (*Typhaceae*). *American Midland Naturalist*, *78*(2), 257. https://doi.org/10.2307/2485231

Smith, S. G. (2000). *Typhaceae Jussieu* (as *Typhae*) - Cat-tail family. In Flora of North America North of Mexico. Vol. 22: *Magnoliophyta*: *Alismatidae*, *Arecidae*, *Commelinidae* (in part) and *Zingiberidae*. Pp 278-285. Oxford University Press, New York, New York.

Snow, A. A., Travis, S. E., Wildová, R., Fér, T., Sweeney, P. M., Marburger, J. E., Windels, S., Kubátová, B., Goldberg, D. E., & Mutegi, E. (2010). Species-specific SSR alleles for studies of hybrid cattails (*Typha latifolia* x *T. angustifolia*; *Typhaceae*) in North America. *American Journal of Botany*, *97*(12), 2061–2067. https://doi.org/10.3732/ajb.1000187

Sojda, R. S., & Solberg, K. L. (1993). Management and control of cattails. *United States Department of the Interior Fish and Wildlife Service, Washington, D.C. Fish and Wildlife Leaflet 13*

Stewart, D., Hood, W. G., & Martin, T. G. (2023). Undetected but widespread: the Cryptic invasion of non-native cattail (*Typha*) in a Pacific Northwest estuary. *Estuaries and Coasts*, *46*(3), 802–817. https://doi.org/10.1007/s12237-023-01171-4

Straka, J. R., Antoine, A., Bruno, R., Campbell, D., Campbell, R., Campbell, R., Cardina, J., Gibot, G., Gray, Q. Z., Irwin, S., Kindopp, R., Ladouceur, R., Ladouceur, W., Lankshear, J., Maclean, B., Macmillan, S., Marcel, F., Marten, G., Marten, L., McKinnon, J., Patterson, L. D., Voyageur, M., Whiteknife, G., Wiltzen, L. & Giguère, N. (2018). We used to say rats fell from the sky after a flood: Temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta. *Arctic*, *71*(2), 218–228. https://doi.org/10.14430/arctic4714

Takos, M. J. (1947). A semi-quantitative study of muskrat food habits. *The Journal of Wildlife Management*, *11*(4), 331–339.

Tangen, B. A., Bansal, S., Freeland, J. R., Travis, S. E., Wasko, J. D., McGonigle, T. P., Goldsborough, L. G., Gow, K., Marburger, J. E., & Meier, J. A. (2022). Distributions of native and invasive Typha (cattail) throughout the Prairie Pothole Region of North America. *Wetlands Ecology and Management*, *30*(1), 1–17. https://doi.org/10.1007/s11273-021-09823-7

Toner, J., Farrell, J. M., & Mead, J. V. (2010). Muskrat abundance responses to water level regulation within freshwater coastal wetlands. *Wetlands*, *30*(2), 211–219. https://doi.org/10.1007/s13157-010-0034-x

Travis, S. E., Marburger, J. E., Windels, S., & Kubátová, B. (2010). Hybridization dynamics of invasive cattail (*Typhaceae*) stands in the Western Great Lakes Region of North America: A molecular analysis. *Journal of Ecology*, *98*(1), 7–16. https://doi.org/10.1111/j.1365-2745.2009.01596.x

Tuchman, N. C., Larkin, D. J., Geddes, P., Wildova, R., Jankowski, K., & Goldberg, D. E. (2009). Patterns of environmental change associated with *Typha* x *glauca* invasion in a Great Lakes coastal wetland. *Wetlands*, *29*(3), 964–975. https://doi.org/10.1672/08-71.1

Vaccaro, L. E., Bedford, B. L., & Johnston, C. A. (2009). Litter accumulation promotes dominance of invasive species of cattails (*Typha* spp.) in Lake Ontario wetlands. *Wetlands*, *29*(3), 1036–1048. https://doi.org/10.1672/08-28.1

Ward, E. M., & Gorelick, S. M. (2018). Drying drives decline in muskrat population in the Peace-Athabasca Delta, Canada. *Environmental Research Letters*, *13*(12), 124026. https://doi.org/10.1088/1748-9326/aaf0ec

Weller, M. W. (1988). Issues and approaches in assessing cumulative impacts on waterbird habitat in wetlands. *Environmental Management*, *12*(5), 695–701. https://doi.org/10.1007/BF01867546

Weller, M. W., & Spatcher, C. S. (1965). Role of habitat in the distribution and abundance of marsh birds. *Special Report, 43*, 4-31.

Wilcox, D. A. (2004). Implications of hydrologic variability on the succession of plants in Great Lakes wetlands. *Aquatic Ecosystem Health and Management*, *7*(2), 223–231. https://doi.org/10.1080/14634980490461579

Wilcox, D. A., & Bateman, J. A. (2018). Photointerpretation analysis of plant communities in Lake Ontario wetlands following 65 years of lake-level regulation. *Journal of Great Lakes Research*, *44*(6), 1306–1313. https://doi.org/10.1016/j.jglr.2018.08.007

Wilcox, D. A., Buckler, K., & Czayka, A. (2017). Controlling Cattail Invasion in Sedge / Grass Meadows. *Wetlands*, *38*(2), 337–347. https://doi.org/10.1007/s13157-017-0971-8

Wilcox, D. A., Ingram, J. W., Kowalski, K. P., Meeker, J. E., Martha, L., Xie, Y., Grabas, G. P., Holmes, K. L., & Patterson, N. J. (2005). Evaluation of water level regulation influences on Lake Ontario and upper St. Lawrence River coastal wetland plant communities. Report to the International Joint Commission, Washington, D.C. and Ottawa, ON.

Wilcox, D. A., Kowalski, K. P., Hoare, H. L., Carlson, M. L., & Morgan, H. N. (2008). Cattail invasion of sedge/grass meadows in Lake Ontario: Photointerpretation analysis of sixteen wetlands over five decades. *Journal of Great Lakes Research*, *34*(2), 301–323. https://doi.org/10.3394/0380-1330(2008)34[301:CIOGMI]2.0.CO;2

Wilcox, D. A., & Xie, Y. (2007). Predicting wetland plant community responses to proposed water-level-regulation plans for Lake Ontario: GIS-based modeling. *Journal of Great Lakes Research*, *33*(4), 751–773. https://doi.org/10.3394/0380-1330(2007)33[751:PWPCRT]2.0.CO;2

Wilcox, D. A., & Xie, Y. (2008). Predicted effects of proposed new regulation plans on sedge/grass meadows of Lake Ontario. *Journal of Great Lakes Research*, *34*(4), 745–754. https://doi.org/10.3394/0380-1330-34.4.745

Woo, I., & Zedler, J. B. (2002). Can nutrients alone shift a sedge meadow towards dominance by the invasive *Typha* x *glauca*? Wetlands, 22(3), 509–521. https://doi.org/10.1672/0277-5212(2002)022[0509:CNASAS]2.0.CO;2

Zapfe, L., & Freeland, J. R. (2015). Heterosis in invasive F1 cattail hybrids (*Typha* x *glauca*). *Aquatic Botany*, *125*, 44–47. https://doi.org/10.1016/j.aquabot.2015.05.004

Chapter 3: Impact of marsh interspersion on muskrat habitat use

Abstract

Muskrat (*Ondatra zibethicus*) populations have been declining in North America for decades. The precise cause of these widespread declines has not yet been identified. Over a similar timeframe, wetlands across large regions of North America have been experiencing an invasion of *Typha*. Non-native *T. angustifolia* readily hybridizes with native *T. latifolia* to produce *T.* x *glauca*, which tends to dominate over parental species and other wetland plants alike. *T.* x *glauca* invasions are associated with many negative consequences for wetlands, including a reduction in biodiversity, open water habitat, and interspersion of water and vegetation. Muskrats are strongly tied to wetlands, especially where there is a high degree of interspersion of water and emergent vegetation. Therefore, we sought to understand the impact of reduced interspersion on muskrat habitat which has been linked to the invasion of *T.* x *glauca*. We measured intensity of habitat use by muskrats in a large, cattail-dominated marsh in south-central Ontario using remote cameras, stratifying camera placement along a gradient of marsh interspersion. We found no correlation between interspersion and intensity of use, which may suggest that factors other than interspersion may drive intensity of use. Our study site, like most marshes in the region, was highly dominated by *T.* x *glauca*. Further research is needed to determine the impact of *T.* x *glauca* invasions on muskrats, as well as the cause of widespread muskrat declines.

Key words: *Ondatra zibethicus*, southern Ontario, *Typha* x *glauca*, invasive species, wetlands, intensity of use, remote cameras

Introduction

Muskrats (*Ondatra zibethicus*) are in decline across their native range of North America (Benoit & Askins, 1999; Roberts & Crimmins, 2010; Brietzke, 2015; Ahlers & Heske, 2017; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Gregory, 2019; Sadowski & Bowman, 2021; Melvin, Chapter 1). This is concerning, as muskrats are widely regarded as ecosystem engineers for their activity in marshes (Higgins & Mitsch, 2000; Toner *et al.*, 2010; Mott *et al.*, 2013; Kua *et al.*, 2020). For example, depending on local habitat, muskrats either construct houses from emergent vegetation or excavate bank dens, creating unique microhabitats that are also used by a multitude of other species (Kiviat, 1978). They are important marsh herbivores (Errington, 1963; Hewitt & Miyanishi, 1997) and are known to selectively remove large quantities of emergent vegetation through feeding and creating channels for navigation (Boutin & Birkenholz, 1987; Hewitt & Miyanishi, 1997; Bomske & Ahlers, 2020). In certain regions, they may eliminate entire swathes of vegetation, playing an important role in marsh succession (Weller & Spatcher, 1965; Errington, 1963; Danell, 1977; Nyman *et al.*, 1993). These activities, including house-building, herbivory, and the creation of channels are associated with increased habitat complexity (Weller & Spatcher, 1965; Errington, 1963; Wilcox & Meeker, 1992; Kua *et al.*, 2020) and biodiversity (Weller & Spatcher, 1965; Kaminski & Prince, 1981; Nyman *et al.*, 1993; Danell, 1996; Kua *et al.*, 2020).

Historically, localized muskrat population declines have been linked to water level fluctuations (Bellrose & Brown, 1941; Errington, 1951), resource limitations (Dozier, 1948; Errington, 1963; Weller & Spatcher, 1965), disease outbreaks (Errington, 1963), and increases in predation (Errington, 1939; Errington, 1951). However, muskrats are hardy, resilient, and highly fecund species (Errington, 1963; Boutin & Birkenholz, 1987; Kroll & Meeks, 2020; Straka *et al.*, 2018; Ganoe *et al.*, 2020; Sadowski & Bowman, 2021). They can occupy a variety of aquatic habitats (Errington, 1963; Virgl & Messier, 1997; Ahlers *et al.*, 2010), they can withstand high levels of harvest (Soper, 1942; Errington, 1951), and they are usually quick to rebound from short-term die-offs (Chatterton, 1944; Errington, 1951). Therefore, population declines of this scale are likely the result of a persistent and widespread stressor that is still poorly understood.

Muskrat abundance is inextricably linked to water levels (Errington, 1939; Errington, 1951; Toner *et al.*, 2010; Sadowski & Bowman, 2021) and emergent vegetation (Dozier, 1950; Weller & Spatcher, 1965; Boutin & Birkenholz, 1987). Recent studies have linked large-scale muskrat population declines to water level management (Toner *et al.*, 2010; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018) and the invasion of cattails (*Typha*; Greenhorn *et al.*, 2017; Sadowski & Bowman, 2021; Melvin, Chapter 1), which are not mutually exclusive. Expansion of emergent vegetation in marsh habitats spanning several decades is well-documented in certain regions, such as the Great Lakes-St. Lawrence Lowlands, where cattail expansion has been largely attributed to water level management in the late 20th and early 21st century (Wilcox *et al.*, 2008; Farrell *et al.*, 2010; IJC, 2014; Markle *et al.*, 2018). Fall drawdowns of Lake Ontario have been shown to reduce muskrat habitat suitability (Toner *et al.*, 2010) but water level stabilization under Plan 1958D has also resulted in a myriad of unintended consequences on coastal ecosystems (IJC, 2014), including widespread invasion of

Typha. The impacts of this invasion on muskrats have not yet been investigated. However, *Typha* invasions are associated with a reduction in open water and interspersion (Wilcox *et al.*, 2005; Tulbure *et al.*, 2007; Schummer *et al.*, 2012; Markle *et al.*, 2018; Smith *et al.*, 2021), which has been linked to reduced muskrat populations (Proulx & Gilbert, 1983; Boutin & Birkenholz, 1987; Melvin, Chapter 1). Since *Typha* invasions are now occurring in many parts of North America (Pieper *et al.*, 2020; Tangen *et al.*, 2022; Stewart *et al.*, 2023; Meeker *et al.*, 2023), it is reasonable to suggest that widespread wetland degradation may play a role in muskrat population declines.

Central to *Typha* invasions in North America is *T.* x *glauca*, a hybrid of native *T. latifolia* and introduced *T. angustifolia* (Smith, 2000). Following the gradual spread of *T. angustifolia* and systematic hybridization with its native counterpart, *T.* x *glauca* has been quick to invade and dominate wetlands in Canada and the United States (Galatowitsch *et al.*, 1999). Both *T. angustifolia* and *T.* x *glauca* are known to form dense, monodominant stands (Grace & Harrison, 1986; Waters & Shay, 1992; Farrer & Goldberg, 2014; Wilcox & Bateman, 2018). However, *T.* x *glauca* has many competitive advantages over other emergent plants, including both parental species. For example, it is tolerant of a broad range of water depths, allowing it to colonize multiple zones within a marsh (Woo & Zedler, 2002; Wilcox *et al.*, 2008) and withstand water level fluctuations of greater frequency and magnitude (Harris & Marshall, 1963; Boers *et al.*, 2007; Lishawa *et al.*, 2010). *T.* x *glauca* generally grows taller than parental species (Travis *et al.*, 2011; Zapfe & Freeland, 2013; Tangen *et al.*, 2022) which may ‘shade out’ adjacent plants and thus suppress growth (Weisner, 1993; Tanaka *et al.*, 2004). Due to a high rate of nutrient uptake (Larkin *et al.*, 2012a), *T.* x *glauca* produces large quantities of biomass, resulting in a thick layer of leaf litter that impedes light penetration, also leading to reduced growth of nearby species (Vaccaro *et al.*, 2009; Larkin *et al.*, 2012b; Farrer & Goldberg, 2014; Lishawa *et al.*, 2015). Furthermore, leachate from the litter of *T.* x *glauca* directly suppresses the growth of both parental species (Szabo *et al.*, 2018). Under stabilized water levels, it has an extremely rapid rate of clonal growth (Boers & Zedler, 2008) which is an important mode of reproduction (Pieper *et al.*, 2020; Tangen *et al.*, 2022). *T.* x *glauca* has now been encountered in many parts of Canada and the United States (Hall, 2008). Given its wide distribution and aggressive tendencies, it is likely that the negative effects of *T.* x *glauca* on wetlands are under-represented in the literature, and that *T.* x *glauca* will continue to colonize wetlands in North America, displacing native species and altering muskrat habitat.

While there is no evidence of *T.* x *glauca* being directly harmful to muskrats, this does not consider the broader changes in habitat structure and composition caused by *T.* x *glauca* invasions and their potential impact on muskrat populations. For example, muskrat populations have been positively linked to marsh interspersion (Weller & Spatcher, 1965; Kaminski & Prince, 1981; Boutin & Birkenholz, 1987; Proulx & Gilbert, 1983; Melvin, Chapter 1), which generally declines with increasing prevalence of *T*. x *glauca* (Wilcox *et al.*, 2008; Schummer *et al.*, 2012; Hohman *et al.*, 2021). Reduced interspersion may result in limited travel routes (Greenhorn *et al.*, 2017) and habitat connectivity (Sadowski & Bowman, 2021). Interspersion is also strongly correlated with the density of emergent-water edges (Melvin, Chapter 1) which has similarly declined as a result of *T.* x *glauca* invasions (Wilcox *et al.*, 2008). Emergent-water edges are important habitat features for muskrat house-building (Sadowski & Bowman, 2021) and likely travel, as muskrats avoid large expanses of open water (Errington, 1963; Ervin, 2011; Larreur *et al.*, 2020) and rely on emergent vegetation for cover (Bellrose & Brown, 1941). Therefore, evidence suggests that muskrats may be negatively affected by a widespread loss in marsh interspersion due to *T.* x *glauca* invasions and may therefore avoid habitat that has been degraded by *T.* x *glauca*. We conducted a study using camera traps to measure muskrat intensity of habitat use in a large cattail-dominated marsh with a mosaic of varying interspersion. We hypothesized that muskrat populations are declining in southern Ontario due to the loss in marsh interspersion caused by the invasion of *T.* x *glauca*, and predicted a positive correlation between muskrat intensity of habitat use and interspersion. The study will improve our understanding of muskrat behaviour in light of changes to wetland habitats caused by *T.* x *glauca*, making the connection between fine-scale habitat use and widespread population trends.

Methods

Overview

We deployed camera traps in a southern Ontario marsh to measure muskrat intensity of use across sample cells representing a range of interspersion. We used recent, high-resolution aerial imagery and Geographic Information Systems (GIS) to identify suitable sample cells and measure interspersion. Twenty cameras were each deployed for approximately one month before being moved to a new location. Camera deployment occurred over four months from late May to late September, 2021, for a total of 80 camera locations. We tallied independent muskrat sightings ("events") in each cell. Sample cells were 0.25 hectares, representing the home range of muskrats in northern marshes (Takos, 1947; MacArthur, 1980; Proulx & Gilbert, 1983). We also sampled cattails throughout the marsh to determine the relative frequency of native, introduced, and hybrid cattail for a comparison with muskrat intensity of use.

Site selection

The study was conducted at Osler Marsh (44.090, -78.920) in Scugog Township, Ontario at the southern end of Lake Scugog (Figure 3.1). The marsh occupies roughly 5 km^2 while the larger wetland complex including marsh, bog, and swamp habitat spans roughly 15 km^2. The marsh is dominated by *Typha*, followed by wild rice (*Zizania* sp.) and water lilies (family *Nymphaeceae*). Other prominent species include water milfoil (*Myriophyllum* spp.), common duckweed (*Lemna minor*), European frogbit (*Hydrocharis morsus-ranae*), ferns (subclass *Polypodiidae*), and various graminoids. To a lesser extent, the marsh contains arrowhead (*Sagittaria* spp.), bulrush (*Schoenoplectus* spp.), alder (*Alnus* sp.), and white cedar (*Thuja occidentalis*). The surrounding land cover is dominated by agriculture and pasture and contains some forest and urban development. The marsh is home to a population of muskrats as determined by historical muskrat trapping as well as recent sightings and house surveys conducted by the author. The wetland is privately owned and access permissions were granted from the land manager. Muskrat trapping has not occurred in the marsh since 1990 (Overgoor, pers. comm.). All locations within the marsh were accessed by watercraft.

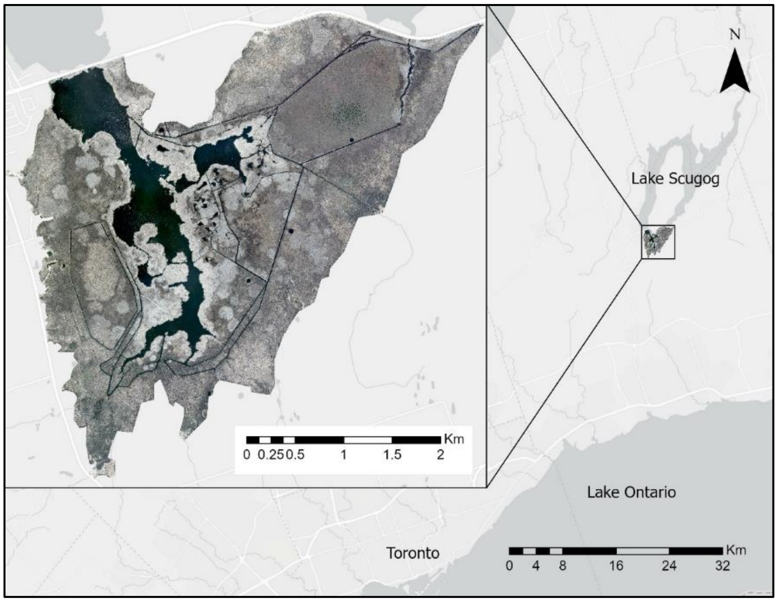

Figure 3.1. Osler Marsh in Durham Region, Ontario.

Land cover classifications

We conducted a land cover classification of Osler Marsh using the Classification Wizard in ArcGIS Pro 2.6 (ESRI, 2021) and imagery from the South-Central Ontario Orthophotography Project 2018 (SCOOP 2018) collected by Land Information Ontario (2019) to map areas of cattail-dominated marsh, open water, and other vegetation, hereafter Cattail, Water, and Other, respectively. We defined Cattail as emergent vegetation stands containing at least 50% cattail relative to other vegetation types. Imagery was acquired in spring 2018 in mostly clear conditions. The imagery contained four bands (RGB + NIR) and had a resolution of 16 cm. SCOOP 2018 was the most recent high-resolution imagery available that was appropriate for our purposes. Specifically, the leaf-off acquisition period showed relatively high contrast between monotypic cattail stands and other land cover types, especially water, and the high resolution allowed us to differentiate habitat classes at a fine scale (i.e. within 0.25-ha sample cells).

We used object-based classification to identify land cover types, which is regarded as superior to pixel-based classification for high-resolution imagery of wetlands (Grenier *et al.*, 2008; Luymes & Chow-Fraser, 2021), and we used an unsupervised classification approach as we did not collect a robust random sample of training data generally required for supervised classification (Lu & Weng, 2007; Hu *et al.*, 2017; Figure 3.2). As part of the object-based classification process, we created a segmented image using a spatial detail of 20, spectral detail of 20, and minimum pixel size of 30; after adjusting settings and running multiple iterations, these parameters best represented the observed habitat classes within the marsh overall (Melvin, Chapter 1). Spectral overlap between certain features (e.g. dense cattail stands and water sheen which may both appear white) caused some misclassifications. We visually compared the classified raster to the imagery and manually reclassified features that were clearly misclassified. We then converted the raster to polygons representing each class for ease of spatial processing. Finally, we applied two additional steps to improve classification accuracy. First, to reduce speckle (i.e. misclassified pixels due to small pixel size and high heterogeneity among neighboring pixels), we converted all Other polygons < 5 m^2 to Cattail; most of these polygons represented cattail shadows, and this reclassification had no perceptible effect on the representation of actual vegetation features in the Other class. Secondly, we corrected for major temporal differences in marsh structure by digitizing (i.e. manually tracing) major changes in marsh structure from 2018 (SCOOP imagery) to 2021 (imagery acquired by Melvin, Chapter 1) and incorporating these changes into our final land cover classification; due to the low contrast between cattail-dominated marsh and other vegetation types in the 2021 imagery, classification of SCOOP 2018 and subsequent polygon editing remained the better option for classifying these landcover types. We used a total of 167 ground-truth points to verify the accuracy of our land cover classification. A minimum of 46 points per class were opportunistically sampled at the marsh throughout 2021. GPS locations were collected with a Garmin handheld GPS unit or iPhone SE 1st generation with ≤ 5 m accuracy. Some ground-truth points were not accessed directly but examined from the water's edge; these points were moved approximately 5 m inland from the water's edge prior to the accuracy assessment. We computed an accuracy assessment using a confusion matrix, resulting in an overall accuracy of 82.0 %.

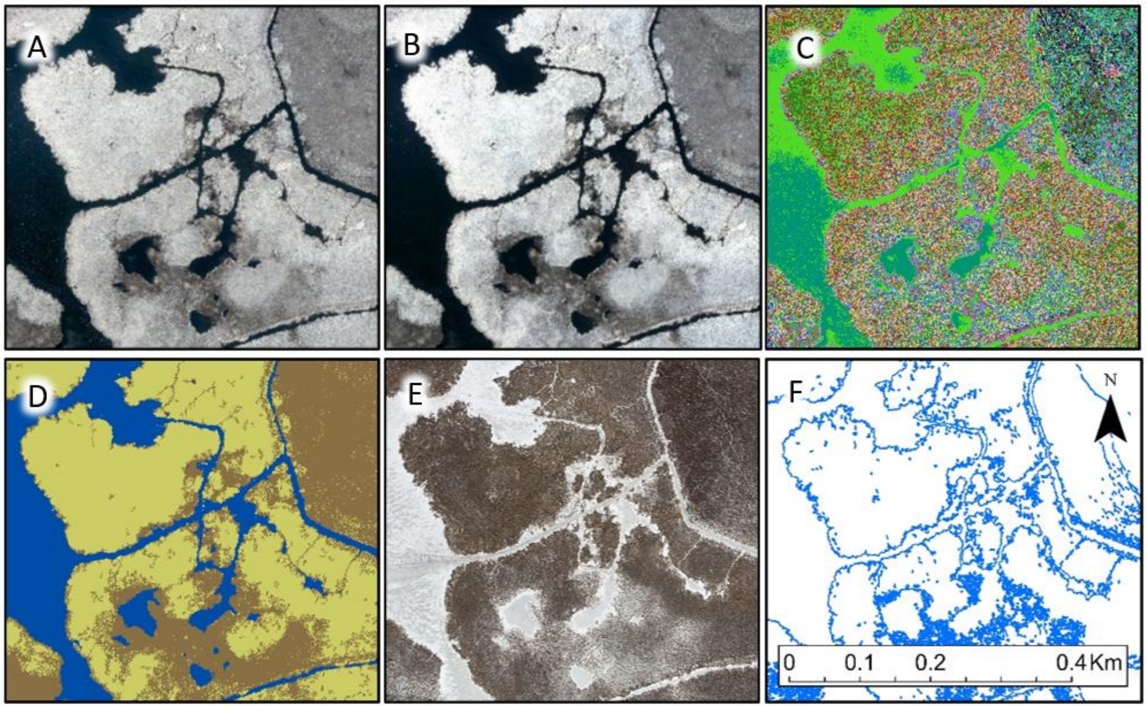

Figure 3.2. Unsupervised object-based classification of SCOOP 2018 imagery and resulting vegetation-water edges using Classification Wizard in ArcGIS Pro. Segment Mean Shift was used on mosaic of SCOOP 2018 imagery tiles (A) to produce a segmented image (B). The segmented image was used with SCOOP 2018 imagery mosaic to produce a classified raster with a maximum of 40 automatically differentiated classes (C). Classes were then merged and assigned a class of interest (D; blue = Water, yellow = Cattail, brown = Other). This process was repeated in full with 2021 winter imagery (E) assigning only Water and Other classes. The classified raster was converted to polygons representing each class. Water polygons were converted to polylines to represent vegetation-water edges used to measure interspersion (F). If necessary, polylines were

then manually digitized to more accurately represent interspersion using SCOOP 2018 imagery as a guide.

Measuring interspersion

We measured interspersion as water-vegetation edges as done by others (Rehm & Baldassarre, 2007; Chabot *et al.*, 2014; Hohman *et al.*, 2021). Due to differences in marsh structure from 2018 to 2021, we did not use our classification of SCOOP 2018 imagery to measure interspersion. Instead, we classified the more recent winter 2021 imagery collected by Melvin (Chapter 1) to make our measurements of interspersion as temporally relevant as possible. This imagery was collected at a resolution of approximately 7.5 cm. Imagery was stitched into an orthomosaic image by DroneMetrics (Ottawa, ON). Due to a spatial offset of up to 75 m, we manually georeferenced the mosaic in ArcGIS Pro using SCOOP 2018 as a reference, which was considered accurate to within 0.45 m at 95%. Snow cover during this time was minimal, and larger (≥ 50 m^2) snow patches represented water features which we confirmed using SCOOP 2018. Like our classification of SCOOP 2018 imagery, we used an unsupervised, object-based classification, but only classified land cover types as water or vegetation. We also used lower spectral and spatial detail (15 and 5, respectively) which was sufficient due to the high contrast generally observed between vegetation and water (i.e. snow). Furthermore, we used a minimum segment size of 180 pixels, thereby allowing for the detection of features of approximately 1 m^2. The interface between water features and cattail-dominated marsh was well-defined, and thus, accurately represented interspersion. However, wind-blown cattail as well as shorter vegetation types allowed for additional buildup of snow cover that did not represent water features. This led to inflated estimates of water, and thus, interspersion, which was evident when comparing with SCOOP 2018. Therefore, we calculated interspersion using only water features (represented by snow) ≥ 50 m^2 within sample cells. This minimum threshold effectively limited our measurements of interspersion to the outermost edges of vegetation and water, which, in addition to being more accurately classified than interior water features, are the most relevant to muskrat habitat use (Ervin, 2011; Sadowski & Bowman, 2021). In only one sample cell, interspersion still appeared to be overestimated since the outermost vegetation edge was not cattail and thus did not form a defined boundary with the adjacent pond. To correct for this, we digitized the portion of vegetation-water edge where interspersion was overestimated using SCOOP 2018 as a guide. Finally, we converted water polygons ≥ 50 m^2 to lines which represented water-vegetation edges, and thus, interspersion.

Interspersion and cell selection

To create sample cells, we used ArcGIS Pro to trace lines along the main water-vegetation edges, adding points at 60 m increments. These points served as cell centroids around which we created circular quarter-hectare buffers. Interspersion was then calculated for each quarter-hectare cell by intersecting water edges with sample cells (Figure 3.3). We also intersected land cover polygons (*Cattail*, *Water*, and *Other*) with sample cells to calculate the proportion of each class per cell. We eliminated any cells that contained < 5% *Cattail* and < 5% *Water* by area, as well as cells that contained ≥ 1500 m^2 of Other. For each sampling rotation, we randomly selected 20 cells in which to deploy cameras. We intended on sampling an equal number of high- and low-interspersion cells per sampling period, each within defined thresholds; however, there were not enough sample cells to meet these criteria. Nevertheless, we sampled similar ranges of interspersion from low (116 m) to high (1094 m) within each sampling period. We ensured that cells did not overlap within sampling periods, maintaining a minimum Euclidean distance of 75 m between centroids and 15 m between cell edges within sampling periods to ensure sample independence.

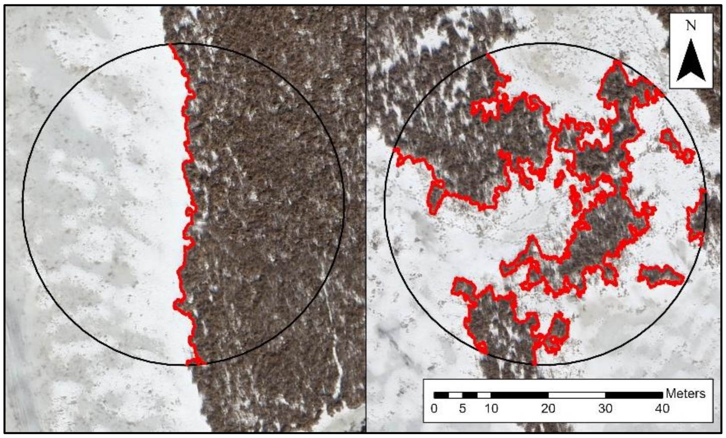

Figure 3.3. Quarter-hectare sample cells with low interspersion (left) and high interspersion (right). Vegetation-water edges used for calculations of interspersion are highlighted in red.

Camera deployment

We used Reconyx Hyperfire 1, Hyperfire 2, and Ultrafire camera traps. We positioned unbaited plywood platforms covered with senesced cattail stalks at the centroid of each sample cell as a focal point and cryptic distance marker which lied along the cattail-water interface. Cameras were fixed to iron T-posts which were inserted into the marsh substrate in open water facing the platform approximately 5 m away (Figure 3.4). Camera height was adjusted to sit approximately 0.75 m from the water's surface. We oriented cameras to face roughly north or south to avoid direct sunlight which reduces visibility and leads to false motion triggers in combination with wave action (Melvin, pers. obs.). We lightly cleared emergent vegetation within the detection zone that we thought would trigger the camera's motion sensor, otherwise leaving the detection zone unaltered. Cameras were loaded with 16 GB SD cards and Energizer Ultimate Lithium AA batteries. Settings were set to a motion trigger sensitivity of HIGH on a 24-hr schedule with no delay period and one shot per trigger. Additionally, cameras were set to take interval timer photos every 5 minutes from 1600-hrs to 0900-hrs to avoid missing nocturnal detections. Cameras were first deployed at the end of May 2021 and were moved to new locations after approximately one month (average of 28 days) until the final deployment ending in September 2021 (Figure 3.5). Sample cells were accessed by watercraft. We could not always exactly locate the cell centroid in the field due to changing GPS accuracy, wind gusts displacing our watercraft, and certain points lying in very shallow water and mucky substrate that could not be accessed. If we could not deploy a camera and platform at the designated location, we deployed them at the nearest location along the cattail-water edge. We then obtained GPS coordinates at the new platform location, created a new buffer around that point in ArcGIS Pro, and recalculated interspersion and land cover proportions.

Figure 3.4. Typical camera configuration.

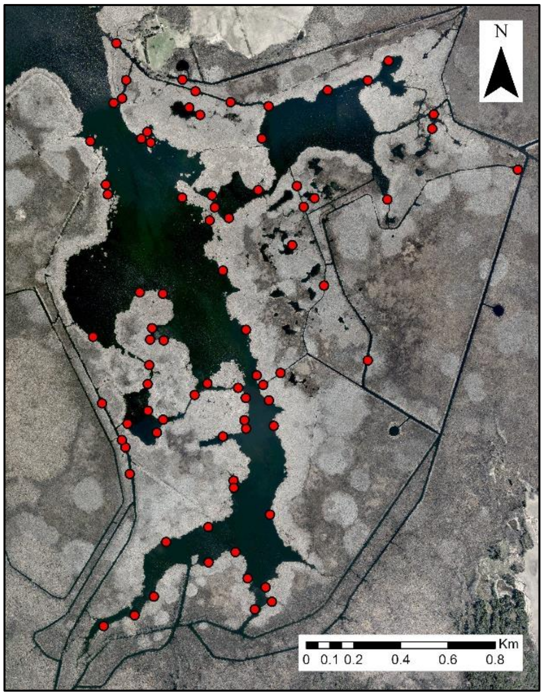

Figure 3.5. All camera locations (red circles).

Image tagging and analysis

We processed and tagged images using Timelapse 2.0 image tagging software (Greenberg, 2023). Due to resemblance with beavers, muskrats were only tagged if the observer was ≥ 90% confident of species identification. We measured intensity of use as the average number of muskrat events per 30 days. We defined events as muskrat sightings ≤ 5 minutes apart, reducing the likelihood of counting the same individual remaining within or repeatedly swimming in and out of the viewshed. Despite attempts to use a standardized approach to camera set-up, each camera's viewshed (i.e. sample area) differed to a certain extent due to differences in vegetation cover, camera angle relative to cattail stands, and frame size among camera models, likely leading to different detection probabilities among camera locations. To eliminate camera detection bias, we limited events to interval-timer photos, omitting all motion-triggered photos. To account for observer detection bias due to differences in camera set-up among locations, we assigned an index for both sample area and viewshed obstruction to each camera location to be used as variables in our models. Sample area was calculated by estimating the relative difference in water area from a standard viewshed, with 0.5 representing 0.5x the water area in the standard viewshed, 1 representing the same water area, and 2 representing 2x the water area. In some cases, much of the viewshed consisted of water, but the area farthest from the camera was too far for muskrats to be consistently detected and accurately identified; therefore, all muskrats detected in this zone were excluded, and this zone was excluded from the sample area index. Persistent camera obstruction from vegetation or glare was estimated using a scale of 0-4 from lowest to greatest obstruction based on photos from midnight on the same day near the middle of each sampling period (Table 3.1). Finally, certain data were corrected or omitted from the study due to technical complications. We omitted data from four camera locations that had very short active periods due to batteries dying or SD cards filling faster than anticipated. We also applied a multiplication factor to total events for three camera locations whose interval timers were accidentally set to > 5 min; this had no effect on two locations that originally had 0 events and only a small effect on one location that had 1 event.

Table 3.1. Index of camera obstruction.

Value	Description
0	Water virtually clear of plant material and other objects. Muskrats can swim freely.
1	Some plant material but likely no impact on muskrat detection or muskrat movement.
2	Some plant material potentially leading to missed muskrat detections. Muskrat movement may be restricted.
3	Thick plant material potentially leading to missed muskrat detections. Muskrat movement may be restricted.
4	Very thick plant material causing near complete obstruction of viewshed. Muskrat navigation unlikely.

Cattail sampling and identification

We replicated methods by Melvin (Chapter 1) to determine the relative frequency of *T. latifolia*, *T. angustifolia*, and *T.* x *glauca* at Osler Marsh. For simplicity, we refer to all hybrid classes between *T. latifolia* and *T. angustifolia* as *T.* x *glauca*. Sampling consisted of collecting a pistillate spike, pollen grains (when present), and two of the youngest leaf tips from three ramets at 3m increments along each transect, beginning at the water's edge. We sampled 21 pre-determined transects throughout the marsh, sampling a total of 62 ramets; only one transect was missing a sample due to the lack of a pistillate spike at the time of sampling. In addition, we sampled ramets that did not appear to be *T.* x *glauca* and ramets that occurred in more remote or otherwise unsampled areas of the marsh. Transects and other sampled ramets were accessed by watercraft. Samples were collected from June 28 to July 30, 2021. We identified cattail ramets by their pistillate spike (bracteole) phenotype as indicated by Smith (2000), and assumed all hybrids to exhibit the phenotype associated with *T.* x *glauca* in this key. Ramet identification by pistillate bracteole phenotype was shown to have a high level of agreement with phenotype identification by pollen morphology (Melvin, Chapter 1) which has been used by others to identify ramets (Finkelstein, 2003; Selbo & Snow, 2004; Shih & Finkelstein, 2008; Pieper *et al*., 2022). Pollen sample phenotypes were also identified according to Smith (2000), but due to the limited pollen-shedding window, pollen could only be collected from a fraction of ramets and was thus only used for validation of phenotype identification derived from pistillate spikes. Leaf tissue was collected for genotyping for future study.

Data analysis

We used Pearson correlation to determine the effect of interspersion (in meters) on intensity of use (daily average muskrat events) within and across sampling periods, as well as correlations with other predictor variables across sampling periods. Additional predictor variables included the estimated indices of sample area (0.4 – 2.0) and camera obstruction (0 – 4), which both have the potential to affect detectability of muskrats by observers, while heavy vegetation cover may also impede muskrats from occupying the area. We further included the continuous variable of water area (in square meters) which is likely an important determinant of muskrat habitat use (Proulx & Gilbert, 1983;

Melvin, Chapter 1) and the binary variable of geometry (channelized vs. non-channelized), since channelized habitat where travel is congested may see higher occurrences of muskrats than in more open habitats (Collinge & Ray, 2006, as cited in Ganoe *et al.*, 2021). Finally, we included the variable of sampling period, as muskrat activity may be seasonal (MacArthur, 1980), with increased activity during periods of house-building (Proulx & Gilbert, 1984; Danell, 1982). We also modelled intensity of use by muskrats using a zero-inflated Poisson model as our data fit a Poisson distribution and contained excess zeros. Intensity of use was standardized to muskrat events per 30 days and rounded to produce positive integers to be used in the zero-inflated Poisson model. Correlations between predictor variables were all < 0.7, so we included all variables in our model.

Results

Intensity of use

From May 25th to September 21st, we detected 261 muskrat events across 76 locations with a mean of 0.13 (± 0.025 SE) events per sample cell per day. Muskrats were detected at 50 locations (66%). The greatest intensity of use at any location was 1.17 events per day. We did not find a significant correlation between interspersion and intensity of use among or within sampling periods (Figures 3.6 and 3.7, respectively). Intensity of use was positively correlated with sampling period ($r = 0.39$, $p < 0.0005$) and was highest during the period of late-August to late-September. Intensity of use was negatively correlated with water area ($r = -0.33$, $p = 0.0034$). Finally, intensity of use was significantly higher in channelized habitats (r = 0.40, p = 0.0003). We did not observe significant correlations between intensity of use and sample area or camera obstruction.

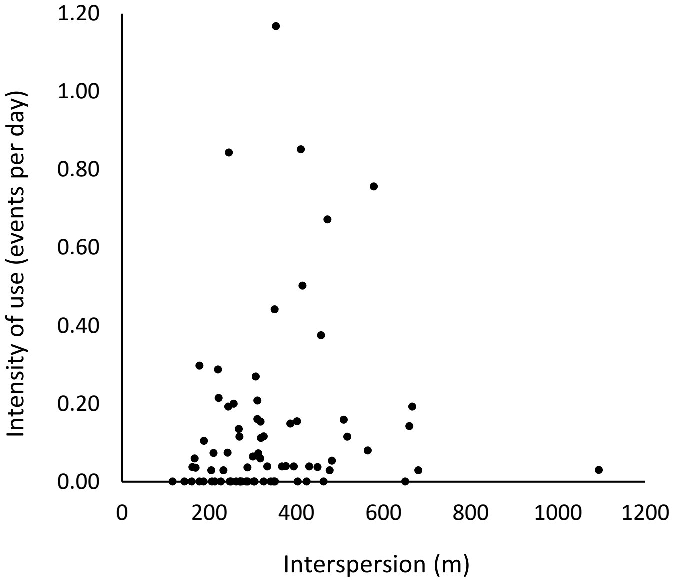

Figure 3.6. Mean daily intensity of use by muskrats in relation to interspersion at Osler Marsh, Ontario across 76 locations over four sampling periods from May 25th to September 21st, 2021.

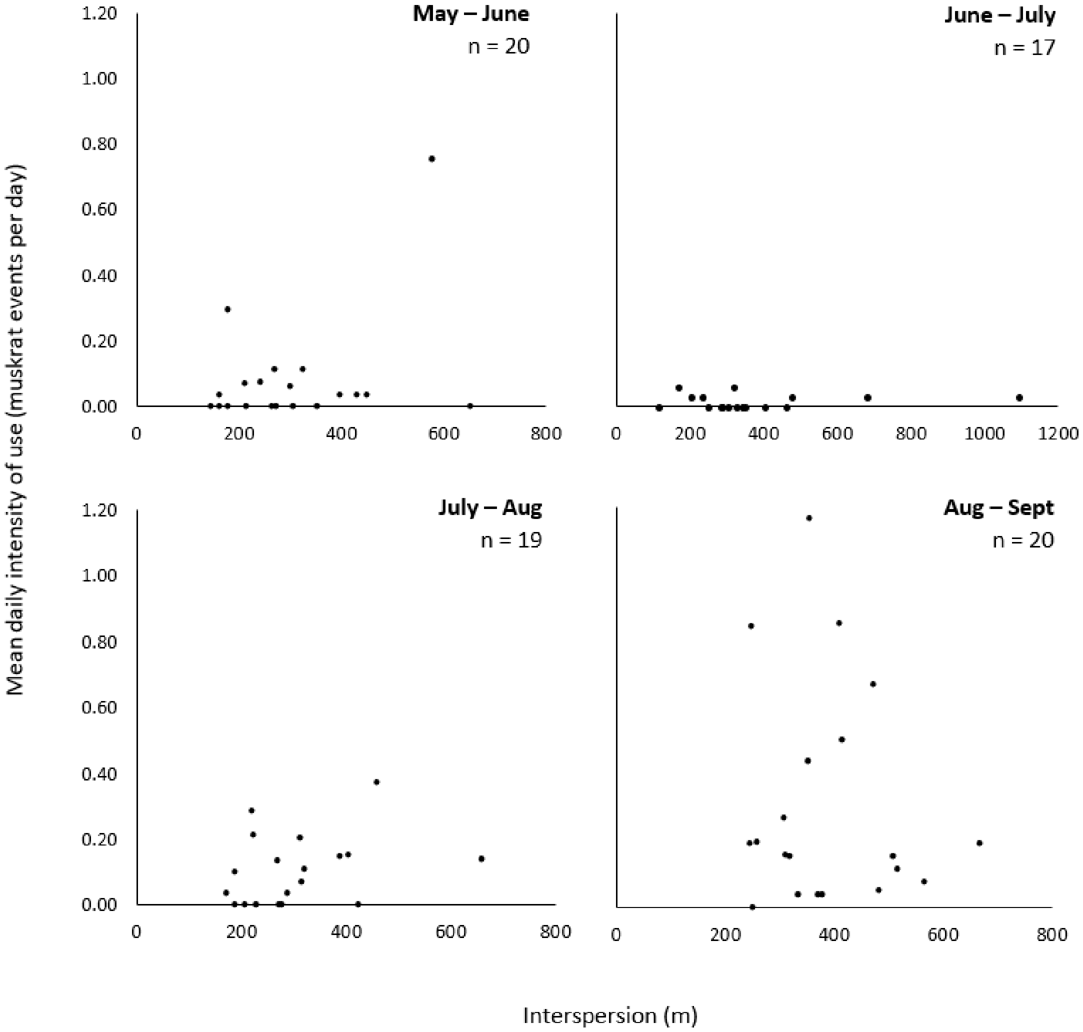

Figure 3.7. Mean daily intensity of use by muskrats in relation to interspersion at Osler Marsh, Ontario across 76 locations during each sampling period from May 25th to September 21st, 2021.

Predictor variables

In our modelling of intensity of use, *Geometry* and *Period* were correlated, and both variables were correlated with *Sample area* and *Water area*. However, since all correlations were below 0.7 (Pearson correlation coefficients), we used all variables in a global model of intensity of use. See supplementary information for a correlation matrix including p-values.

Zero-inflated Poisson models

Geometry and water area were both highly significant predictors of intensity of use in the global model. To a lesser degree, sampling period, followed by interspersion, were also significant predictors. Camera obstruction and sample area did not have a significant effect on intensity of use (Table 3.2).

Table 3.2. Summary of the strength and direction of the relationship between six predictor variables and intensity of use by muskrats at Osler Marsh, Ontario, as determined from the Poisson portion of a zero-inflated Poisson model. Significant predictors are indicated in bold text.

Variable	Estimate	Std. Error	z-value	p-value
Geometry	**1.95**	**0.28**	**6.98**	**$3.06e^{-12}$**
Water area	**0.0017**	**0.00028**	**5.88**	**$4.05e^{-9}$**
Period	**0.32**	**0.092**	**3.47**	**0.00051**
Interspersion	**-0.0010**	**0.00047**	**-2.24**	**0.025**
Obstruction	-0.14	0.085	-1.64	0.10
Sample area	-0.044	0.24	-0.18	0.85

Cattail distribution

T. x *glauca* was the dominant taxon observed in the marsh (89 % of transect samples), followed by *T. angustifolia* (11 % of transect samples; Figure 3.8). *T. latifolia* was not observed on transects but was observed elsewhere in the marsh.

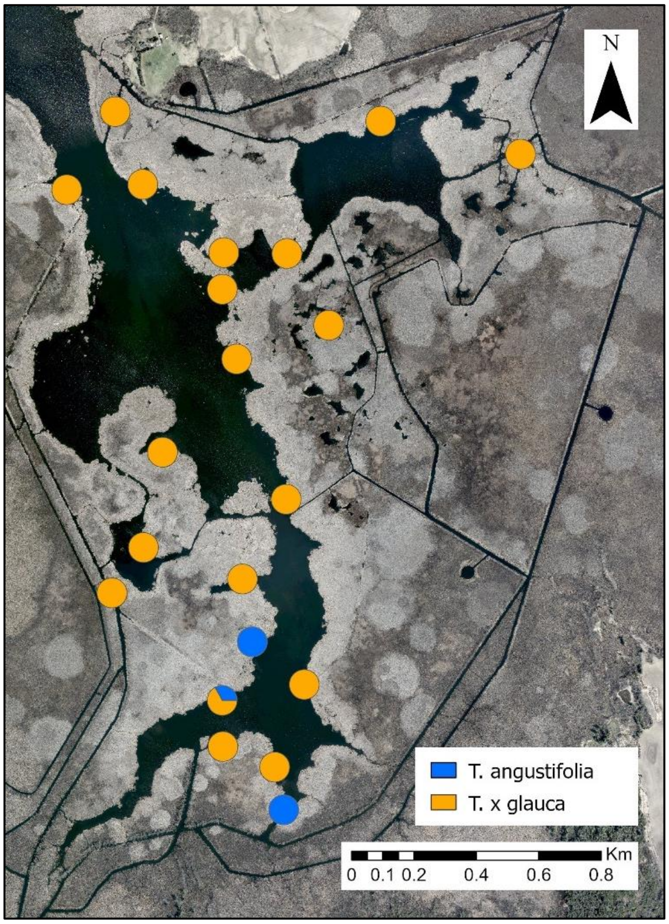

Figure 3.8. Relative frequency of cattail taxa along 21 transects at Osler Marsh, Ontario. Cattail taxa were identified by pistillate bracteole and pollen cluster phenotype according to Smith (2000).

Discussion

Contrary to our prediction, we did not find that interspersion was positively correlated with interspersion, though interspersion was a significant predictor in the global model of intensity of use. Intensity of use was more heavily influenced by other factors, including habitat geometry, sampling period, and water area. However, due to correlations among these variables, it is unclear whether there is a single mechanism driving intensity of use in muskrats or if multiple factors are at play. Though camera sampling area increased over the study period, this did not affect muskrat detections. Hybrid cattail (*T.* x *glauca*) was the dominant taxon in the marsh and very little native cattail (*T. latifolia*) was found.

The lack of correlation between interspersion and intensity of use in this study is likely due to site-specific habitat characteristics. For example, intensity of use was most strongly and significantly correlated with habitat geometry, with greater use of channelized over non-channelized habitats. Channels at Osler Marsh were dredged for boat travel nearly two centuries ago (Hvidsten, 2017). They are narrow (< 5 m wide), sheltered, and relatively still compared to the large ponds central to the marsh which frequently experience strong wind gusts (Melvin, pers. obs.). Muskrats typically avoid travelling across large, wind-exposed water bodies (Ervin, 2011; Larreur *et al.*, 2020), potentially making these channels more suitable habitat. These channels are also cleared of wild rice annually for ease of navigation, likely facilitating travel for muskrats as well, compared to pond edges where other cameras were located which became thick with rice and lilies over the summer. Channels may also act as constricted travel corridors leading to a higher volume of travelling muskrats (Collinge & Ray, 2006). Finally, it is possible that channelized habitat at Osler Marsh supports greater numbers of muskrats than open marsh as some channels had sloping banks suitable for bank dens. The degree to which muskrats use bank dens or houses may vary (MacArthur & Aleksiuk, 1979; Proulx & Gilbert, 1983), but is limited to the availability of sloping banks which are generally only present near the peripheries of a marsh. Recent population estimates at Osler Marsh did not account for bank-dwelling muskrats, though the area surveyed contained a smaller proportion of sloping banks than the current study (Melvin, Chapter 1). Due to limited suitable sample cells, we included mostly channelized habitat in the fourth sampling period, potentially confounding the effects of channelization with the effects of seasonality. However, channelized habitat had twice the effect on muskrat intensity of use than sampling period as determined by our regression model. Limiting cell selection to a single habitat type (e.g. channelized or non-channelized) would improve inferences of intensity of use in future studies.

Interspersion in the context of marsh habitat is often measured as the ratio of water to emergent vegetation (Weller & Spatcher, 1965; Kaminski & Prince, 1981; Proulx & Gilbert, 1983). By this definition, interspersion is highest where there are equal proportions of water and emergent vegetation in a given area, otherwise known as hemi-marsh (Weller & Spatcher, 1965; Kaminski & Prince, 1981). However, this concept of interspersion only acknowledges the total area of water and vegetation stands and does not take marsh structure into account. For example, a 1-ha pond and an adjacent 1-ha stand of densely-packed cattail would meet the criteria of hemi-marsh, as would a

2-ha marsh containing numerous interconnected pools and channels where the ratio of water and vegetation are equal. The latter is most likely to attract a host of marsh species (Weller & Spatcher, 1965; Kaminski & Prince, 1981; Chabot *et al.*, 2014; Kua *et al.*, 2020). As water-vegetation edge length increases within a given area, the ratio of water to vegetation will also generally approach 1:1 since these edges are associated with both water and vegetation. Melvin (Chapter 1) found that vegetation-water edge density was significantly correlated with water area approaching hemi-marsh conditions (i.e. 0 – 50 % water per unit area). Therefore, by measuring vegetation-water edges, we accounted for both structural complexity and the ratio of water to vegetation using a single variable. Additionally, since we calculated the area of water and vegetation per cell, we were also able to measure interspersion as a ratio of water to vegetation, using water area as a direct proxy. The significant negative correlation between water area and intensity of use in this study is surprising. The average proportion of water relative to vegetation across sample cells was less than 50%, or less than 1250 m^2 (1030 m^2, ± 50 SE). Therefore, one might expect a positive correlation between intensity of use and water area as the proportion of water approaches hemi-marsh conditions. Though muskrat population density tends to be highest in hemi-marsh conditions (Weller & Spatcher, 1965; Weller, 1978; Proulx & Gilbert, 1983; Melvin, Chapter 1), population density may not directly correlate with intensity of use. At the relatively fine scale used in this study, factors other than interspersion may be more important to intensity of use by muskrats, including site specific characteristics such as habitat geometry.

The scale at which interspersion is important to muskrats is not widely reported in the literature. Proulx & Gilbert (1983) found high levels of interspersion within muskrat home ranges in a southern Ontario marsh, ranging from 484 m^2 in early summer to 1112 m^2 in late summer. Melvin (Chapter 1) showed that interspersion within 1-ha grid cells, averaged within 39 southern Ontario marshes, was a significant predictor of muskrat population density. Since we measured interspersion at a scale of 0.25-hectare sample cells, it is likely that we appropriately captured the scale at which interspersion should be relevant to muskrats. Furthermore, vegetation-water edge density should be less constrained by scale than the traditional hemi-marsh definition of interspersion. For example, a 50 m^2 pool beside a 50 m^2 cattail stand may represent a valuable patch of muskrat habitat, but if these areas are multiplied 10-fold, the ratio of water to vegetation may be less relevant since muskrats typically concentrate their activity near emergent-water edges (Ervin, 2011; Sadowski & Bowman, 2021) and avoid large expanses of open water (Errington, 1963; Ervin, 2011; Larreur *et al.*, 2020). While vegetation-water edge has been used in few studies to measure marsh interspersion in the context of muskrats (Melvin, Chapter 1), we believe this to be a valuable tool in assessing marsh habitat quality.

While the average muskrat home range may be roughly 0.25 ha, home range size can vary widely, from a radius of as little as 15 m (MacArthur, 1978, as cited in Willner *et al.*, 1980) to 230 m (MacArthur, 1980) from a dwelling. Studies suggest that muskrat home range size is negatively correlated with population density (Proulx & Gilbert, 1983; Marinelli & Messier, 1993), as seen in other rodents (Maza *et al.*, 1973; Cameron &

Spencer, 1985; Erlinge *et al.*, 1990). The population density at Osler Marsh at the time this study was conducted was low compared to other marshes in south central Ontario (Melvin, Chapter 1) which were also low, on average, compared to historical densities in cattail-dominated marshes in Canada (Proulx & Gilbert, 1984; Messier & Virgl, 1992; Sadowski & Bowman, 2021). This suggests that muskrat home ranges at Osler Marsh could be relatively large, and thus, it is possible that we did not capture entire home ranges in our 0.25 ha (25 m radius) sample cells. We also assumed equal home range sizes throughout the marsh, though evidence suggests that linear water features may promote increased length of home range size relative to non-channelized features (Ahlers *et al.*, 2010). This may have resulted in home ranges of muskrats that spanned multiple sample cells in the marsh. One may expect fewer passes in front of a given camera in home ranges spanning multiple cameras, though this may be compensated by increased movement of individuals typical in large home ranges (Alt *et al.*, 1980; Gehring & Swihart, 2004; Keim *et al.*, 2019). Furthermore, muskrat home ranges may overlap considerably (Ching and Chih-tanc, 1962, as cited in Ganoe *et al.*, 2021; Ganoe *et al*, 2021). Therefore, home range is not likely a critical factor in determining the size of sample cells when studying intensity of use in muskrats.

Osler Marsh was highly dominated by invasive hybrid cattail *T.* x *glauca*, as determined by the relative proportion of *T.* x *glauca* samples along representative transects throughout the marsh and identification of ramets by pistillate bracteole phenotypes. This method of ramet identification has been shown to have high agreement with identification by pollen cluster morphology (Melvin, Chapter 1), which has been used by others to identify *T. latifolia*, *T. angustifolia*, and *T.* x *glauca* in the absence of genetic data (Finkelstein, 2003; Selbo & Snow, 2004; Bhargav *et al.*, 2022). Since we did not collect cattail samples in all camera sample cells, and the marsh was highly dominated by *T.* x *glauca*, we did not conduct any statistical comparisons between the distribution of *T.* x *glauca* and intensity of use by muskrats. Melvin (Chapter 1) found little correlation between *T.* x *glauca* relative frequency and muskrat population density; however, their inference was also limited by the high degree of dominance by *T.* x *glauca* across sites. A study of muskrat habitat use stratified by cattail taxa in a wetland with a highly variable cattail community would likely provide further insight into the effects of *T.* x *glauca* invasions on muskrats.

Studies have also linked muskrat population declines to water level management (Toner *et al.*, 2010; Ervin, 2011; Ahlers & Heske, 2017; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018). While altered water level regimes can have direct consequences on muskrat populations (Errington, 1963; Phaneuf, 1979; Toner *et al.*, 2010), allowing a system to return to a natural equilibrium should permit muskrat populations to rebound, given their high reproductive output (Errington, 1963). However, preliminary evidence suggests that the recently implemented Plan 2014, which was intended to improve the overall health of coastal Lake Ontario wetlands by allowing more natural water level fluctuations to occur, has not led to an increase in muskrat populations (Melvin, Chapter 1). After decades of succession toward an ecosystem that is dominated by invasive cattail, largely the result of stabilized water levels under Plan 1958, returning muskrat habitat to the way it once was may not be so simple. Wetland succession can be slow (Meeks, 1969; Keddy & Reznicek, 1986; Weller, 1988; Wilcox *et al.*, 2004), so reversing the invasion of *T.* x *glauca*, if possible, may take decades. Other efforts to control *T.* x *glauca* have been met with limited success (Boers *et al.*, 2007; Elgersma *et al.*, 2017; Wilcox *et al.*, 2017) and may be difficult and costly to carry out on a broad scale (Sojda and Solberg 1993; Stewart *et al.*, 2023). More extensive and long-term monitoring is required to determine the effectiveness of Plan 2014 in controlling *T.* x glauca and whether muskrat populations will eventually increase in Lake Ontario coastal wetlands under this new plan.

In addition to the negative impacts on wetland habitats associated with the invasion of *T.* x *glauca*, floating cattail mats may be a concern for muskrats. For reasons that are not yet clear, floating mats are avoided by muskrats (Bishop *et al.*, 1979; Kadlec *et al.*, 2007; Ervin, 2011). This may be due to the reduction of relatively shallow open water required for house-building (Sather, 1958; Proulx & Gilbert, 1984; Toner *et al.*, 2010), as floating cattail mats are not constrained by water depth and thus expand into deeper water than rooted stands (Larreur *et al.*, 2020; Melvin, Chapter 1). These mats are bound by rhizomal networks which create a buoyant substrate (Hogg & Wein, 1988) that can be traversed by terrestrial predators (Hewitt & Miyanishi, 1997; Melvin, pers. obs.). Furthermore, floating mats may be dry or covered only by shallow water, and the water column beneath is dense with organic material and sediment (Hogg & Wein, 1988), possibly deterring muskrats from habitat use. Notably, nearly all sampled cattail ramets at Osler Marsh occurred on floating mats, and water depth at sampled ramets averaged over 1 m. This may have contributed to the low population density observed at Osler Marsh, as suitable water depths for house-building were scarce. Both *T*. x *glauca* and *T. angustifolia* stands have been reported to expand vegetatively via floating mats (Wilcox *et al.*, 2005; Wilcox *et al.*, 2008; Larreur *et al.*, 2020) which may have implications for muskrats. We recommend further research into floating mat formation as it relates to cattail invasions, wetland habitat quality, and muskrat population declines.

Conclusion

We found that interspersion was not an important predictor of intensity of use by muskrats at Osler Marsh. Intensity of use was most influenced by habitat geometry, followed by sampling period and water area. Though interspersion is an important habitat feature for muskrats, this may not be reflected in studies of intensity of use. We also present further evidence of extensive *T.* x *glauca* invasion in southern Ontario, with near total coverage of *T.* x *glauca* in a large, cattail-dominated marsh. The spread of *T.* x *glauca* in North America is extensive and its effects on wetland biodiversity are numerous. While there remains little empirical evidence demonstrating a link between *T.* x *glauca* invasions and muskrat population declines, the widespread and long-term transformations of muskrat habitat due to this invasive hybrid are difficult to ignore. It is important that agencies continue to monitor marsh communities and muskrat populations across the muskrat's native range. We also recommend investigating the impacts of floating mats on muskrat habitat selection and population density. Invasive species pose a major threat to biodiversity and ecosystems worldwide (IUCN, n.d.). With the number of invasive species entering non-native regions steadily increasing (IUCN, n.d.), maintaining the integrity of native ecosystems and biodiversity while simultaneously engineering landscapes for human benefit will require increasingly complex and innovative solutions. Controlling and reversing the spread of *T.* x *glauca* may be a necessary step in conserving muskrat populations, but this will not happen overnight. However, more research is needed to determine the precise cause or causes of muskrat population declines in North America.

References

Ahlers, A. A., & Heske, E. J. (2017). Empirical evidence for declines in muskrat populations across the United States. *Journal of Wildlife Management*, *81*(8), 1408–1416. https://doi.org/10.1002/jwmg.21328

Ahlers, A. A., Heske, E. J., Schooley, R. L., & Mitchell, M. A. (2010). Home ranges and space use of muskrats Ondatra zibethicus in restricted linear habitats. *Wildlife Biology*, *16*(4), 400–408. https://doi.org/10.2981/10-044

Alt, G. L., Matula, G. J., Alt, F. W., & Lindzey, J. S. (1980). Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. *International Association for Bear Research and Management*, *4*(February 1977), 131–136.

Bansal, S., Lishawa, S. C., Newman, S., Tangen, B. A., Wilcox, D., Albert, D., Anteau, M. J., Chimney, M. J., Cressey, R. L., DeKeyser, E., Elgersma, K. J., Finkelstein, S. A., Freeland, J., Grosshans, R., Klug, P. E., Larkin, D. J., Lawrence, B. A., Linz, G., Marburger, J., Noe, G., Otto, C., Reo, N., Richards, J., Richardson, C., Rodgers, L., Schrank, A., Svedarsky, D., Travis, S., Tuchman, N., & Windham-Myers, L. (2019). *Typha* (cattail) invasion in North American wetlands: Biology, regional problems, impacts, ecosystem services, and management. *Wetlands, 39*, 645–684. https://doi.org/10.1007/s13157-019-01174-7

Bellrose, F. C., & Brown, L. G. (1941). The effect of fluctuating water levels on the muskrat population of the Illinois River Valley. *The Journal of Wildlife Management*, *5*(2), 206. https://doi.org/10.2307/3795587

Benoit, L. K., & Askins, R. A. (1999). Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *The Society of Wetland Scientists*, *19*(1), 194–208.

Bhargav, V. V., Freeland, J. R., & Dorken, M. E. (2022). Evidence of hybrid breakdown among invasive hybrid cattails (*Typha* x *glauca*). *The Genetics Society*, *March*, 1–7. https://doi.org/10.1038/s41437-022-00557-7

Bishop, R. A., Andrews, R. D., & Bridges, R. J. (1979). Marsh management and its relationship to vegetation, waterfowl and muskrats. *Proceedings - Iowa Academy of Science*, *86*(2), 50–56.

Boers, A. M., & Zedler, J. B. (2008). Stabilized water levels and *Typha* invasiveness. *Wetlands*, *28*(3), 676–685. https://doi.org/10.1672/07-223.1

Boers, A. M., Veltman, R. L. D., & Zedler, J. B. (2007). *Typha* x *glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering*, *29*(3), 232–244. https://doi.org/10.1016/j.ecoleng.2006.04.011

Bomske, C. M., & Ahlers, A. A. (2020). How do muskrats *Ondatra zibethicus* affect ecosystems? A review of evidence. *Mammal Review*, 1–11. https://doi.org/10.1111/mam.12218

Boutin, S., & Birkenholz, D. E. (1987). Muskrat and round-tailed muskrat. In Novak, M., Baker, J.A., Obbard, M. E., & Malloch, B. (Eds.), *Wild Furbearer Management and Conservation in North America*, 314–325. Ontario Ministry of Natural Resources.

Brietzke, C. (2015). Muskrat ecology in the Mackenzie Delta: Insights from local knowledge and ecological field surveys. *Arctic*, *68*(4), 527–531. https://doi.org/10.14430/arctic4538

Cameron, G. N., & Spencer, S. R. (1985). Assessment of space-use patterns in the hispid cotton rat (*Sigmodon hispidus*). *Oecologia*, *68*(1), 133–139.

Chabot, D., Carignan, V., & Bird, D. M. (2014). Measuring habitat quality for least bitterns in a created wetland with use of a small unmanned aircraft. *Wetlands*, *34*(3), 527–533. https://doi.org/10.1007/s13157-014-0518-1

Chatterton, H. J. (1944). The muskrat fur industry of Louisiana. *Journal of Geography*.

Danell, K. (1977). Short-term plant successions following the colonization of a northern Swedish lake. *British Ecological Society*, *14*(3), 933–947.

Danell, K. (1996). Introductions of aquatic rodents: Lessons of the muskrat *Ondatra zibethicus* invasion. *Wildlife Biology*, *2*(3), 213–220. https://doi.org/10.2981/wlb.1996.021

Danell, K. 1982. CRC Handbook of Census Methods for Terrestrial Vertebrates. 1st ed.

Dozier, H. L. (1948). Estimating muskrat populations by house counts. *Thirteenth North American Wildlife Conference*, 372-392.

Dozier, H. L. (1950). Muskrat trapping on the Montezuma National Wildlife Refuge, New York. *The Journal of Wildlife Management*, *14*(4), 403–412.

Elgersma, K. J., Martina, J. P., Goldberg, D. E., & Currie, W. S. (2017). Effectiveness of cattail (*Typha* spp.) management techniques depends on exogenous nitrogen inputs. *Elementa*, *5*. https://doi.org/10.1525/elementa.147

Environmental Systems Research Institute [ESRI]. 2021. ArcGIS Pro Desktop: Version 2.6. Environmental Systems Research Institute, Redlands, California.

Erlinge, A. S., Hoogenboom, I., Agrell, J., Nelson, J., & Sandell, M. (1990). Density-related home-range size and overlap in adult field voles (*Microtus agrestis*) in southern Sweden. *American Society of Mammologists*, *71*(4), 597–603.

Errington, P. L. (1939). Reaction of muskrat populations to drought. *Ecology*, *20*(2), 168–186.

Errington, P. L. (1951). Concerning fluctuations in populations of the prolific and widely distributed muskrat. *The American Naturalist*, *85*(824), 273–292. https://doi.org/10.1086/281680

Errington, P. L. (1963). Muskrat populations. The Iowa State University Press, Ames, Iowa, USA.

Ervin, M. D. (2011). Population characteristics and habitat selection of muskrats (*Ondatra zibethicus*) in response to water level management at the Summerberry Marsh Complex, The Pas (M.Sc. Thesis). Iowa State University, Iowa, USA.

Farrell, J. M., Murry, B. A., Leopold, D. J., Halpern, A., Rippke, M. B., Godwin, K. S., & Hafner, S. D. (2010). Water-level regulation and coastal wetland vegetation in the upper St. Lawrence River: Inferences from historical aerial imagery, seed banks, and *Typha* dynamics. *Hydrobiologia*, *647*(1), 127–144. https://doi.org/10.1007/s10750-009-0035-z

Farrer, E. C., & Goldberg, D. E. (2014). Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. *Aquatic Botany*, *116*, 35–43. https://doi.org/10.1016/j.aquabot.2014.01.002

Finkelstein, S. A. (2003). Identifying pollen grains of *Typha latifolia*, *Typha angustifolia*, and *Typha* x *glauca*. *Canadian Journal of Botany*, *81*(9), 985–990. https://doi.org/10.1139/b03-084

Galatowitsch, S. M., Anderson, N. O., Ascher, P. D., & Hall, A. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*(4), 733–755.

Ganoe, L. S., Brown, J. D., Yabsley, M. J., Lovallo, M. J., & Walter, W. D. (2020). A Review of Pathogens, Diseases, and Contaminants of Muskrats (Ondatra zibethicus) in North America. *Frontiers in Veterinary Science*, *7*(May), 1–13. https://doi.org/10.3389/fvets.2020.00233

Ganoe, L. S., Lovallo, M. J., Brown, J. D., & Walter, W. D. (2021). Ecology of an isolated muskrat population during regional population declines. *Northeastern Naturalist*, *28*(1), 49–64. https://doi.org/10.1656/045.028.0104

Gehring, T. M., & Swihart, R. K. (2004). Home range and movements of long-tailed weasels in a landscape fragmented by agriculture. *Journal of Mammalogy*, *85*(1), 79–86. https://doi.org/10.1644/1545-1542(2004)085<0079:HRAMOL>2.0.CO;2

Grace, J. B., & Harrison, J. S. (1986). The biology of Canadian weeds. *Journal of Plant Science*, *379*.

Greenberg, S. 2023. Timelapse 2.0. University of Calgary.

Greenhorn, J. E., Sadowski, C., Holden, J., & Bowman, J. (2017). Coastal wetlands connected to Lake Ontario have reduced muskrat (*Ondatra zibethicus*) abundance. *Wetlands*, *37*(2), 339–349. https://doi.org/10.1007/s13157-016-0874-0

Gregory, G. J., Dibblee, R., Daoust, P.-Y., & Van Den Heuvel, M. R. (2019). Declines in muskrat (*Ondatra zibethicus*) population density in Prince Edward Island, Canada. *Canadian Wildlife Biology and Management*, *8*(2), 46–60.

Grenier, M., Labrecque, S., Benoit, M., & Allard, M. (2008). Accuracy assessment method for wetland object-based classification. *GEOBIA 2008 - Pixels, Objects, Intelligence*, 6. http://www.isprs.org/proceedings/XXXVIII/4-C1/Sessions/Session1/6589_Y_Gao_Proc_pap.pdf

Hall, S. (2008). *Typha* x *glauca* (hybrid cattail). CABI Digital Library. https://doi.org/10.1079/cabicompendium.107745

Harris, S. W., & Marshall, W. H. (1963). Ecology of water-level manipulations on a northern marsh. *Ecology*, *44*(2), 331–343.

Hewitt, N., & Miyanishi, K. (1997). The role of mammals in maintaining plant species richness in a floating *Typha* marsh in southern Ontario. *Biodiversity and Conservation*, *6*(8), 1085–1102. https://doi.org/10.1023/A:1018380000881

Higgins, C., & Mitsch, W. J. (2000). The role of muskrats (*Ondatra zibethicus*) as ecosystem engineers in created freshwater marshes. *Biomass*, 81–86.

Hogg, E., & Wein, R. W. (1988). The contribution of *Typha* components to floating mat buoyancy. *Ecology*, *69*(4), 1025–1031.

Hohman, T. R., Howe, R. W., Tozer, D. C., Gnass Giese, E. E., Wolf, A. T., Niemi, G. J., Gehring, T. M., Grabas, G. P., & Norment, C. J. (2021). Influence of lake levels on water extent, interspersion, and marsh birds in Great Lakes coastal wetlands. *Journal of Great Lakes Research*, *47*(2), 534–545. https://doi.org/10.1016/j.jglr.2021.01.006

Hu, S., Niu, Z., & Chen, Y. (2017). Global Wetland Datasets: A review. *Wetlands*, *37*(5), 807–817. https://doi.org/10.1007/s13157-017-0927-z

Hvidsten, J. P. (2007). Scugog marshlands: Creation of the syndicate game preserve.

International Joint Commission [IJC]. (2014). Lake Ontario St. Lawrence River Plan 2014: Protecting against extreme water levels, restoring wetlands and preparing for climate change. https://ijc.org/sites/default/files/IJC_LOSR_EN_Web.pdf

International Union for the Conservation of Nature [IUCN]. (n.d.). Invasive alien species. https://www.iucn.org/our-work/topic/invasive-alien-species#:~:text=Invasive%20alien%20species%20are%20animals,human%20economy%20and%20well-being. Accessed August 2023.

Kadlec, R. H., Pries, J., & Mustard, H. (2007). Muskrats (*Ondatra zibethicus*) in treatment wetlands. *Ecological Engineering*, *29*(2), 143–153. https://doi.org/10.1016/j.ecoleng.2006.06.008

Kaminski, R. M., & Prince, H. H. (1981). Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. *The Wildlife Society*, *45*(1), 1–15.

Keddy, P. A., & Reznicek, A. A. (1986). Great Lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research*.

Keim, J. L., Lele, S. R., DeWitt, P. D., Fitzpatrick, J. J., & Jenni, N. S. (2019). Estimating the intensity of use by interacting predators and prey using camera traps. *Journal of Animal Ecology*, *88*(5), 690–701. https://doi.org/10.1111/1365-2656.12960

Kiviat, E. (1978). Vertebrate use of muskrat lodges and burrows. *Estuaries*, *1*(3), 196–200. https://doi.org/10.2307/1351464

Kua, Z. X., Stella, J. C., & Farrell, J. M. (2020). Local disturbance by muskrat, an ecosystem engineer, enhances plant diversity in regionally-altered wetlands. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3256

Larreur, M. R., Windels, S. K., Olson, B. T., & Ahlers, A. A. (2020). Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. *Landscape Ecology*, *35*(1), 59–68. https://doi.org/10.1007/s10980-019-00925-5

Lishawa, S. C., Albert, D. A., & Tuchman, N. C. (2010). Water level decline promotes *Typha* x *glauca* establishment and vegetation change in Great Lakes coastal wetlands. *Wetlands*, *30*(6), 1085–1096. https://doi.org/10.1007/s13157-010-0113-z

Lu, D., & Weng, Q. (2007). A survey of image classification methods and techniques for improving classification performance. *International Journal of Remote Sensing*, *28*(5), 823–870. https://doi.org/10.1080/01431160600746456

Luymes, N., & Chow-Fraser, P. (2021). Detection of potential vernal pools on the Canadian Shield (Ontario) using object-based image analysis in combination with machine learning. *Canadian Journal of Remote Sensing*, *47*(4), 519–534. https://doi.org/10.1080/07038992.2021.1900717

MacArthur, R. A. (1980). Daily and seasonal activity patterns of the muskrat *Ondatra zibethicus* as revealed by radiotelemetry. *Ecography*, *3*(1), 1–9. https://doi.org/10.1111/j.1600-0587.1980.tb00702.x

Macarthur, R. A., & Aleksiuk, M. (1979). Seasonal microenvironments of the muskrat (*Ondatra zibethicus*) in a northern marsh. *American Society of Mammologists*, *60*(1), 146–154.

Marinelli, L., & Messier, F. (1993). Space use and the social system of muskrats. *Canadian Journal of Zoology*, *71*(5), 869–875. https://doi.org/10.1139/z93-113

Markle, C. E., Chow-Fraser, G., & Chow-Fraser, P. (2018). Long-Term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. *PLoS ONE*, *13*(2), 1–15. https://doi.org/10.1371/journal.pone.0192134

Maza, A. B. G., French, N. R., & Aschwanden, A. P. (1973). Home range dynamics in a population of heteromyid rodents. *American Society of Mammologists*, *54*(2), 405–425.

Meeker, J. E., Wilcox, D. A., Johnson, S. E., & Tillison, N. (2023). Tracking vegetation transitions due to invasion of cattail (*Typha*) in Lake Superior coastal peatlands. *Wetlands*, *43*(2). https://doi.org/10.1007/s13157-023-01664-9

Meeks, R. L. (1969). The effect of drawdown date on wetland plant succession. *The Journal of Wildlife Management*, *33*(4), 817–821.

Melvin, G. P. Chapter 2: Impact of *T.* x *glauca* invasions and interspersion on muskrat populations in southern Ontario. In: Impacts of invasive hybrid cattail *Typha* x *glauca* and reduced marsh interspersion on muskrats (*Ondatra zibethicus*) in North America (M.Sc. Thesis). Trent University, Peterborough, Ontario.

Messier, F., & Virgl, J. A. (1992). Differential use of bank burrows and lodges by muskrats, Ondatra zibethicus, in a northern marsh environment. *Canadian Journal of Zoology*, *70*(6), 1180–1184. https://doi.org/10.1139/z92-165

Mott, C. L., Bloomquist, C. K., & Nielsen, C. K. (2013). Within-lodge interactions between two ecosystem engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). *Behaviour*, *150*(11), 1325–1344. https://doi.org/10.1163/1568539X-00003097

Nyman, J. A., Chabreck, R. H., & Kinler, N. W. (1993). Some effects of herbivory and 30 years of weir management on emergent vegetation in Brackish Marsh. *Wetlands*, *13*(3), 165–175. https://doi.org/10.1007/BF03160877

Nyman, J. A., Chabreck, R. H., & Kinler, N. W. (1993). Some effects of herbivory and 30 years of weir management on emergent vegetation in Brackish Marsh. *Wetlands*, *13*(3), 165–175. https://doi.org/10.1007/BF03160877

Phaneuf, R. (1979). Indian reserve band rights: Enforcement on the St. Lawrence River. *Canadian Water Resources Journal*, *4*(3), 30–34. https://doi.org/10.4296/cwrj0403030

Pieper, S. J., Freeland, J., & Dorken, M. (2022). Patterns of pollen dispersal and pollen capture in the hybridizing cattails, *Typha latifolia* and *T. angustifolia*. *Botany*. https://doi.org/10.1139/cjb-2021-0166

Pieper, S., Dorken, M., & Freeland, J. (2020). Genetic structure in hybrids and progenitors provides insight into processes underlying an invasive cattail (*Typha* x *glauca*) hybrid zone. *Heredity*, *124*(6), 714–725. https://doi.org/10.1038/s41437-020-0307-y

Proulx, G., & Gilbert, F. F. (1983). The ecology of the muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario. *Canadian Field-Naturalist*, *97*(4), 377–390.

Proulx, G., & Gilbert, F. F. (1984). Estimating muskrat population trends by house counts. *The Journal of Wildlife Management*, *48*(3), 917–922.

Rehm, E. M., & Baldassarre, G. A. (2007). The influence of interspersion on marsh bird abundance in New York. *Wilson Journal of Ornithology*, *119*(4), 648–654. https://doi.org/10.1676/06-060.1

Roberts, N. M., & Crimmins, S. M. (2010). Do trends in muskrat harvest indicate widespread population declines? *Northeastern Naturalist*, *17*(2), 229–238. https://doi.org/10.1656/045.017.0206

Sadowski, C., & Bowman, J. (2021). Historical surveys reveal a long-term decline in muskrat populations. *Ecology and Evolution*, *11*(12), 7557–7568. https://doi.org/10.1002/ece3.7588

Sather, J. H. (1958). Biology of the Great Plains Muskrat in Nebraska. *Wildlife Monographs*, *2*, 1–35.

Schummer, M. L., Palframan, J., McNaughton, E., Barney, T., & Petrie, S. A. (2012). Comparisons of bird, aquatic macroinvertebrate, and plant communities among dredged ponds and natural wetland habitats at Long Point, Lake Erie, Ontario. *Wetlands*, *32*(5), 945–953. https://doi.org/10.1007/s13157-012-0328-2

Selbo, S. M., & Snow, A. A. (2004). The potential for hybridization between *Typha angustifolia* and *Typha latifolia* in a constructed wetland. *Aquatic Botany*, *78*(4), 361–369. https://doi.org/10.1016/j.aquabot.2004.01.003

Shih, J. G., & Finkelstein, S. A. (2008). Range dynamics and invasive tendencies in *Typha latifolia* and *Typha angustifolia* in eastern North America derived from herbarium and pollen records. *Wetlands*, *28*(1), 1–16. http://www.ncdc.noaa.gov/paleo/

Smith, I. M., Fiorino, G. E., Grabas, G. P., & Wilcox, D. A. (2021). Wetland vegetation response to record-high Lake Ontario water levels. *Journal of Great Lakes Research*, *47*(1), 160–167. https://doi.org/10.1016/j.jglr.2020.10.013

Smith, S. G. (2000). *Typhaceae Jussieu* (as *Typhae*) - Cat-tail family. In Flora of North America North of Mexico. Vol. 22: *Magnoliophyta*: *Alismatidae*, *Arecidae*, *Commelinidae* (in part) and *Zingiberidae*. Pp 278-285. Oxford University Press, New York, New York.

Sojda, R. S., & Solberg, K. L. (1993). Management and control of cattails. *United States Department of the Interior Fish and Wildlife Service, Washington, D.C. Fish and Wildlife Leaflet 13*

Soper, D. (1942). Mammals of Wood Buffalo Park, northern Alberta and District of Mackenzie. *Academy of Management Review*, *31*(2), 386–408.

Stewart, D., Hood, W. G., & Martin, T. G. (2023). Undetected but widespread: The cryptic invasion of non-native cattail (*Typha*) in a Pacific Northwest estuary. *Estuaries and Coasts*, *46*(3), 802–817. https://doi.org/10.1007/s12237-023-01171-4

Straka, J. R., Antoine, A., Bruno, R., Campbell, D., Campbell, R., Campbell, R., Cardina, J., Gibot, G., Gray, Q. Z., Irwin, S., Kindopp, R., Ladouceur, R., Ladouceur, W., Lankshear, J., Maclean, B., Macmillan, S., Marcel, F., Marten, G., Marten, L., McKinnon, J., Patterson, L. D., Voyageur, M., Whiteknife, G., Wiltzen, L. & Giguère, N. (2018). We used to say rats fell from the sky after a flood: Temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta. *Arctic*, *71*(2), 218–228. https://doi.org/10.14430/arctic4714

Szabo, J., Freeland, J. R., & Dorken, M. E. (2018). The effects of leaf litter and competition from hybrid cattails (*Typha* x *glauca*) on the seed germination and seedling performance of its parental species. *Aquatic Botany*, *145*(November 2017), 29–36. https://doi.org/10.1016/j.aquabot.2017.11.009

Takos, M. J. (1947). A semi-quantitative study of muskrat food habits. *The Journal of Wildlife Management*, *11*(4), 331–339.

Tangen, B. A., Bansal, S., Freeland, J. R., Travis, S. E., Wasko, J. D., McGonigle, T. P., Goldsborough, L. G., Gow, K., Marburger, J. E., & Meier, J. A. (2022). Distributions of native and invasive *Typha* (cattail) throughout the Prairie Pothole Region of North America. *Wetlands Ecology and Management*, *30*(1), 1–17. https://doi.org/10.1007/s11273-021-09823-7

Toner, J., Farrell, J. M., & Mead, J. V. (2010). Muskrat abundance responses to water level regulation within freshwater coastal wetlands. *Wetlands*, *30*(2), 211–219. https://doi.org/10.1007/s13157-010-0034-x

Travis, S. E., Marburger, J. E., Windels, S., & Kubátová, B. (2010). Hybridization dynamics of invasive cattail (*Typhaceae*) stands in the western Great Lakes Region of North America: A molecular analysis. *Journal of Ecology*, *98*(1), 7–16. https://doi.org/10.1111/j.1365-2745.2009.01596.x

Tulbure, M. G., Johnston, C. A., & Auger, D. L. (2007). Rapid invasion of a Great Lakes coastal wetland by non-native *Phragmites australis* and *Typha*. *Journal of Great Lakes Research*, *33*(SPEC. ISS. 3), 269–279. https://doi.org/10.3394/0380-1330(2007)33[269:RIOAGL]2.0.CO;2

Vaccaro, L. E., Bedford, B. L., & Johnston, C. A. (2009). Litter accumulation promotes dominance of invasive species of cattails (*Typha* spp.) in Lake Ontario wetlands. *Wetlands*, *29*(3), 1036–1048. https://doi.org/10.1672/08-28.1

Virgl, J. A., & Messier, F. (1997). Habitat suitability in muskrats: A test of the food limitation hypothesis. *Journal of Zoology*, *243*(2), 237–253. https://doi.org/10.1111/j.1469-7998.1997.tb02779.x

Ward, E. M., & Gorelick, S. M. (2018). Drying drives decline in muskrat population in the Peace-Athabasca Delta, Canada. *Environmental Research Letters*, *13*(12), 124026. https://doi.org/10.1088/1748-9326/aaf0ec

Waters, I., & Shay, J. M. (1992). Effect of water depth on population parameters of a Typha glauca stand. *Canadian Journal of Botany*, *70*(2), 349–351. https://doi.org/10.1139/b92-046

Weller, M. W. (1988). Issues and approaches in assessing cumulative impacts on waterbird habitat in wetlands. *Environmental Management*, *12*(5), 695–701. https://doi.org/10.1007/BF01867546

Weller, M. W., & Spatcher, C. S. (1965). Role of habitat in the distribution and abundance of marsh birds. *Special Report No. 43*, 4-31.

Wilcox, D. A. (2004). Implications of hydrologic variability on the succession of plants in Great Lakes wetlands. *Aquatic Ecosystem Health and Management*, *7*(2), 223–231. https://doi.org/10.1080/14634980490461579

Wilcox, D. A., & Bateman, J. A. (2018). Photointerpretation analysis of plant communities in Lake Ontario wetlands following 65 years of lake-level regulation. *Journal of Great Lakes Research*, *44*(6), 1306–1313. https://doi.org/10.1016/j.jglr.2018.08.007

Wilcox, D. A., & Meeker, J. E. (1992). Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. *Wetlands*, *12*(3), 192–203. https://doi.org/10.1007/BF03160609

Wilcox, D. A., & Xie, Y. (2008). Predicted effects of proposed new regulation plans on sedge/grass meadows of Lake Ontario. *Journal of Great Lakes Research*, *34*(4), 745–754. https://doi.org/10.3394/0380-1330-34.4.745

Wilcox, D. A., Buckler, K., & Czayka, A. (2017). Controlling cattail invasion in sedge/grass meadows. *Wetlands*, *38*(2), 337–347. https://doi.org/10.1007/s13157-017-0971-8

Wilcox, D. A., Ingram, J. W., Kowalski, K. P., Meeker, J. E., Martha, L., Xie, Y., Grabas, G. P., Holmes, K. L., & Patterson, N. J. (2005). Evaluation of water level regulation influences on Lake Ontario and upper St. Lawrence River coastal wetland plant communities. Report to the International Joint Commission, Washington, D.C. and Ottawa, ON.

Wilcox, D. A., Kowalski, K. P., Hoare, H. L., Carlson, M. L., & Morgan, H. N. (2008). Cattail invasion of sedge/grass meadows in Lake Ontario: Photointerpretation analysis of sixteen wetlands over five decades. *Journal of Great Lakes Research*, *34*(2), 301–323. https://doi.org/10.3394/0380-1330(2008)34[301:CIOGMI]2.0.CO;2

Willner, B. G. R., Feldhamer, G. A., Zucker, E. E., & Chapman, J. A. (1980). *Ondatra zibethicus*. *The American Society of Mammologists*, *141*, 1–8.

Woo, I., & Zedler, J. B. (2002). Can nutrients alone shift a sedge meadow towards dominance by the invasive Typha × glauca? Wetlands, 22(3), 509–521. https://doi.org/10.1672/0277-5212(2002)022[0509:CNASAS]2.0.CO;2

Zapfe, L., & Freeland, J. R. (2015). Heterosis in invasive F1 cattail hybrids (*Typha* x *glauca*). *Aquatic Botany*, *125*, 44–47. https://doi.org/10.1016/j.aquabot.2015.05.004

Chapter 4: General discussion

Summary of findings

I present regional-scale muskrat population estimates using house counts as a proxy, along with a comprehensive inventory of cattail (*Typha*) in south-central Ontario. Muskrat house counts in the region are low, on average, compared to historical house counts in Ontario and elsewhere in North America, and invasive hybrid cattail *T.* x *glauca* has become dominant over parental *Typha* species. Despite these findings, I found no correlation between the relative frequency of *T.* x *glauca* and muskrat population density. This may be due to the overwhelming dominance of *T.* x *glauca* and resulting lack of variation in its relative frequency across sites. Therefore, I cannot reject the hypothesis that muskrat populations are declining in southern Ontario due to the invasion of *T.* x *glauca.* I found a nearly significant correlation between marsh interspersion and the relative frequency of *T.* x *glauca* across the study area, which may indicate that other factors are also driving interspersion. Support for my reduced interspersion hypothesis was mixed. Muskrat population density was significantly correlated with interspersion across the study area, but we did not observe a correlation between interspersion and intensity of habitat use at our fine-scale study site, Osler Marsh. Instead, intensity of use was more strongly correlated with habitat geometry (higher in channelized habitats), water area, and sampling period. Though these variables were correlated, the highly significant effect of channelized habitat suggests that this was the primary driver of intensity of use. My work marks the first investigation of the impact of invasive cattails and reduced marsh interspersion on muskrat populations and sheds light on continental declines of this once-prolific furbearer.

Muskrats and cattails

While muskrat population declines appear to be widespread in North America (Benoit & Askins, 1999; Roberts & Crimmins, 2010; Ahlers & Heske, 2017; Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Gregory *et al.*, 2019; Sadowski & Bowman, 2021), the invasion of *T.* x *glauca* has not been widely reported outside of eastern and central North America. This may suggest that other factors are influencing muskrat population declines throughout the continent. Indeed, large-scale declines in Canada's northwest have been linked to climate change (Ward & Gorelick, 2018; Turner *et al.*, 2020) and water management (Ward & Gorelick, 2018), and few reports of *T.* x *glauca* exist in that region. Additionally, in Lake Ontario coastal wetlands, notwithstanding major invasions of *T.* x *glauca*, low muskrat population densities have been more directly linked to water level management (Toner *et al.*, 2010; Greenhorn *et al.*, 2017). Nevertheless, the extent of *T.* x *glauca* invasions continues to expand (Tangen *et al.*, 2022; Meeker *et al.*, 2023; Stewart *et al.*, 2023), is likely underestimated due to the plant's cryptic appearance relative to parental species (Stewart *et al.*, 2023), and may be under-reported in the literature. Furthermore, evidence supporting the competitive advantages of *T.* x *glauca* over parental *T. latifolia* and *T. angustifolia* is overwhelming (Bansal *et al.*, 2019), suggesting that *T.* x *glauca* will continue to dominate invaded wetlands in North America. However, recent evidence shows that the dominance of *T.* x *glauca* will eventually be limited by the low relative frequency of *T. angustifolia* (Bhargav *et al.*,

2022) which almost exclusively acts as the maternal parent to F1 hybrids (Ball & Freeland, 2013). Although *T.* x *glauca* appears scarce in certain regions of North America, even despite the coexistence of both parental species, other cattail species are exhibiting similar invasive tendencies. For example, *T. domingensis* has become more prevalent in the Florida Everglades in recent decades, forming monotypic stands in certain areas (Newman *et al.*, 1997), much like *T.* x *glauca.* And, like *T.* x *glauca*, the increase in *T. domingensis* has been attributed to water level management and increased nutrient concentrations (Newman *et al.*, 1997). Muskrats are absent from the Florida Everglades, which are instead occupied by the closely-resembling round-tailed muskrat (*Neofiber alleni*). Due to lack of harvest, round-tailed muskrats have garnered little attention compared to their relative, the common muskrat (Boutin & Birkenholz, 1987). Recent evidence suggests population declines in round-tailed muskrat as well (Taillie *et al.*, 2021), but this is likely linked to predation by invasive Burmese pythons (Dorcas *et al.*, 2012). It remains unclear whether and to what degree cattail invasions are impacting muskrat populations in North America. More extensive and systematic sampling of *Typha*, other aquatic plants, and muskrats in wetlands across the United States and Canada would improve our understanding of the distribution and abundance of cattail species and their hybrids, which may help to determine their potential role in muskrat population declines.

Muskrats and invasive species

Despite some debate (Gurevitch & Padilla, 2004; Didham *et al.*, 2005), biological invasions are likely a major cause of extinctions worldwide (Clavero & García-Berthou, 2005; IUCN, n.d.). Cattails are not the only invasive plants that may be negatively impacting muskrat populations in North America. Common reed (*Phragmites australis* subsp. *australis*, hereafter *P. australis*) has also become a prolific invader in Canada and the United States in recent decades (Galatowitsch *et al.*, 1999; Catling & Mitrow, 2011), in some cases likely supplanting *T.* x *glauca* (Benoit & Askins, 1999; Bellavalence & Brisson, 2010; Robichaud & Rooney, 2017). This invasion has been associated with local vertebrate population declines (Benoit & Askins; 1999; Greenberg & Green, 2013; Robichaud Rooney, 2017), reduced biodiversity (Ailstock *et al.*, 2001; Whyte *et al.,* 2005; OMNRF, 2017), and degradation of critical marsh habitat (Robichaud & Rooney, 2017; Markle *et al.*, 2018). Benoit & Askins (1999) report steep declines in muskrat populations in Connecticut tidal marshes following the invasion of *P. australis*. Notably, one marsh included in their study became progressively infilled by *P. australis* leading to a gradual reduction in marsh interspersion. Efforts to control *T.* x *glauca* and *P. australis* have been successful in restoring wetland ecosystems to varying degrees (Ailstock *et al.*, 2001; Tozer & Mackenzie, 2019; Johnson *et al.*, 2021; Silva *et al.*, 2021; Polzer & Wilcox, 2022). However, the positive effects of restoration may be temporary (Ailstock *et al.*, 2001; Farrer & Goldberg, 2014; Keyport *et al.*, 2019), and may even promote secondary invasions (Robichaud & Rooney, 2021). Moreover, controlling invasive species using current methods (e.g. cutting, burning, and use of herbicides) indefinitely on a large scale is likely to be extremely costly and labour-intensive, and it seems highly likely that new species will continue to invade and disrupt ecosystems across North America. The switch to water-level management Plan 2014 for Lake Ontario will be a test of whether allowing more natural water level fluctuations to occur can more passively suppress *T.* x *glauca* invasions in the long term and restore the health of coastal Lake Ontario ecosystems, including muskrat populations within them.

Muskrats and marsh interspersion: a 'chicken or egg' scenario

The positive association between muskrats and interspersion observed in this investigation reflects previous findings (Weller & Spatcher, 1965; Proulx & Gilbert, 1983; Kua *et al.*, 2020). Since muskrats are known to increase heterogeneity in wetlands (Weller & Spatcher, 1965; Errington, 1963; Wilcox & Meeker, 1992; Kadlec *et al.*, 2007; Kua *et al.*, 2020), gaining the title "ecosystem engineer" (Higgins & Mitsch, 2000; Toner *et al.*, 2010; Mott *et al.*, 2013; Kua *et al.*, 2020), one may question whether interspersion is an important habitat feature or whether it is simply a byproduct of muskrat activity. The answer, it seems, is both. Through herbivory and house-building, muskrats create patterns of interspersion in marshes (Weller & Spatcher, 1965; Bishop *et al.*, 1979; Higgins & Mitsch, 2000; Kadlec *et al.*, 2007; Kua *et al.*, 2020). At the same time, muskrats select habitat with high interspersion for house-building (Proulx & Gilbert, 1983), and, since muskrats are simultaneously limited by the presence of water for travel and mostly emergent vegetation for foraging (Boutin & Birkenholz, 1987; Errington, 1963; Proulx & Gilbert, 1983; Clark *et al.*, 1994; Ahlers *et al.*, 2010), it is reasonable to assume that muskrats generally select for habitat with high interspersion of both cover types. Furthermore, muskrats likely benefit from high interspersion, particularly as emergent-water edge density, due to the increased availability of both forage and cover (Brinson *et al.*, 1995). Therefore, muskrat activity in marshes may cause a positive feedback loop, where muskrats create the habitat conditions for which they select. The significant correlation found between muskrat population density and interspersion in this investigation supports the idea that muskrats select habitat with high interspersion. This idea was not supported by my findings in Chapter 2, where no correlation was found between interspersion and intensity of use. This may suggest that other habitat characteristics are more important in fine-scale habitat use where site-level interspersion is generally high. However, further research is needed to test this hypothesis.

Will muskrats adapt to changing habitat?

Given the muskrat's hardy nature and flexible habitat requirements (Errington, 1963; Boutin & Birkenholz, 1987), widespread population declines are surprising. Most recent large-scale population estimates have used house counts to estimate population density (Greenhorn *et al.*, 2017; Ward & Gorelick, 2018; Sadowski & Bowman, 2021; Melvin, Chapter 1) which does not account for bank-dwelling muskrats. In certain regions where natural wetland habitat has been converted to cropland, drainage ditches represent some of the only suitable habitats for muskrats (Ahlers *et al.*, 2010). In this investigation, I suggest that the expansion of floating mats into deep water may limit house-building in marshes. In Chapter 2, I demonstrated greater use of channelized habitat at Osler Marsh over more open marsh habitat; these channels included elevated banks and were generally closer to upland habitat which likely provided suitable conditions for bank dens. The choice of dwelling is largely dependent on available habitat and conditions therein (Errington, 1963; Kurta, 1995), and perhaps in certain regions, seasonality (Dozier, 1948; MacArthur & Aleksiuk, 1979). Aside from the basic requirement of solid, sloping banks, bank dens may be preferred where water levels are unstable. For example, bank dens can serve as important spring dwellings where the annual freshet destroys winter houses (Dozier, 1948, Sather, 1958; Danell, 1966). Where water levels decline below a minimum threshold, muskrats may abandon houses (Proulx & Gilbert, 1983; Danell, 1978) and house-building may be reduced (Toner *et al.*, 2010). Bank dens may be preferred in warmer months as they remain cooler than houses (MacArthur & Aleksiuk, 1979). Houses can also be vulnerable to predation (Danell, 1978; Proulx *et al.*, 1987) as they are easy to destroy, potentially leading to reduced house-building in areas with high densities of predators. Muskrats have a tendency to crowd habitats either currently or previously occupied by other muskrats, even when suitable habitat is nearby, likely owing to the presence of existing dwellings, and thus, the reduced cost of establishment (Errington, 1963). In light of widespread changes to the structure and composition of marshes in North America, in conjunction with an increase in roadside ditches and other engineered habitats tied to human infrastructure, what once may have been marginal habitat for certain muskrat populations may now be more valuable and frequently used. Quantifying habitat selection in the face of changing landscapes would provide insight into whether muskrats are adapting to a shift in available habitat types. However, declines in muskrat harvest across much of North

America are not biased toward dwelling type, indicating widespread population declines despite a potential increase in the use of bank dens relative to houses.

Other potential causes of population declines

Muskrat population declines in North America are likely the result of several factors, some of which, such as water level management and species invasions, are clearly related. As with most contemporary extinctions and population declines, it is very likely that the ultimate cause of muskrat population declines stems from human activity, either directly or indirectly. This investigation does not provide an answer to the continental decline in muskrat populations, but contributes to our understanding of the influence of habitat change. In addition to the negative impact of reduced marsh interspersion in southern Ontario marshes I present here, I also suggest that the formation of floating cattail mats, which may also be associated with the invasion of *T.* x *glauca*, is a plausible avenue for future investigation. Despite the widespread occurrence of floating cattail mats, the avoidance of these mats by muskrats, and the numerous potential negative consequences of floating mats on muskrat habitat suitability, such as increased predation, reduced winter food availability, and limited substrate for house-building, the effects of cattail mat formation on muskrat populations have not yet been studied. Water level management is clearly having direct negative consequences on certain muskrat populations due to drawdowns, diversion, and intensive use by industry. Managing water level regimes for both ecological and economic values will be required to maintain healthy aquatic ecosystems, including muskrat populations. Ongoing monitoring and research will help gauge the success of

Plan 2014 in restoring coastal ecosystems in Lake Ontario, which, if successful, may act as a global example of ecologically effective water level management. Though muskrat populations are generally tolerant of diseases and contaminants (Ganoe *et al.*, 2021), monitoring the effects of novel diseases and contaminants on muskrats may also be beneficial. Finally, climate change is predicted to bring a higher frequency of weather extremes to North America, such as floods (Marsooli *et al.*, 2019) and droughts (Ebi et al, 2021) in certain regions, and muskrats have been shown to be sensitive to both extremes (Errington, 1939; Errington, 1951; Errington, 1963; Phaneuf, 1979; Miller, 2018). Strategies to conserve or increase muskrat populations in North America, therefore, will likely require a broad range of considerations.

The use of remote cameras for studying muskrats

Studies using remote cameras to monitor muskrats are scarce but have been increasing in recent years (Gregory, 2012; Mott *et al.*, 2013; Matykiewicz *et al.*, 2021). In our study, differences in sample area and camera obstruction had little effect on muskrat detections. Nevertheless, using the same camera model across locations would improve consistency and limit the need for correction factors in modelling. Measuring the distance of the camera from the focal target as well as the height and angle of the camera would ensure similar viewshed sizes across sites, similarly reducing the need for corrections in modelling. We did not find platforms to be useful as we observed very few muskrats using them as perches, and only 1 out of 8 of these events triggered a motion detection. Swaying cattail stands in the background approximately 4 – 5 m from the camera rarely caused motion triggers on high sensitivity. Conversely, the movement of individual plants closer to the camera frequently triggered the camera. We attempted to clear the viewshed of such plants, though this became increasingly difficult in the summer with the heavy growth of wild rice. However, this had little impact on muskrat detections. Motion detections can be highly variable depending on the distance of the animal to the camera, camera obstructions, and time of day. Regular interval photos at high frequencies, as used in this study, provide a high volume of data that is generally more objective than motion-triggered detections. This approach should be considered for future camera trap studies involving species that are non-cryptic and relatively abundant, and may be particularly useful for semi-aquatic, nocturnal mammals which seldom trigger motion detections at night (Lerone *et al.*, 2015; this study).

Conclusion

This marks one of the first targeted investigations into widespread muskrat population declines in North America. I studied marshes in southern Ontario to test whether invasive hybrid cattail *T.* x *glauca* and associated reductions in marsh interspersion are contributing to these declines in Canada and the United States. I conclude that reductions in marsh interspersion may be contributing to muskrat population declines, but the direct impact of increased *T.* x *glauca* relative frequency in North American marshes is inconclusive. I recommend the following: (1) increased monitoring of muskrat populations throughout their range in North America and comparing current population estimates to historical data where possible; (2) increased monitoring of wetland plant communities where data on cattail taxa distribution and abundance are limited; (3) research into the impacts of floating mats on muskrat fitness and population density, specifically with respect to a potential increase in predation, limited food access in winter, and deep water limiting house-building as potential consequences of floating mat formation; (4) detailed assessments of areas and habitats with high and low muskrat densities in North America which may shed additional light on causes of population declines; (5) use remote sensing data to track habitat changes, such as marsh interspersion, over time; and (6) continue monitoring the effects of Plan 2014 on coastal wetlands, including changes to marsh vegetation and muskrat populations.

References

Ahlers, A. A., & Heske, E. J. (2017). Empirical evidence for declines in muskrat populations across the United States. *Journal of Wildlife Management*, *81*(8), 1408–1416. https://doi.org/10.1002/jwmg.21328

Ahlers, A. A., Heske, E. J., Schooley, R. L., & Mitchell, M. A. (2010). Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. *Wildlife Biology*, *16*(4), 400–408. https://doi.org/10.2981/10-044

Ailstock, M. S., Norman, C. M., & Bushmann, P. J. (2001). Common reed *Phragmites australis*: Control and effects upon biodiversity in freshwater nontidal wetlands. *Restoration Ecology*, *9*(1), 49–59. https://doi.org/10.1046/j.1526-100X.2001.009001049.x

Bansal, S., Lishawa, S. C., Newman, S., Tangen, B. A., Wilcox, D., Albert, D., Anteau, M. J., Chimney, M. J., Cressey, R. L., DeKeyser, E., Elgersma, K. J., Finkelstein, S. A., Freeland, J., Grosshans, R., Klug, P. E., Larkin, D. J., Lawrence, B. A., Linz, G., Marburger, J., Noe, G., Otto, C., Reo, N., Richards, J., Richardson, C., Rodgers, L., Schrank, A., Svedarsky, D., Travis, S., Tuchman, N., & Windham-Myers, L. (2019). *Typha* (cattail) invasion in North American wetlands: Biology, regional problems, impacts, ecosystem services, and management. *Wetlands, 39*, 645–684. https://doi.org/10.1007/s13157-019-01174-7

Bellavance, M. E., & Brisson, J. (2010). Spatial dynamics and morphological plasticity of common reed (*Phragmites australis*) and cattails (*Typha* sp.) in freshwater marshes and roadside ditches. *Aquatic Botany*, *93*(2), 129–134. https://doi.org/10.1016/j.aquabot.2010.04.003

Benoit, L. K., & Askins, R. A. (1999). Impact of the spread of *Phragmites* on the distribution of birds in Connecticut tidal marshes. *The Society of Wetland Scientists*, *19*(1), 194–208.

Bhargav, V. V., Freeland, J. R., & Dorken, M. E. (2022). Evidence of hybrid breakdown among invasive hybrid cattails (*Typha* x *glauca*). *The Genetics Society*, *March*, 1–7. https://doi.org/10.1038/s41437-022-00557-7

Boutin, S., & Birkenholz, D. E. (1987). Muskrat and round-tailed muskrat. In Novak, M., Baker, J.A., Obbard, M. E., & Malloch, B. (Eds.), *Wild Furbearer Management and Conservation in North America*, 314–325. Ontario Ministry of Natural Resources.

Brinson, M. M., Rheinhardt, R. D., Hauer, F. R., Lee, L. C., Nutter, W. L., Smith, R. D., Whigham, D., & Smith, R. D. (1995). A Guidebook for Application of Hydrogeomorphic Assessments to Riverine Wetlands. *Wetlands Research Program Technical Report WRP-DE-11*, *December 1995*, 219. http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA308365

Catling, P. M., & Mitrow, G. (2011). The recent spread and potential distribution of phragmites australis subsp. Australis in Canada. *Canadian Field-Naturalist*, *125*(2), 95–104. https://doi.org/10.22621/cfn.v125i2.1187

Clark, W. R. (1994). Habitat selection by muskrats in experimental marshes undergoing succession. In *Canadian Journal of Zoology*, *72*(4). https://doi.org/10.1139/z94-091

Clavero, M., & Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. Trends in Ecology and Evolution. *Trends in Ecology & Evolution*, *20*(3), 110. https://digitalcommons.unl.edu/usgsstaffpub/45%0Ahttp://dx.doi.org/10.1016/j.tree.2010.06.006%0Ahttps://doi.org/10.1016/j.rala.2018.11.002

Danell, K. (1978). Population dynamics of the muskrat in a shallow Swedish lake. *Journal of Animal Ecology*, *47*(3), 697–709.

Danell, K. (1996). Introductions of aquatic rodents: Lessons of the muskrat *Ondatra zibethicus* invasion. *Wildlife Biology*, *2*(3), 213–220. https://doi.org/10.2981/wlb.1996.021

Dorcas, M. E., Willson, J. D., Reed, R. N., Snow, R. W., Rochford, M. R., Miller, M. A., Meshaka, W. E., Andreadis, P. T., Mazzotti, F. J., Romagosa, C. M., & Hart, K. M. (2012). Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(7), 2418–2422. https://doi.org/10.1073/pnas.1115226109

Dozier, H. L. (1948). Estimating muskrat populations by house counts. *Thirteenth North American Wildlife Conference*, 372-392.

Ebi, K. L., Vanos, J., Baldwin, J. W., Bell, J. E., Hondula, D. M., Errett, N. A., Hayes, K., Reid, C. E., Saha, S., Spector, J., & Berry, P. (2020). Extreme weather and climate change: Population health and health system implications. *Annual Review of Public Health*, *42*, 293–315. https://doi.org/10.1146/annurev-publhealth-012420-105026

Errington, P. L. (1939). Reaction of muskrat populations to drought. *Ecology*, *20*(2), 168–186.

Errington, P. L. (1951). Concerning fluctuations in populations of the prolific and widely distributed muskrat. *The American Naturalist*, *85*(824), 273–292. https://doi.org/10.1086/281680

Errington, P. L. (1963). Muskrat populations. The Iowa State University Press, Ames, Iowa, USA.

Farrer, E. C., & Goldberg, D. E. (2014). Mechanisms and reversibility of the effects of hybrid cattail on a Great Lakes marsh. *Aquatic Botany*, *116*, 35–43. https://doi.org/10.1016/j.aquabot.2014.01.002

Galatowitsch, S. M., Anderson, N. O., Ascher, P. D., & Hall, A. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*(4), 733–755.

Ganoe, L. S., Brown, J. D., Lovallo, M. J., Yabsley, M. J., Garrett, K. B., Thompson, A. T., Poppenga, R. H., Ruder, M. G., & Walter, W. D. (2021). Surveillance for diseases, pathogens, and toxicants of muskrat (*Ondatra zibethicus*) in Pennsylvania and surrounding regions. *PLoS ONE*, *16*(12 December), 1–21. https://doi.org/10.1371/journal.pone.0260987

Greenhorn, J. E., Sadowski, C., Holden, J., & Bowman, J. (2017). Coastal wetlands connected to Lake Ontario have reduced muskrat (*Ondatra zibethicus*) abundance. *Wetlands*, *37*(2), 339–349. https://doi.org/10.1007/s13157-016-0874-0

Gregory, G. J. (2012). Investigating the potential causes of muskrat (*Ondatra zibethicus*) density decline on Prince Edward Island (M.Sc. Thesis). University of Prince Edward Island, Charlottetown, Prince Edward Island.

Gregory, G. J., Dibblee, R., Daoust, P.-Y., & Van Den Heuvel, M. R. (2019). Declines in muskrat (*Ondatra zibethicus*) population density in Prince Edward Island, Canada. *Canadian Wildlife Biology and Management*, *8*(2), 46–60.

Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution*, *19*(9), 470–474. https://doi.org/10.1016/j.tree.2004.07.005

Higgins, C., & Mitsch, W. J. (2000). The role of muskrats (*Ondatra zibethicus*) as ecosystem engineers in created freshwater marshes. *Biomass*, 81–86.

Johnson, O. F., Panda, A., Lishawa, S. C., & Lawrence, B. A. (2021). Repeated large-scale mechanical treatment of invasive Typha under increasing water levels promotes floating mat formation and wetland methane emissions. *Science of the Total Environment*, *790*, 147920. https://doi.org/10.1016/j.scitotenv.2021.147920

Kadlec, R. H., Pries, J., & Mustard, H. (2007). Muskrats (*Ondatra zibethicus*) in treatment wetlands. *Ecological Engineering*, *29*(2), 143–153. https://doi.org/10.1016/j.ecoleng.2006.06.008

Keyport, S., Carson, B. D., Johnson, O., Lawrence, B. A., Lishawa, S. C., Tuchman, N. C., & Kelly, J. J. (2019). Effects of experimental harvesting of an invasive hybrid cattail on wetland structure and function. *Restoration Ecology*, *27*(2), 389–398. https://doi.org/10.1111/rec.12859

Kua, Z. X., Stella, J. C., & Farrell, J. M. (2020). Local disturbance by muskrat, an ecosystem engineer, enhances plant diversity in regionally-altered wetlands. *Ecosphere*, *11*(10). https://doi.org/10.1002/ecs2.3256

Kurta, A. Mammals of the Great Lakes Region. 3rd Ed. The University of Michigan Press, Ann Arbor, Michigan, USA.

Lerone, L., Carpaneto, G. M., & Loy, A. (2015). Why camera traps fail to detect a semi-aquatic mammal: Activation devices as possible cause. *Wildlife Society Bulletin*, *39*(1), 193–196. https://doi.org/10.1002/wsb.508

Macarthur, R. A., & Aleksiuk, M. (1979). Seasonal microenvironments of the muskrat (*Ondatra zibethicus*) in a northern marsh. *American Society of Mammologists*, *60*(1), 146–154.

Markle, C. E., Chow-Fraser, G., & Chow-Fraser, P. (2018). Long-term habitat changes in a protected area: Implications for herpetofauna habitat management and restoration. *PLoS ONE*, *13*(2), 1–15. https://doi.org/10.1371/journal.pone.0192134

Marsooli, R., Lin, N., Emanuel, K., & Feng, K. (2019). Climate change exacerbates hurricane flood hazards along US Atlantic and Gulf Coasts in spatially varying patterns. *Nature Communications*, *10*(1), 1–9. https://doi.org/10.1038/s41467-019-11755-z

Matykiewicz, B. R., Windels, S. K., Olson, B. T., Plumb, R. T., Wolf, T. M., & Ahlers, A. A. (2021). Assessing translocation effects on the spatial ecology and survival of muskrats *Ondatra zibethicus*. *Wildlife Biology*, *2021*(2). https://doi.org/10.2981/wlb.00823

Meeker, J. E., Wilcox, D. A., Johnson, S. E., & Tillison, N. (2023). Tracking vegetation transitions due to invasion of cattail (*Typha*) in Lake Superior coastal peatlands. *Wetlands*, *43*(2). https://doi.org/10.1007/s13157-023-01664-9

Melvin, G. P. Chapter 2: Impact of *T.* x *glauca* invasions and interspersion on muskrat populations in southern Ontario. In: Impacts of invasive hybrid cattail *Typha* x *glauca* and reduced marsh interspersion on muskrats (*Ondatra zibethicus*) in North America (M.Sc. Thesis). Trent University, Peterborough, Ontario.

Miller, J. E. (2018). Muskrats. *Wildlife Damage Management Technical Series, 14*. https://digitalcommons.unl.edu/nwrcwdmts/14

Mott, C. L., Bloomquist, C. K., & Nielsen, C. K. (2013). Within-lodge interactions between two ecosystem engineers, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*). *Behaviour*, *150*(11), 1325–1344. https://doi.org/10.1163/1568539X-00003097

Newman, S., Reddy, K. R., DeBusk, W. F., Wang, Y., Fisher, M. M., & Shih, G. (1997). Spatial Distribution of Soil Nutrients in a Northern Everglades Marsh: Water Conservation Area 1. *Soil Science Society of America Journal*, *61*(4), 1275–1283. https://doi.org/10.2136/sssaj1997.03615995006100040038x

Phaneuf, R. (1979). Indian reserve band rights: Enforcement on the St. Lawrence River. *Canadian Water Resources Journal*, *4*(3), 30–34. https://doi.org/10.4296/cwrj0403030

Polzer, E. L., & Wilcox, D. A. (2022). Testing restoration methods for Lake Ontario wetlands at a wetland scale. *Journal of Great Lakes Research*, *48*(3), 756–767. https://doi.org/10.1016/j.jglr.2022.03.002

Proulx, G., & Gilbert, F. F. (1983). The ecology of the muskrat, *Ondatra zibethicus*, at Luther Marsh, Ontario. *Canadian Field-Naturalist*, *97*(4), 377–390.

Roberts, N. M., & Crimmins, S. M. (2010). Do trends in muskrat harvest indicate widespread population declines? *Northeastern Naturalist*, *17*(2), 229–238. https://doi.org/10.1656/045.017.0206

Robichaud, C. D., & Rooney, R. C. (2017). Long-term effects of a Phragmites australis invasion on birds in a Lake Erie coastal marsh. *Journal of Great Lakes Research*, *43*(3), 141–149. https://doi.org/10.1016/j.jglr.2017.03.018

Robichaud, C. D., & Rooney, R. C. (2021). Effective suppression of established invasive Phragmites australis leads to secondary invasion in a coastal marsh. *Invasive Plant Science and Management*, *14*(1), 9–19. https://doi.org/10.1017/inp.2021.2

Sadowski, C., & Bowman, J. (2021). Historical surveys reveal a long-term decline in muskrat populations. *Ecology and Evolution*, *11*(12), 7557–7568. https://doi.org/10.1002/ece3.7588

Sather, J. H. (1958). Biology of the Great Plains Muskrat in Nebraska. *Wildlife Monographs*, *2*, 1–35.

Silva, A. O., Wilcox, D. A., & Polzer, E. L. (2021). Wetland restoration in *Typha*-dominated Braddock Bay of Lake Ontario. *Ecological Restoration*, *39*(4), 247–259. https://doi.org/10.3368/er.39.4.247

Stewart, D., Hood, W. G., & Martin, T. G. (2023). Undetected but widespread: The cryptic invasion of non-native cattail (*Typha*) in a Pacific Northwest estuary. *Estuaries and Coasts*, *46*(3), 802–817. https://doi.org/10.1007/s12237-023-01171-4

Taillie, P. J., Hart, K. M., Sovie, A. R., & McCleery, R. A. (2021). Native mammals lack resilience to invasive generalist predator. *Biological Conservation*, *261*(July), 109290. https://doi.org/10.1016/j.biocon.2021.109290

Tangen, B. A., Bansal, S., Freeland, J. R., Travis, S. E., Wasko, J. D., McGonigle, T. P., Goldsborough, L. G., Gow, K., Marburger, J. E., & Meier, J. A. (2022). Distributions of native and invasive *Typha* (cattail) throughout the Prairie Pothole Region of North America. *Wetlands Ecology and Management*, *30*(1), 1–17. https://doi.org/10.1007/s11273-021-09823-7

Toner, J., Farrell, J. M., & Mead, J. V. (2010). Muskrat abundance responses to water level regulation within freshwater coastal wetlands. *Wetlands*, *30*(2), 211–219. https://doi.org/10.1007/s13157-010-0034-x

Tozer, D. C., & Mackenzie, S. A. (2019). Control of invasive *Phragmites* increases marsh birds but not frogs. *Canadian Wildlife Biology and Management*, *8*(2), 66–82.

Turner, C. K., Lantz, T. C., & Fisher, J. T. (2020). Muskrat distributions in a changing Arctic delta are explained by patch composition and configuration. *Arctic Science*, *6*(2), 77–94. https://doi.org/10.1139/as-2018-0017

Ward, E. M., & Gorelick, S. M. (2018). Drying drives decline in muskrat population in the Peace-Athabasca Delta, Canada. *Environmental Research Letters*, *13*(12), 124026. https://doi.org/10.1088/1748-9326/aaf0ec

Weller, M. W., & Spatcher, C. S. (1965). Role of habitat in the distribution and abundance of marsh birds. *Special Report No. 43*, 4-31

Whyte, R. S., Bocetti, C. I., & Klarer, D. M. (2015). Bird assemblages in phragmites dominated and non-phragmites habitats in two Lake Erie coastal marshes. *Natural Areas Journal*, *35*(2), 235–245. https://doi.org/10.3375/043.035.0204

Wilcox, D. A., & Meeker, J. E. (1992). Implications for faunal habitat related to altered macrophyte structure in regulated lakes in northern Minnesota. *Wetlands*, *12*(3), 192–203. https://doi.org/10.1007/BF03160609

Appendix

Table A.1. Site locations, muskrat house densities, relative frequency of *Typha* taxa along transects, and marsh interspersion of 39 marshes across south-central Ontario (Chapter 2).

Site	Latitude	Longitude	House density (houses/ha)	n (sampled ramets)	% *T. angustifolia*	% *T. latifolia*	% *T.* x *glauca*	Average Interspersion (m/ha)
Big Island	44.11724	-77.2143	0.20	24	0	0	100	139
Birdsall 1	44.26858	-78.0691	0.30	15	0	7	93	692
Birdsall 2	44.27073	-78.0412	0.40	15	0	0	100	529
Buckley Lake	44.42865	-78.2313	0.00	21	19	0	81	695
Corbett Creek	43.85439	-78.8886	0.10	10	20	0	80	235
Cowan's Bay	44.33033	-78.5381	0.30	15	7	0	93	354
Cranberry Marsh	43.84515	-78.9628	0.20	6	100	0	0	808
Dead Creek	44.05968	-77.6087	0.10	12	0	0	100	141
Duffins Creek	43.82525	-79.0421	0.90	9	0	0	100	504
East Lake	43.94638	-77.1655	0.10	18	0	0	100	175
Emily Creek	44.41775	-78.5809	0.20	20	10	0	90	301
Frenchman's Bay	43.82348	-79.0958	0.40	14	0	0	100	249
Gosport	44.03044	-77.7157	0.00	21	14	0	86	169
Huyck's Bay	43.94481	-77.4655	0.00	15	0	0	100	205
Hydro Marsh	43.81534	-79.0766	0.22	11	0	0	100	238
Indian River Mouth	44.23015	-78.1419	0.10	18	11	33	56	60
Lakefield Marsh	44.43357	-78.2785	0.30	20	25	0	75	543
Lynde Creek	43.85728	-78.9606	0.10	11	0	0	100	119
Murray Marsh	44.24014	-77.7242	0.10	18	0	0	100	101
North Lake Scugog 1	44.2186	-78.9245	0.20	18	0	0	100	219

North Lake Scugog 2	44.23508	-78.8436	0.00	18	0	0	100	176
Oshawa Second Marsh	43.87172	-78.8141	0.80	17	12	0	88	863
Osler Marsh	44.08083	-78.9193	0.10	62	11	0	89	263
Otonabee River Mouth	44.15292	-78.2408	0.20	21	0	0	100	386
Pigeon Lake 1	44.36746	-78.5181	0.00	15	13	0	87	481
Pigeon Lake 2	44.41329	-78.4963	0.00	18	0	0	100	422
Pigeon Lake 3	44.43646	-78.4949	0.20	18	17	0	83	417
Pigeon Lake 5	44.41092	-78.5072	0.10	15	13	0	87	456
Port Darlington Marsh	43.89065	-78.6675	0.10	14	0	0	100	204
Presqu'Ile North	44.01147	-77.7358	0.10	19	32	0	68	202
Presqu'Ile South	44.00036	-77.7175	0.30	15	80	0	20	273
Rice Lake West	44.10018	-78.3306	0.10	15	0	7	93	188
Serpent Mounds	44.19326	-78.1788	0.30	18	28	0	72	126
Southeast Lake Scugog	44.14023	-78.8573	0.30	21	0	0	100	281
Weller's Bay	44.02742	-77.5767	0.10	16	0	0	100	260
West Lake	43.96269	-77.2826	0.10	15	0	0	100	107
Westside Beach	43.88783	-78.6800	0.86	12	25	0	75	915
Wicklow Beach	43.97701	-77.9828	0.56	12	0	0	100	156
Wilmot Creek	43.89651	-78.5975	0.00	12	0	0	100	255

Table A.2. Correlation matrix with variables used in zero-inflated Poisson modelling of muskrat intensity of habitat use with Pearson correlations (upper) and p-values (lower).

Interspersion	-0.15	0.0057	0.011	0.16	0.14
0.20	**Water area**	0.31	-0.33	-0.61	-0.58
0.62	0.0069	**Obstruction**	0.11	-0.022	0.15
0.93	0.0041	0.36	**Sample area**	0.26	0.63
0.18	< 0.001	0.84	0.025	**Geometry**	0.55
0.22	< 0.001	0.18	< 0.001	< 0.001	**Period**