Multiscale habitat use by muskrats in lacustrine wetlands

by

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B.S., Franklin College, 2015

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

Department of Horticulture and Natural Resources
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2018

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Abstract

The muskrat (*Ondatra zibethicus*) is an economically and ecologically important furbearer species that occupy wetlands throughout North America. However, populations across the United States (US) are declining and there is little evidence as to the cause of this decline. Wetlands in the upper Midwest, US, are shifting into more homogeneous vegetation states due to an invasive hybrid cattail species, *Typha x glauca* (hereafter '*T. x glauca*'), outcompeting native vegetation. This hybrid cattail species is now an abundant potential resource for muskrats and has outcompeted native wetland vegetation. I investigated how landscape composition and configuration affected multiscale habitat use by muskrats during the summers of 2016 – 2017. Additionally, I assessed how fetch (impact of wind and wave action), a process dictated by large-scale landscape configuration, influenced muskrat habitat use at a local-scale representing a resource patch. I randomly selected 71 wetland sites within Voyageurs National Park, Minnesota, and used presence/absence surveys to assess site occupancy by muskrats. Each year, multiple surveys were conducted at each site and I used multiseason occupancy modeling to investigate how both local and landscape factors affect site occupancy and turnover. I predicted a positive relationship between local-scale (2 ha) sites, characterized by shallower and less open water, and muskrat occupancy and colonization rates. I also predicted increased occupancy probabilities and colonization rates in wetlands that contain higher amounts of *T. x glauca*. However, I expected the amount of fetch at each site to negatively influence site occupancy probabilities and colonization rates. At the landscape-scale (2 km), I expected habitat use by muskrats to be positively related to the percentage of *T. x glauca* and area of wetlands surrounding sites. At the local-scale, muskrats occupied wetlands that contained shallower water depths and less open water. As predicted, site occupancy probabilities were greater in areas with

greater amounts of *T. x glauca* coverage. My results revealed a cross-scale interaction between the severity of fetch impacts and percent of *T. x glauca* coverage at sites. Muskrats were more likely to colonize areas with greater fetch impacts if there was also greater coverage of *T. x glauca* at these sites. At the landscape-scale, site-occupancy probabilities were positively influenced by the percent of open water and landscape heterogeneity surrounding each site. My study was the first to document how invasive *T. x glauca* populations can mitigate negative effects that high wave intensity may have on muskrat spatial distributions. I was also the first to identify multiscale factors affecting the spatial distribution of muskrats in lacustrine ecosystems.

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Acknowledgements

I couldn't be more thankful and appreciative for all the help and guidance I've received throughout my time at Kansas State University. I am incredibly grateful to have Adam Ahlers as my mentor and advisor as I have learned so much from him in my 2 years here. He has helped me expand my knowledge within this field and has been a great role model for me to learn from. He's always been there to help, provide advice, guidance, and educate me on anything and everything. Saying I'm incredibly thankful for all the times he has sat down and answered my relentless questions, preparing me for professional conferences, and late nights editing, organizing, and finalizing this whole project is a huge understatement.

I was also lucky to have Drew Ricketts as a member of my committee and had the great benefit to learn from him while here at K-State. Drew was incredibly helpful with any questions I had about foreign topics, random questions, and providing advice, all of which have helped with my professional development. David Haukos has been another member of my committee that has provided me with so much great advice and information with getting me ready to start my wildlife career. I was lucky to have Dave as a professor for Habitat Ecology and even used some of the principles he taught in my own personal research.

Steve Windels and Bryce Olson have been great role models as well and have provided so much support for me throughout this whole project. I hope to one day have a great wildlife career like they have had within the National Park Service. Everyone within Kansas State University and the National Park Service has been great to work with and incredibly helpful. K-State and all the faculty I've come into contact with have been so kind and helpful, which has provided me with a great graduate experience. I would also like to thank Spencer Wesche and

Justin Patterson for their hard work over the past 2 summers. I wouldn't have been able to do this without everyone's help.

Dedication

To my parents, Roger and Kelly, and all my family and friends who have supported me in all my endeavors and have given me the opportunity to follow my passion.

Thank you

Chapter 1 - Introduction

Muskrats (*Ondatra zibethicus*) play a major role in maintaining wetland ecosystems and are considered a wetland-obligate species (Weller 1981). This semiaquatic mammal can control wetland vegetation characteristics through lodge construction and the accumulation of food resources (Danell 1977, 1979; Messier and Virgl 1992; Erb and Perry 2003). Muskrats are found throughout North America and have been a key economic resource due to the value of their pelts (Erb and Perry 2003) that has made them a major component of the North American fur trade dating back to the 1800s (Erb and Perry 2003). Using historic fur harvest data, Ahlers and Heske (2017) found that muskrat populations across the United States have been declining since 1970. However, there have not been contemporary studies investigating the mechanistic cause of these declines. Ahlers and Heske (2017) proposed testable hypotheses for the observed population declines such as habitat loss and degradation, wetland hydrological changes, predation, and changes in trapping culture. Future management Ahlers and Heske (2017) further posit that management of this species will require long-term studies with cooperation from multiple agencies to coordinate research directions and replicable data-collection methods across large spatial scales.

Muskrats select wetlands in lentic or slow moving lotic waters (Erb and Perry 2003), and avoid large bodies of open water due to the potential negative effects of wave action and food resources growing near the littoral zone (Bellrose 1950; Errington 1963). Habitat-use patterns can vary by season, with muskrats focusing on emergent vegetation growing along shallow shorelines during the summer (Jelinski 1989). Muskrats also chose to create burrows that occur near shallower water in areas with gentler slopes and greater overhead cover (Jelinski 1989).

However, Jelinski (1989) found that muskrats switched to sites with deeper water in the winter to have ice-free access to procure necessary resources for winter survival.

With wetlands serving as critical habitat for muskrats across the US, threats to the stability and health of wetlands could have a dramatic influence on muskrats occupying these areas. An invasive hybrid cattail species is rapidly encroaching into novel wetlands. Species hybridization can potentially lead to adaptive evolution that favors robust invasive species (Ellstrand and Schierenbeck 2000). Invasive hybridized plant species are generally more aggressive and display increased vigor, reduced genetic load, and broad ecological tolerances (Hall et al. 2006). The ability of a hybrid species to rapidly invade native areas relies on the compatibility between the hybridizing species (Hall et al. 2006). *Typha x glauca* (hereafter '*T. x glauca*'), a hybrid cattail formed between native *Typha latifolia* (broad-leaf cattail) and the introduced *Typha angustifolia* (narrow-leaf cattail) is an aggressive invasive hybrid affecting wetland ecosystems in the United States. *T. x glauca* is a genetically robust species that has been rapidly expanding across wetlands throughout the United States as well as Europe. *T. x glauca* has traits similar to those of other invasive wetland plant species such as its large size, rapid root growth, and the ability to grow in a range of water depths outside the range of the parent species (Waters and Shay 1990; Galatowitsch et al. 1999). Dense stands of *T. x glauca* can reduce open-water habitats, displace native vegetation, and increase litter and organic matter. Farrer and Goldberg (2009) suggest that the litter accumulation of *T. x glauca* could be limiting light penetration and increasing its overall height leading to *T. x glauca's* dominance in invaded wetlands.

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Wetland habitat availability can also be affected by fetch, the unobstructed distance that wind can travel over open water leading to intense wind and wave action (Rohweder et al. 2008). Greater fetch results in wind-generated waves that can cause sediment to suspend in the water column and exacerbate shoreline erosion (Rohweder et al. 2008). Greater fetch can also erode muskrat huts and beaver lodges, reduce soil formation, and prevent plants from rooting. The configuration and composition of landscapes can potentially affect the distribution of muskrats by influencing the magnitude and direction of large wind-generated waves which limit access to resources or other potentially good-quality habitats. These high energy waves could increase the amount of energy needed for muskrats to disperse or forage making it more labor intensive for them to occupy areas with greater wave intensity. Slough and Sadleir (1977) found that beavers (*Castor canadensis*) require stable water levels and intense wave action can potentially alter lake environments that contain slow flowing non-fluctuation water levels that beaver prefer. They observed that the complex spatial arrangement of shorelines could reduce the effect of large wind-generated waves and provide adequate refuge for beavers occurring on large open water lakes (Slough and Sandleir 1977). The few studies that have observed species distribution changes due to potential wind and wave effects have been mostly anecdotal. Thus, there is a need to empirically quantify these potential effects to control for them in species distribution models.

Cross-scale interactions refer to ecological processes at broad-scales that affect patterns and processes at fine-scales, and vice versa (Holling 1992; Levin 1992; Ludwig et al. 2000; Thompson et al. 2001). High wind and wave intensity can have dramatic effects on the distribution of prey species in the water column, as well as, the feeding and dispersal behavior of marine mammals in the North Pacific (Mackas et al. 2005; Sterlin et al. 2014). Female northern

fur seals (*Callorhinus ursinus*) affected by strong wind and wave impact are able to use the configuration of the landscape to their advantage when foraging. Effects of wind-generated waves on many ecological processes is determined by landscape configuration and composition at very large spatial scales, and can potentially affect ecological patterns and processes occurring at much finer spatial scales (e.g., fine-scale habitat use). To my knowledge, this cross-scale interaction has not been quantified but could have a significant effect on the spatial distributions of muskrats throughout wetland habitats.

My thesis research focuses on the effects of landscape pattern and composition, local-scale resources, and cross-scale interactions on the spatial distribution of muskrats, a wetland obligate species, in lacustrine wetlands. I used non-invasive survey techniques to document the presence/absence of muskrats throughout lacustrine wetland areas in the national park. I also used a multiseason occupancy modeling approach to understand habitat-use patterns of muskrats in relation to both local and landscape-scale variables. To my understanding, this is one of the first studies to investigate how habitat use by muskrats is influenced by landscape composition and configuration, and resource availability in boreal lake ecosystems.

Chapter 2 - Cross-scale interactions and landscape heterogeneity affect habitat use by a wetland-obligate species

Introduction

Habitat selection is a scale-sensitive process that requires multiscale assessments to understand species' resource requirements (Orians and Wittenberger 1991; Manly et al 2007). Because habitat use is scale dependent (Johnson 1980; Orians and Wittenberger 1991; Chalfoun and Martin 2007), both local and landscape effects can be important drivers of habitat-use patterns. Misleading interpretations can occur when extrapolating habitat-use patterns at one spatial scale across alternate scales (Mayor et al. 2009). For instance, river otters (*Lontra canadensis*) use riparian sites with greater amounts of woodland cover and decreasing amounts of grassland and cropland cover at the local-scale (Jeffress et al. 2011). At the landscape-scale, however, river otter occupancy and latrine site location were best predicted by shoreline diversity, waterbody and stream density, and habitat that is beneficial for fish, a potential prey source (Jeffress et al. 2011; Crowley et al. 2012). However, river otter presence and intensity at latrine sites at a fine scale is dependent on local shoreline tree cover and characteristics (Crowley et al. 2012).

Cross-scale interactions can also influence ecological processes (Holling 1992; Levin 1992; Thompson et al 2001) as broad-scale effects can dictate patterns at much finer scales (Ludwig et al. 2000). Thus, spatially broad environmental factors could have an effect on the distribution and habitat use of species at much finer spatial scales. For example, wind impact mediated by the landscape position of marine islands can structure prey distributions at local-

scales and, in turn, influence fine-scale resource selection by marine predators (Mackas et al. 2005; Sterling et al. 2014). Female northern fur seals (*Callorhinus ursinus*) are less likely to forage in areas exposed to high wind impact where prey species occur deeper in the water column. Instead, they will utilize areas shielded from high wind impacts where prey occur at reasonable foraging depths (Sterling et al. 2014).

The severity of wind impact in water bodies, or 'fetch' (Finlayson 2005; Rohweder et al. 2008), is a function of the unobstructed distance that wind can travel over a particular landscape. The effect fetch has on a coastline is greater where wind can travel longer distances without obstruction to create more wave energy. Thus, configuration and composition of landscapes at large spatial scales can funnel wind and influence fetch effects at much smaller scales. It is plausible that fetch may influence habitat use by wetland-obligate species by disrupting feeding activities, destroying nests or lodges, or precluding movement between resources. In freshwater lakes with large amounts of open water, habitat use by American beaver (*Castor canadensis*) may be negatively affected by wind and wave action along shorelines (Slough and Sandleir 1977; Allen 1983). Resource use by wetland-obligate species may be influenced by fetch; however, these patterns are not well understood and have not been quantified in previous studies.

My objectives were to understand how multiscale habitat use by muskrats (*Ondatra zibethicus*), a freshwater semiaquatic mammal, is influenced by landscape pattern, composition, and local-scale resources. Additionally, I explored the potential for cross-scale interactions between landscape-scale pattern and fine-scale habitat use by muskrats. Muskrats are small (~1 kg) herbivorous rodents that are obligately associated with wetlands. Space use by muskrats is

generally restricted to the water or shoreline (Ahlers et al. 2010, 2015) and movements in terrestrial space are rare (Ahlers et al. 2015). They are considered multiple central-place foragers (Ahlers et al. 2010) with regular movements up to 260 m from burrows or lodges (Errington 1939; MacArthur 1978, 1980). Muskrats primarily feed on wetland vegetation (e.g., cattails [*Typha* spp.]) and occur in areas with shallow water depths (Errington 1963). Throughout the upper Midwest, USA, a hybrid invasive cattail species (*Typha x glauca*; hereafter '*T. x glauca*') is expanding into wetland ecosystems, displacing native vegetation (including native cattail species) and reducing the extent of open-water areas (Frieswyk & Zedler 2006; Travis et al 2010). The relationship between *T. x glauca* expansions and muskrats is unclear. Landscape heterogeneity has been linked to greater species diversity (Bell et al. 1991). However, our understanding of muskrat habitat use in spatially heterogeneous landscapes is limited. Spatially heterogeneous areas have been previously identified affecting habitat use of another small mammal species due to these areas offering high quality resources (Ostfeld et al. 1985).

I used 2 years of presence/absence data and a multiseason occupancy modeling approach to assess how habitat use by muskrats is influenced by both local and landscape factors and also by potential interactions across these scales. Because muskrats forage on cattails, I expected site occupancy probabilities and colonization rates to be greater in areas with greater coverage of *T. x glauca*. At the local-scale, I expected sites with deeper and more open water would have fewer resources for muskrats (Sather 1958; Errington 1963) and predicted lower occupancy probabilities and colonization rates at sites with these characteristics. Lacustrine wetlands exposed to large amounts of fetch may be unfavorable for muskrats due to the potential negative impacts of wave intensity along the shoreline. I predicted sites exposed to higher fetch values

would have lower site occupancy probabilities and colonization rates. Additionally, I

investigated how the spatial coverage of *T. x glauca* at wetland sites may mediate any potential

effects of wave action in these areas. At the landscape-scale, I predicted site occupancy

probabilities to be larger in areas with a greater percentage would increase as area of wetland

habitat and *T. x glauca* coverage increased, as these areas may provide more resources for

muskrats.

Materials and Methods

Site selection

I conducted my study in and around Voyageurs National Park (VNP; 88,220 ha) located

near International Falls, Minnesota, USA (48.51896° N, -92.91938° E; Figure 1A). This area

occurs at the southern edge of the boreal forest region and is characterized by conifer and

hardwood forests, with both lentic and lotic water bodies. Annual precipitation (rain and snow

combined) averages 66.04 cm and annual mean temperatures range from -3.3° – 9.3° C. I

centered my sampling in the Rainy and Kabetogama Lake watersheds, which contain ~230,000

ha of open water areas (Figure 1A). This region also has hundreds of small islands and irregular

shorelines that can obstruct wind and influence the effect of fetch in wetland areas (Figure 1 A).

T. x glauca populations have expanded throughout areas near the shore, or littoral zones, and

shorelines within VNP and displaced nearly all native cattail populations (Travis et al. 2011;

Windels et al. 2013).

I used ArcGIS (ESRI 2017) and a digitized vegetation map (Faber-Langendoen et al.

2007) to identify lacustrine wetland areas in VNP. I randomly selected 71 points within these

wetlands and delineated sampling sites (100 m x 200 m; 2 ha) centered on these points (Figure

1A). Sampling sites were smaller than average muskrat home ranges (MacArthur 1978, 1980) and reflect local-scale habitat use. All sites were separated by an average Euclidian distance of 1247 m (SD = 377 m). The dominant vegetation at all sites was *T. x glauca* but also consisted of wild rice (*Zizania* spp.), common reed (*Phragmites australis*), arrowhead (*Sagittaria* sp.), water lilies (*Nymphaea* spp. and *Nuphar* spp.), submergent vegetation (*Ceratophyllum demersum*, *Potamogeton* spp., *Myriophyllum* spp.), bulrush (*Schohenoplectus acutus*), reed canary grass (*Phalaris arundinacea*), and various species of sedges (*Carex* sp.; Kallemeyn et al. 2003, Windels et al. 2013). Water depths varied among sites (mean = 0.54 m: 2016 range: 0.03 – 3.00 m: 2017 range 0.05 – 2.06 m).

Occupancy surveys

I surveyed for the presence/absence of muskrats at 71 sites from 7 June – 12 August 2016 and 69 sites from 5 June – 28 July 2017. I employed 2 survey methods (walking surveys and floating raft surveys) to document site occupancy by muskrats. For walking surveys, 2 trained observers searched for muskrat sign (e.g., tracks, scat, huts, clippings, or animal) by systematically surveying the area within the boundaries of each site. Each site was visited twice each year (2 site visits) and observers used a combined survey effort during each site visit. Thus, each site visit was considered 1 independent survey. I conducted both site visits within 7 days to ensure population closure (MacKenzie et al. 2017). There were 3 observers that conducted walking surveys between 2016 and 2017. I participated in all surveys. Average survey time at each site was ~30 minutes per observer.

In conjunction with walking surveys, I conducted floating raft surveys (hereafter 'rafts'). The rafts used a clay/sand tracking medium to capture tracks of animals walking across them, a method used successfully to document habitat use by American mink (*Neovison vison*) in North America and Europe (Reynolds et al. 2004; Schooley et al. 2012). I constructed rafts by securing 0.6-cm plywood sheets (122 x 61 cm) to the top and bottom of a 3.8-cm polystyrene sheet (122 x 61 cm) with 6 evenly-spaced carriage bolts. I positioned a plastic basket filled with floral foam into a cut-out portion in the center of the raft (27 x 20 x 5 cm) such that the top of the basket was flush with the surface of the raft. I spread a tracking surface (clay/sand medium) on top of the floral foam to capture tracks of muskrats walking on the basket. Because the bottom of the basket was constantly exposed to water, the floral foam remained saturated with water maintaining a viable clay/sand tracking surface. I covered the tracking surface with a 3-panel, plywood tunnel to prevent clay from washing away via rain or waves. Rafts were camouflaged with local vegetation, left unbaited, and tethered with a nylon rope to nearby cattails or other sturdy vegetation. For a detailed description of raft construction see Reynolds et al. (2004).

I positioned 2 rafts 100 m apart and centered them within each site (Figure 1B). I checked rafts for muskrat sign (e.g., scat, clippings, feeding stations, tracks) 7 days after securing them at a site (1st survey). I rechecked rafts after an additional 7 days (2nd survey) resulting in 2 primary surveys for each site. After each raft survey, rafts were reset and cleared of an sign that was collected. Both primary surveys for rafts occurred during the same week as the site visits for walking surveys resulting in 4 independent sign surveys per site. For each site, my detection histories included 2 independent walking surveys and 2 independent raft surveys per year. I

considered a site occupied by muskrats during a given year if muskrat sign was found on ≥1 raft or detected during ≥1 site visit.

Local-scale habitat

I measured local-scale habitat characteristics at each site during 2016 and 2017 immediately following the first site occupancy survey. At each site, I established 5 parallel transects spaced 50 m apart and measured habitat characteristics at 5 evenly spaced positions along each transect (Figure 1B). I estimated the percent coverage of *T. x glauca*, open water, and emergent vegetation at each position along transects using a 1-m x 1-m Daubenmire frame. At each position, I also measured water depths (m). I averaged all measurements (n = 25) for each habitat characteristic to obtain a mean value for each site. Water depth and percent open water at sites were correlated (2016, $r = 0.71$; 2017, $r = 0.77$), so I used a principal components analysis (PCA: SAS Institute Inc. 2017) to combine these 2 variables into a single composite variable (Water).

Landscape-scale habitat

I used landcover data compiled by the United States National Park Service and United States Department of Agriculture CropScape Database (USDA 2017) to derive landscape-scale variables for my analyses. I extracted raster (30 m x 30 m) landcover information (Forest, Open Water, *T. x glauca*, and Wetlands) from within circular buffers surrounding each site at multiple scales (500 m, 1000 m, and 2000 m; ESRI 2017). For each site, I quantified percent forest (Forest), open water (Open Water), coverage by *T. x glauca* (Typha), and wetland areas (Wetland) within each scale-specific buffer (FRAGSTATS V4.2; McGarigal 2012). I

characterized landcover heterogeneity by using a Shannon's diversity index (SHDI) of all

landcover types and also calculated the proportion of edge length (Edge) at each site. A *post hoc*

analysis revealed that variables at all spatial scales were correlated ($|r| \geq 0.70$). Therefore, I

chose the 2000-m scale for subsequent analyses because it best represented the scale of current

wetland-management efforts in VNP.

 Fetch

I used the Fetch Analysis Tool in ArcMap 10.5 (ESRI 2017) to quantify wave fetch (m)

across VNP based on the United States Army Corps of Engineers Shore Protection Manual

(SPM; USACE 1984; Finlayson 2005; Rohweder et al. 2008). This tool has generally been used

to estimate fetch impact values across shorelines for informing infrastructure design projects

(Finlayson 2005; Rohweder et al. 2008). I obtained wind distribution and direction data from 36

compass directions (at 10° angular increments) from the International Falls, Minnesota, weather

station recorded during ice free months (May – November) from 1992 – 2016 (NOAA 2017). I

calculated distance (m), using 9 radials (3° angular increments), from the center of every water

raster cell to the nearest land raster cell in all 36 wind directions. The Fetch Analysis Tool

function created 36 fetch raster layers each representing different wind directions. Each layer

was populated with raster data that represented the average fetch distance (m) for each respective

compass direction. Finally, I used the Spatial Analyst's Raster Calculator Tool (ESRI 2017) to

create a single spatial fetch-impact landscape. This tool averaged all fetch values from the 36

wind fetch exposure layers, weighted by the distribution of wind in each direction, then assigned

averaged weighted-fetch exposure values (m) to 10 x 10-m raster cells distributed across the

spatial extent of all open water and wetland areas in VNP (Figure 2). To quantify the endpoint

impact of fetch at each site, I averaged fetch values from all raster cells within a 200-m circular buffer of the centroid of each site.

Analysis

I used multiseason occupancy models (Program PRESENCE, Version 12.7) to estimate site occupancy and turnover dynamics of muskrats at both local and landscape-scales. Due to model-convergence issues, I did not model extinction rates for either scale or colonization at the landscape-scale. I evaluated 3 survey-specific detection covariates (day of year, precipitation, and survey method) found important for muskrat detection in previous studies (Cotner and Schooley 2011; Ahlers et al. 2015). I predicted that detection probabilities for muskrat would be negatively related to the day of year (DOY; continuous variable corresponding to sampling date).To account for the potential for sign to be washed away prior to a site visit, I summed the total precipitation 7 days prior to each survey using data from the National Oceanic and Atmospheric Administration weather station located on Kabetogama Lake (Precip). To account for variation between my 2 sampling techniques (walking surveys vs. rafts), I also included 'Method' as a covariate.

My candidate set of detection models (n = 8) included the single or additive effects of my covariates along with a constant model (DOY; Method; Precip; DOY + Method; DOY + Precip; Precip + Method; DOY + Precip + Method; *Constant*). For my local-scale analyses, my candidate set of initial occupancy and colonization models were identical (n = 13) and included all single effects (Typha; Fetch; Water; Total Emergent) additive effects (Water + Typha; Water + Typha + Fetch; Water + Fetch; Water + Total Emergent; Total Emergent + Fetch; Fetch + Typha; Water + Fetch + Total Emergent) and a constant model (*Constant*). I also considered the

potential for a cross-scale interaction between the proportion of Typha and Fetch at sites (Typha + Fetch + Typha*Fetch). Due to a high correlation between Typha and Total Emergent coverage at the local-scale (r > 0.78), I did not include these 2 covariates in the same model. At the landscape-scale, for my candidate set of initial occupancy models (n = 17) considered 6 models with single effects (SHDI; Edge; Wetlands; Open Water; Typha; Forest), 10 models with additive effects (SHDI + Open Water; SHDI + Wetlands; SHDI + Open Water + Typha; SHDI + Open Water + Wetlands; SHDI + Edge + Open Water; SHDI + Typha; SHDI + Edge; SHDI + Forest; SHDI + Edge + Typha; Edge + Open Water), and a constant model (*Constant*).

I ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) and considered all models with ΔAIC$_c$ values ≤ 2.00 as competitive. I did not include covariates that were correlated ($\vert r \vert \geq 0.70$) in the same model. I used an information-theoretic approach to choose the most-supported model from each candidate set (Burnham and Anderson 2002, Arnold 2010). I used model-averaging for all parameter estimates (derived from all models included in the $\Sigma_w = 0.95$) to reduce bias that may have existed due to model-selection uncertainty (Burnham and Anderson 2002).

Results

I conducted 284 independent surveys in 2016 (walking = 142, rafts = 142) and 276 independent surveys in 2017 (walking = 138, rafts = 138) for a total of 560 surveys. Observers surveyed 560 ha of wetlands and positioned 560 rafts during the duration of the study. Naïve occupancy estimates for muskrats were 0.69 in 2016 and 0.77 in 2017 and varied by survey method (2016 naïve occupancy: walking = 0.5775, rafts = 0.4507; 2017 naïve occupancy:

walking = 0.5797, rafts = 0.6522). I did not detect muskrat sign at 10 sites and always detected

muskrat sign at 43 sites. I documented 12 colonization and 4 extinction events between 2016 and

2017.

My constant model of detection indicated that per-survey detection probability was

moderate (0.5336, SE = 0.0272). My top detection model indicated that day of year (DOY) and

survey method (Method) influenced my ability to detect muskrats at sites (Table 1). Detection

probabilities were lower later in the year (DOY; β = -0.0154, SE = 0.0011) and varied by survey

method (Method; β = -0.3597, SE = 0.1938). I detected muskrats at more sites with raft surveys

(n = 56) than walking surveys (n = 41) across both years. After correcting for imperfect

detection, initial site occupancy probability was 0.7366 (SE = 0.0591) and colonization

probability was 0.5196 (SE = 0.1341).

At the local-scale, my most-supported initial occupancy model included the additive

effects of Typha and Water (Table 1). Muskrats were more likely to occur at sites with greater

percentages of *T. x glauca* coverage (Typha; β = 0.0457, SE = 0.0006) and at sites with

shallower water depths and less open-water area (Water; β = -0.0466, SE = 0.0006; Figure 3). I

had 2 other models including the covariate 'Fetch' that were also competitive (Table 1).

However, I choose to subsequently model colonization with my most parsimonious initial

occupancy model (Typha + Water). My only supported colonization model ($\Delta AIC_c < 2.00$)

included the positive interaction (β = 0.0038, SE = 0.0021) between Typha (β = 0.0949, SE =

0.0173) and Fetch (β = -0.0029, SE = 0.0008; Figure 4; Table 1). Muskrats were more likely to

colonize greater fetch-exposed sites if those sites also had greater coverage of *T. x glauca* (Figure 4).

At the landscape-scale, my most-supported initial occupancy model included the additive effects of landcover diversity (SHDI) and open water areas (Open Water; Table 2), though there was some model-selection uncertainty (Table 2). Muskrats occupied wetland sites with greater landscape diversity (β = 4.5978, SE = 1.9089) and greater coverage of open water areas (β = 0.0320, SE = 0.0046; Figure 5). There were 5 other competitive models ($\Delta AIC_c \leq 2.00$), each including the covariate SHDI. However, minimal changes in deviance suggest additional covariates were piggybacking on the explanatory power of SHDI. Furthermore, SHDI was included in models containing the majority of model weights ($\Sigma_w SHDI$ = 0.9627; Table 2).

Discussion

My results suggest that the effects of fetch, along with local and landscape composition, affect habitat use by muskrats. As predicted, muskrats occupied sites with greater coverage of *T. x glauca*, shallower water depths, and less open water. My findings also suggest that muskrats may likely colonize sites with large exposed to greater amounts of fetch if those sites also have increased *T. x glauca* coverage. At the landscape-scale, site occupancy probabilities were associated with greater landcover diversity and greater amounts of open water surrounding sites.

Muskrats were more likely to occur in areas with shallower water depths and less open water. This result is consistent with previous findings (Takos 1947; Sather 1958) and likely reflects conditions available for feeding and lodge construction and maintenance. Messier et al.

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(1990) reported muskrat population expansions where water levels were maintained at ~85 cm but saw dramatic declines in the muskrat population size during periods of shallower water. Muskrat huts are generally constructed in 43 – 101 cm of water (Sather 1958), and muskrats are generally sensitive to fluctuating water levels and select areas with stable water depth and sufficient resources (Messier et al. 1990; Thurber et al. 1991; Messier and Virgl 1992; Toner et al. 2010). Water depths can influence food resources, predation risk, and body composition of muskrats (Messier et al. 1990; Clark 1994; Virgl and Messier 1997). Low water depths can cause muskrat to abandon their huts (Proulx and Gilbert 1983) and can affect whether they experience a freeze out during winter (Bellrose 1950). Deeper water depths increase the difficulty that muskrats have in keeping their huts intact in areas with greater wave impact (Bellrose 1950). Suitable water levels may provide muskrats with necessary resources for winter survival, while water drawdowns may increase predation risk and reduce access to resources (Thurber et al. 1991; Ahlers et al. 2015).

As predicted, muskrats were more likely to occur at sites with greater coverage of *T. x glauca*. Native cattails are important food sources for muskrats (Toner et al. 2010) and *T. x glauca*, an invasive hybrid species, may also serve as an important resource. Muskrats are wetland obligate species that may use *T. x glauca* as a key food source and for lodge construction material due to its abundance (Higgins and Mitsch 2001). Long-term habitat-use studies revealed muskrats chose lodge locations surrounded by *T. x glauca* (Clark 1994). This pattern is likely because of increased access to food resources and building materials, which could have a positive influence on winter survival probabilities (Clark 1994). *T. x glauca* may have similar nutritional values to other native plants along with increased nitrogen content (Campbell and

MacArthur 1994). There may be an upper threshold response associated with muskrat habitat use in wetlands that are heavily invaded by *T. x glauca*. However, I did not survey wetlands that were completely (100%) dominated by *T. x glauca* and was unable to detect a potential threshold response.

Muskrats were less likely to colonize sites positioned in wetlands with greater fetch impacts unless those sites also had greater coverage of *T. x glauca*. This suggests that *T. x glauca* may mitigate negative effects of fetch in areas that are more exposed to intense wind-generated waves. High wind and wave activity could potentially cut off access for muskrats to other wetlands (Allen 1983). To my knowledge, the effects of fetch on semiaquatic mammals has not been previously quantified. However, previous studies have observed and described high impact from wind and wave activity negatively affecting other species that are associated with wetland habitats (Bergman et al. 1970; Cuthbert and Louis 1993; Allen et al. 2008). Impacts from fetch have been found to negatively influence wetland vegetation growth. Thomasen et al. (2013) noted that turbulent wave action could potentially prevent native wetland vegetation from developing in highly exposed areas. However, in my study, the proportion of *T. x glauca* at sites and calculated fetch impacts were not correlated (r < -0.07). Because *T. x glauca* can rapidly encroach into novel environments, expansions of *T. x glauca* in high-fetch areas may facilitate muskrat (and other wetland-obligate species) distributions onto otherwise inferior habitats. However, negative effects of *T. x glauca* expansions on native wetland vegetation communities and wetland structure are still undermining overwhelmingly negative for biodiversity and ecosystem function (Galatowitsch et al. 1999; Larkin et al. 2012).

At a landscape-scale, muskrats were more likely to occur in areas with greater landcover diversity (SHDI) and greater amounts of open water. In my study, landcover diversity was constrained to 4 specific landscape compositions: percent landcover by forest, open water, wetlands, and *T. x glauca*. It is unclear why muskrat occupancy was greater at sites with diverse landcover in this region, but it is likely that these sites may provide adequate resources for food, shelter, and refugia from predation. For instance, muskrats utilize wetland ecosystems containing *T. x glauca* as these areas likely provide the necessary food resources and stable water levels that muskrats require in order to survive, especially during the harsh winters that VNP experience. Female California voles (*Microtus californicus*) inhabit areas with greater habitat heterogeneity as these areas may provide diverse resources (Ostfeld et al. 1985). In the northwestern edge of the boreal forest region, muskrat burrows are often found along shoreline covered by green alder (*Alnus crispa*), a tree species that can grow close to shorelines and along forest edges, which can potentially act as cover for muskrats (Jelinski 1989). Forested areas could act as cover from predators, such as eagles and ospreys, while muskrats are foraging or building huts.

Throughout VNP there are hundreds of small bays, islands, and creeks that contain pristine wetlands that add to the complexity and connectivity of the landscape. Previous studies have documented muskrats, and other semiaquatic mammals, occupying open-water wetlands and assumed these areas were more spatially connected to each other (Higgins and Mitsch 2001; Toner et al. 2010; Schooley and Branch 2011). Wetlands that are larger and more spatially connected to each other within the landscape increased wetland colonization by round-tailed muskrats (*Neofiber alleni*; Schooley and Branch 2011). However, mountainous landscapes with minimal hydrologic connectivity between 2 regions in Scotland restricted gene flow of another semiaquatic mammal, American mink (*Neovison vison*; Zalewski et al. 2009). Thus, functional

connectivity among wetlands may increase with more open water between sites. At the-

landscape scale, sites positioned in wetlands with more open water may have had increased

functional connectivity to other wetlands in VNP. Muskrats leave huts and burrows when they

experience freeze outs that cut off foraging access underneath the ice. These highly connected

landscapes allow for muskrats to easily disperse to other wetlands if the stability of the currently

occupied wetland was to diminish. However, winter occupancy was not something we measured

and future work could look to analyze muskrat winter occupancy in connected and diverse areas.

My study revealed multiscale scale factors that can affect habitat use by muskrats. I

found that muskrats occupied and colonized wetlands with greater amounts of invasive *T. x

glauca*. With little previous research focusing on the effects of wind and wave action on

semiaquatic mammals, I found that fetch impacts had a significant influence on habitat use by

muskrats in a lacustrine ecosystem. However, my study revealed that greater *T. x glauca*

coverage has the potential to mitigate the negative effect that fetch has on muskrat spatial

distributions. Current wetland management in VNP includes large-scale *T. x glauca* removal

efforts focused on restoring native biodiversity in the region. Understanding the post-

management effects of *T. x glauca* on the spatial distribution of muskrats is essential for

informing future management plans for invaded wetlands. Future research should also assess the

nutritional content of *T. x glauca* and compare its nutritional content to native cattails and other

native food sources for muskrats.

Figure 1 (A) Location of survey sites (n = 71) used to assess site occupancy by muskrat (*Ondatra zibethicus*) within Voyageurs National Park near International Falls, Minnesota, USA, during summer 2016-2017. (B) Schematic of my sampling sites (200 m x 100 m) including habitat-sampling transects (vertical lines) and individual habitat sampling points (black squares).
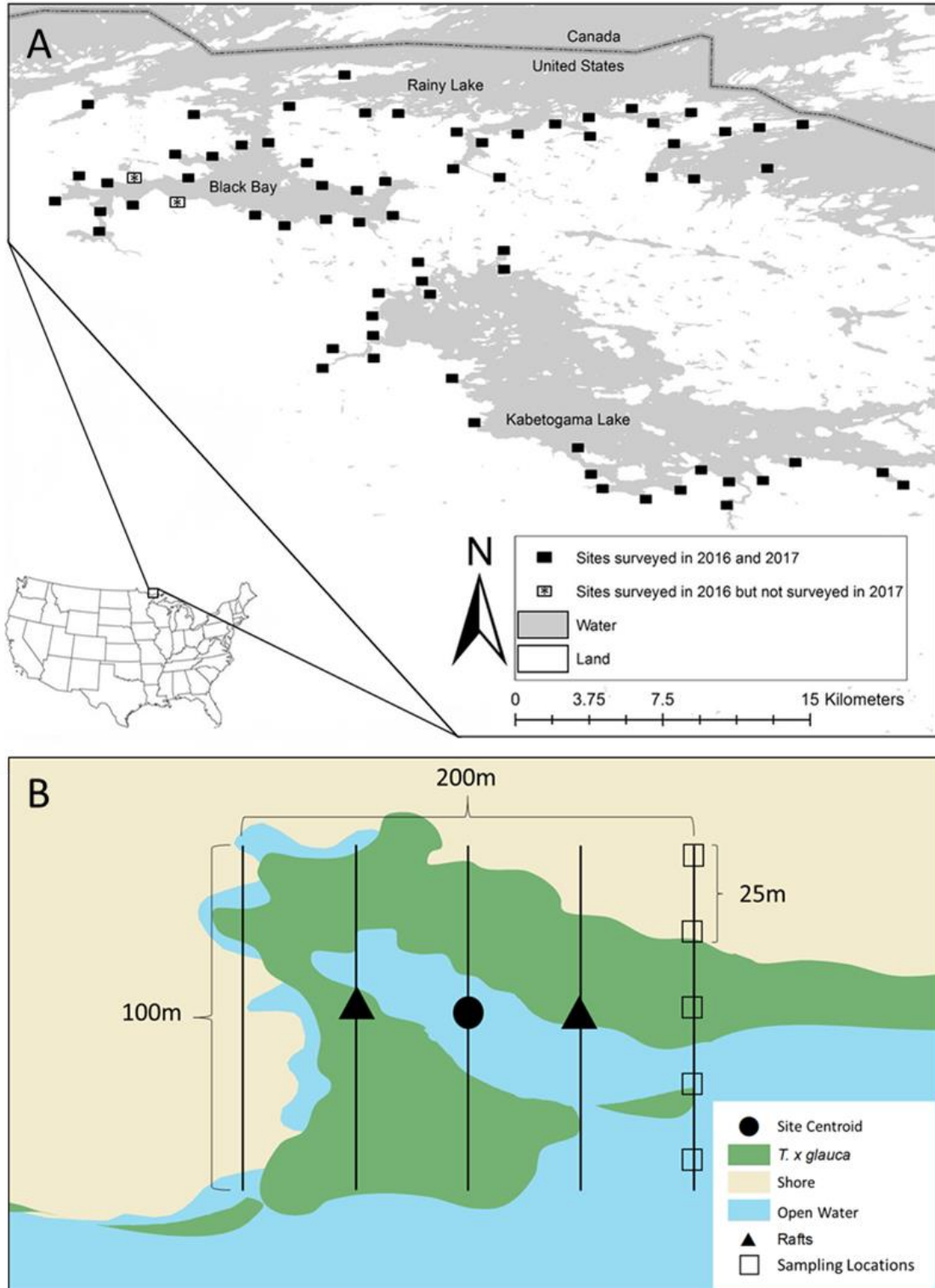
Figure 2 Fetch exposure map of Voyageurs National Park (VNP) located in International Falls, Minnesota, USA. Color ramp indicates the areas of high and low fetch impact across VNP using wind data collected from International Falls weather stations during the ice-free months of May – November of 1992 – 2016.
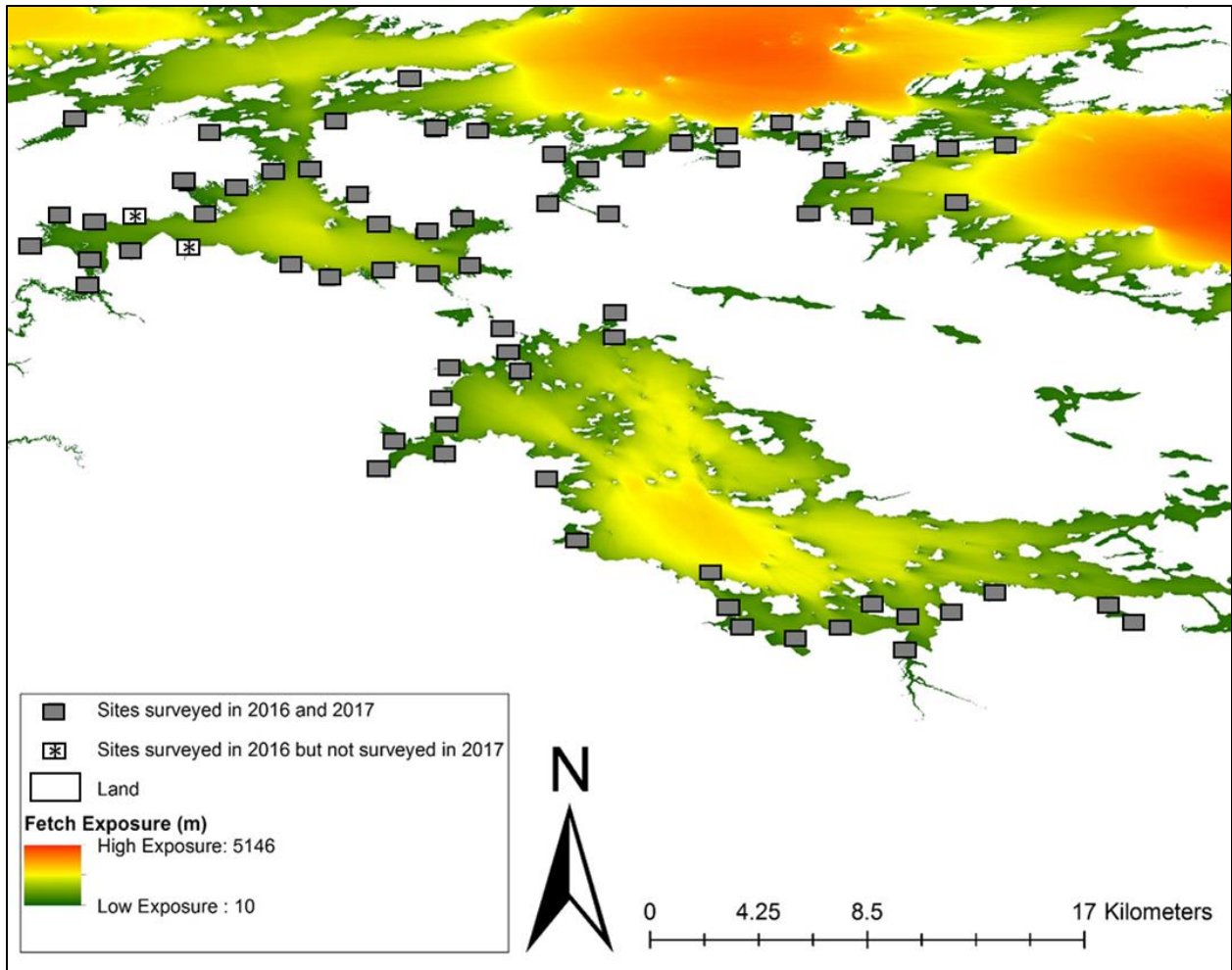
Figure 3 Local-scale site occupancy by muskrats (*Ondatra zibethicus*) at 71 wetland sites in Voyageurs National Park, International Falls, Minnesota, USA, during 2016 and 2017. Relationship between initial site occupancy rates and the percentage of *Typha x glauca* and a composite variable representing water depths and amount of open water areas.
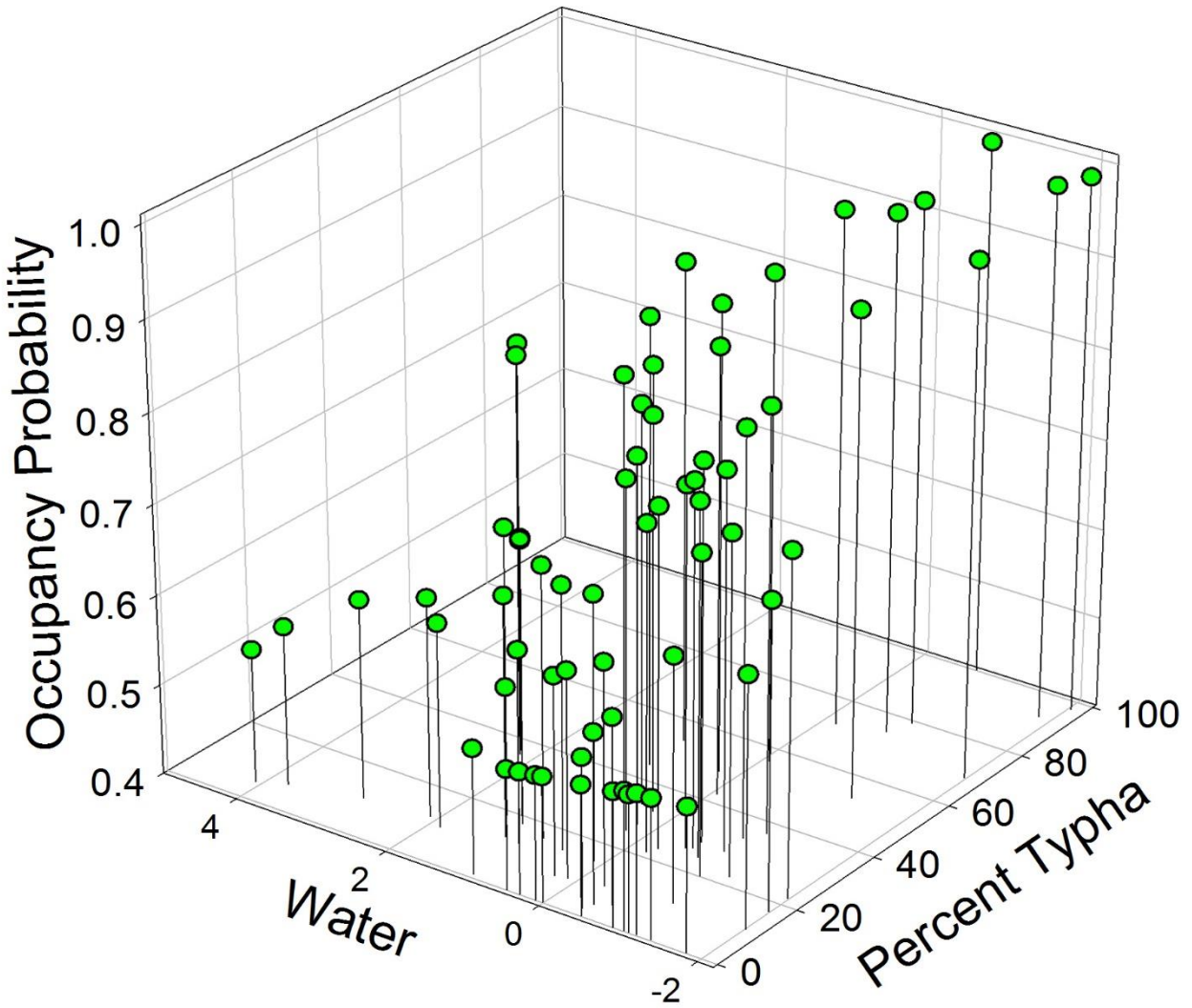
Figure 4 Local-scale site colonization by muskrats (*Ondatra zibethicus*) at 71 wetland sites in Voyageurs National Park, International Falls, Minnesota, USA, during 2016 and 2017. Relationship between percentage of *Typha x glauca* coverage and fetch impacts on site colonization rates. Colonization rates were derived from model-averaged estimates from colonization models ($\Sigma_w = 0.95$).
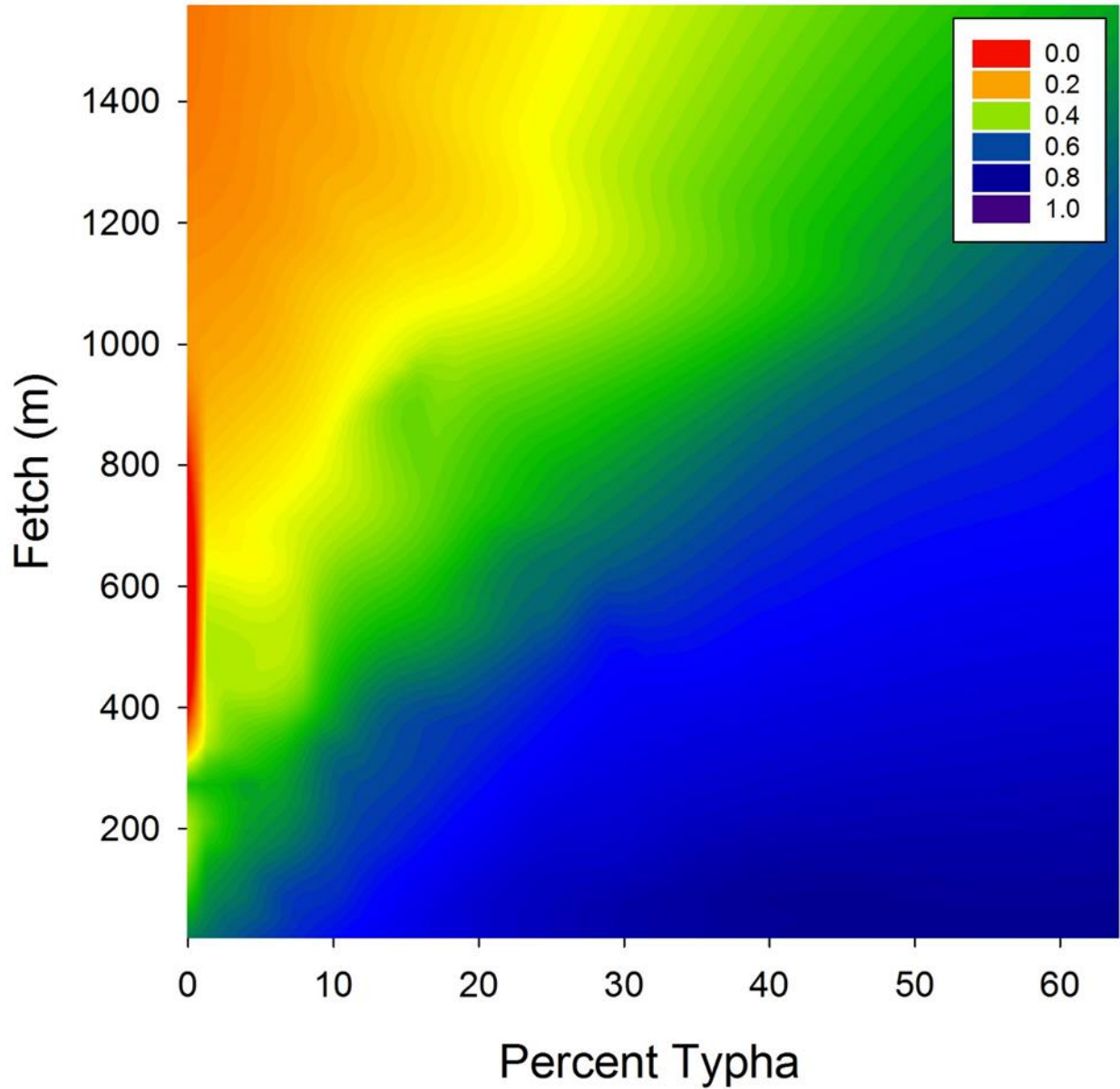
Figure 5 Landscape-scale relationship between muskrat (*Ondatra zibethicus*) site occupancy probabilities and the percentage of open water (Open Water), and landscape diversity (Diversity) at 71 wetland sites in Voyageurs National Park, International Falls, Minnesota, USA, during 2016.
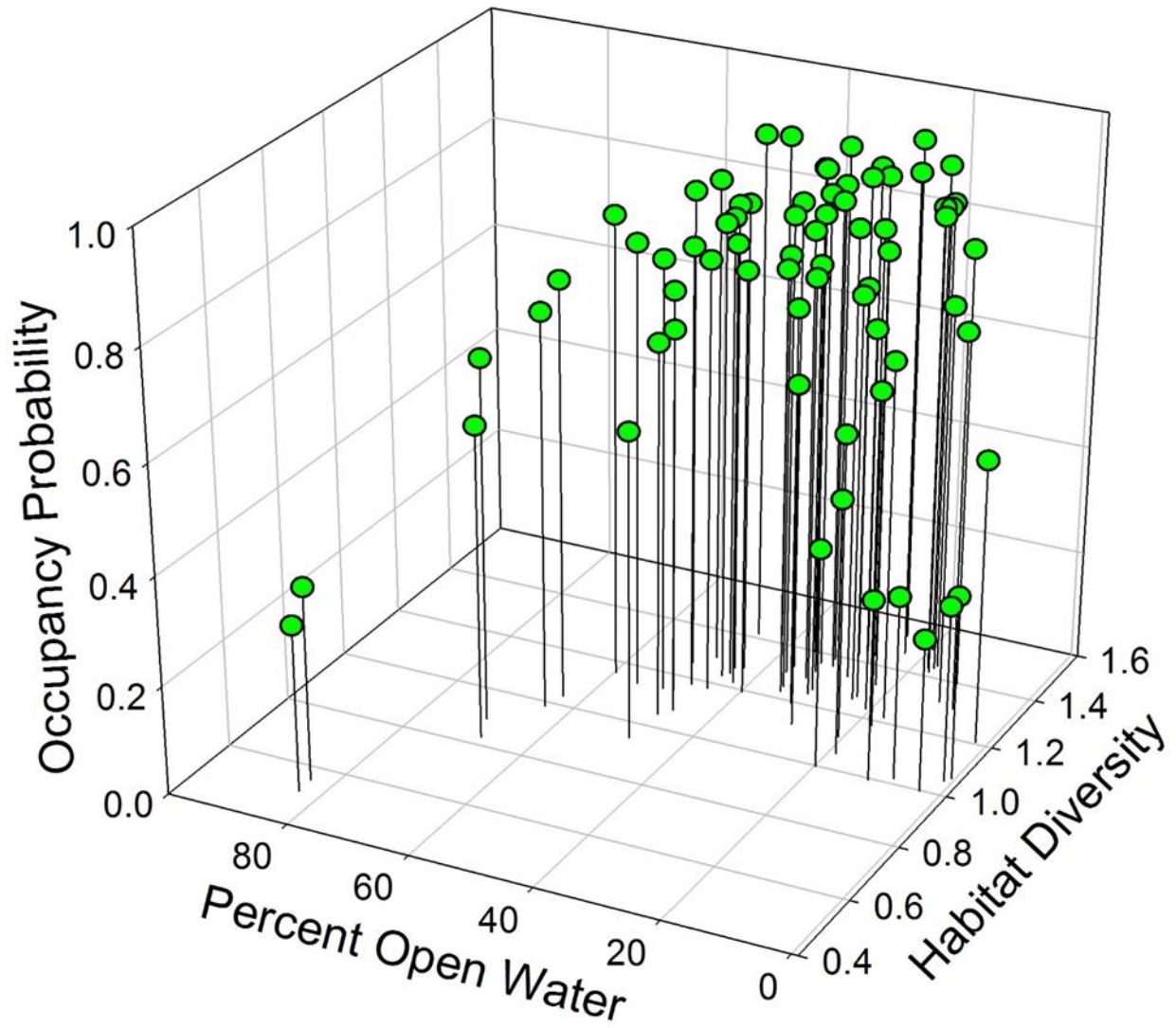
Table 1 Local-scale multiseason models used to assess detection, initial site occupancy, and colonization by muskrats (*Ondatra zibethicus*) in Voyageurs National Park, International Falls, Minnesota, USA, during the summers of 2016 and 2017. I ranked models by descending ΔAIC_c values and included all models with a $\Delta AIC_c \leq 2.00$ as well as the intercept model (Constant). Day of Year (day of year surveys were conducted), Method (method used for presence/absence of muskrat), Precip (7-day cumulative precipitation leading up to each site survey), Typha (percent coverage of Typha), Water (combined water depth and percent open water measurements), Fetch (wave impact within a 200-m buffer centered around each site), and a constant (intercept model). K = number of parameters in each model; w = model weight; Deviance = -2Log(Likelihood).

Model	ΔAIC_c	w	K	Deviance
Detection$_{2016\text{-}2017}$				
Day of Year + Method	0.00	0.46	6	695.84
Day of Year	1.47	0.22	5	699.31
Day of Year + Precip + Method	1.88	0.18	7	695.72
Constant	7.50	0.01	4	707.34
Initial Occupancy$_{2016}$				
Typha + Water	0.00	0.27	8	689.32
Typha + Fetch + Typha*Fetch	1.07	0.14	9	688.39
Typha + Water + Fetch	1.31	0.14	9	688.63
Constant	2.52	0.08	6	695.84
Colonization$_{2017}$				
Typha + Fetch + Typha*Fetch	0.00	0.41	11	678.90
Constant	4.42	0.11	8	689.32

Table 2 Landscape-scale multiseason occupancy models used to assess muskrat (*Ondatra zibethicus*) habitat occupancy Voyageurs National Park, International Falls, Minnesota, USA. I included all models with a $\Delta AIC_c \leq 2.00$ as well as the intercept model (Constant) and ranked them by descending ΔAIC_c. SHDI (Shannon's diversity index of habitat heterogeneity), Open Water (percent of open water habitat within a 2000-m buffer centered around each site), Wetland (percent of wetland habitat within a 2000-m buffer centered around each site), Typha (percent cover of Typha within a 2000m buffer centered around each site), edge (total amount of habitat edge surround each site), and a constant (intercept model). K = number of parameters in each model; *w* = model weight; Deviance = -2Log(Likelihood).

Model	ΔAIC_c	*w*	K	Deviance
Initial Occupancy$_{2016}$				
SHDI + Open Water	0.00	0.24	8	688.08
SHDI	1.36	0.12	7	691.44
SHDI + Wetland	1.46	0.11	8	689.54
SHDI + Open Water + Typha	1.97	0.09	9	688.05
SHDI + Open Water + Wetland	1.99	0.09	9	688.07
SHDI + Edge + Open Water	2.00	0.09	9	688.08
Constant	4.73	0.02	6	696.81

Chapter 3 - Conclusion

Muskrat populations across the Unites States are believed to be declining, however, there is no mechanistic explanation for these widespread declines (Roberts and Crimmins 2010; Ahlers and Heske 2017). This semiaquatic mammal is an economically important furbearer with some of the greatest harvest rates of any furbearer species, and occupy wetlands throughout North America (Erb and Perry 2003; White et al. 2015). Muskrats are also considered ecosystem engineers that can regulate wetland vegetation growth, act as small agents of disturbance, and increase plant species richness in wetlands (Danell 1996; Connors et al. 2000). Their reported decline across the United States supports the need to create management plans across their native range. However, estimating muskrat population size and occupied range at such large spatial and temporal scales is difficult (Ahlers and Heske 2017).

The goal of my research was to identify how muskrat habitat use is affected by local and landscape-scale factors, and the effects that landscape composition and configuration have across multiple scales. I used 2 seasons of presence/absence data and multiseason occupancy modeling to reveal factors affecting the spatial distributions of muskrats within Voyageurs National Park (VNP). After conducting walking and raft surveys throughout wetlands in VNP, I quantified effects of local and landscape composition, and cross-scale interactions have on muskrat occupancy. My results indicate: 1) muskrats occupy local-scale wetlands that contain greater amounts of *T. x glauca*, an invasive hybrid cattail species; 2) muskrats also occupy local-scale wetlands with shallow and less amounts of open water; and 3) muskrats colonize local areas that receive low amounts of wind and wave impact. However, muskrats will colonize local areas that receive greater amounts of wind and wave action if these areas contain greater amounts of *T. x*

glauca. Finally, 4) at a broader landscape-scale, muskrats seem to be occupying areas with greater habitat diversity and open water.

My study provides more insight into invasive hybrid cattail, intense wind-generated waves , and landscape composition and how they affect the spatial distribution of a wetland-obligate semiaquatic mammal. The effects of expanding *T. x glauca* on muskrats have not been well documented and this study is one of the first to document these effects on habitat use by muskrats. My results suggest that management of *T. x glauca* should potentially focus on containment, and not complete eradication, of this invasive species as it may provide a critical food source or lodge material for muskrats. Management plans should also consider wetlands that are protected from wind-generated waves as muskrats colonizing these less impacted wetlands. My results are similar to another study documenting the effects fetch on another semiaquatic mammal, American beaver (*Castor canadensis*; Allen 1983). Management plans for muskrat populations and wetlands should also focus on maintaining habitat diversity and open water connectivity as these resources may provide functional connectivity for muskrats into other wetlands that provide resources for food and lodge construction.

ThePrior to the decline of muskrat populations throughout the US (Ahlers and Heske 2017), the spread of invasive hybrid *T. x glauca* across the United States, and loss of natural wetlands have occurred simultaneously (Johnston 1994; Galatowitsch et al. 1999). This research represents one of the first studies to test local and landscape composition and cross-scale interactions on the habitat use of muskrats. Using non-invasive sign surveys, presence/absence data, and multiseason occupancy modeling, I documented local and landscape variables that have

the greatest effects on muskrat habitat use. Understanding species interactions with fine and broad scale variables can help inform and shape management plans targeted at restoring declining populations. Future research should measure nutritional value of *T. x glauca* to understand if this invasive hybrid species provides similar nutritional values (compared to native vegetation communities) to muskrat populations. Additionally, studying the pre- and post-effects of management for invasive hybrid *T. x glauca* on muskrat spatial distributions could inform future wetland management plans.

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