Supplementary Materials for “Evaluate Control Methods for Invasive Hybrid Cattails”

Submitted by Steve Windels, Ph.D., Project Manager

Copies of manuscripts in peer-reviewed science journals (published), and reports/dissertations/theses.

Manuscripts in peer-reviewed science journals (published or submitted):

1. Aarrestad O, Matykiewicz BR, Windels SK, Ahlers AA, Olson BT, Rendahl A, Burton E, and Wolf TM. 2021. Baseline physiologic and hematologic health in wild-caught muskrats (*Ondatra zibethicus*) from a near-pristine ecosystem in northern Minnesota. *Journal of Zoo and Wildlife Medicine* 52: 698-703.
2. Matykiewicz BR, Windels SK, Olson BT, Plumb RT, Wolf TM, and Ahlers AA. 2021. Assessing translocation effects on the spatial ecology and survival of muskrats (*Ondatra zibethicus*). *Wildlife Biology* 2: 1-11.
3. Ahlers AA, Wolf TM, Aarrestad O, Windels SK, Olson BT, Matykiewicz BR, and Dubey JP. 2020. Survey of *Toxoplasma gondii* exposure in muskrats in a relatively pristine ecosystem. *Journal of Parasitology* 106: 346-349.
4. Larreur M, Windels SK, Olson BT, and Ahlers AA. 2020. Cross-scale interactions and non-native cattails affect the spatial distribution of a wetland-obligate species. *Landscape Ecology* 35: 59 68.

Reports/dissertations/theses:

1. Benjamin Matykiewicz. Post-translocation spatial ecology and survival of muskrats (*Ondatra zibethicus*) in lacustrine wetlands. M.S. Completed May 2020 (Kansas State University).

BASELINE PHYSIOLOGIC AND HEMATOLOGIC HEALTH IN WILD-CAUGHT MUSKRATS (ONDATRA ZIBETHICUS) FROM A NEAR-PRISTINE ECOSYSTEM IN NORTHERN MINNESOTA

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BASELINE PHYSIOLOGIC AND HEMATOLOGIC HEALTH IN WILD-CAUGHT MUSKRATS (*ONDATRA ZIBETHICUS*) FROM A NEAR-PRISTINE ECOSYSTEM IN NORTHERN MINNESOTA

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Abstract: Muskrat (*Ondatra zibethicus*) populations show long-term and widespread declines across North America, necessitating research into potential mechanistic explanations, including population health. Previous research established reference hematology values, a proxy of individual health, of muskrats occurring in highly modified ecosystems. However, our knowledge of hematology metrics in muskrat populations occurring in more natural ecosystems is limited. We measured several hematological parameters of wild-caught muskrats ($n = 73$) in the Greater Voyageurs Ecosystem in northern Minnesota in 2018–2019 to establish baseline muskrat health in a relatively intact, near-pristine ecosystem. Additionally, we measured rectal temperature and heart and respiratory rates and collected whole blood for complete blood cell count assessment. We established baseline physiologic and hematologic reference ranges for the population and describe variations between total white blood cells, nucleated cell differentials, and basic erythron and platelet estimates and demonstrate methods of estimation to be poor proxies for more standardized counting methods. Our results establish a baseline to compare muskrat health assessments for populations affected by landscape change or in decline.

INTRODUCTION

Muskrats (*Ondatra zibethicus*) are small (~1.0–1.5kg) semiaquatic herbivores that play an important role in wetland ecosystems but appear to be declining across North America.[1,6,17] Landscape changes (e.g. urbanization, agriculture) can enhance pathogen transmission into wetlands, which can negatively affect muskrat health and population growth.[2] Although population health parameters (i.e. hematology and serum chemistry) are established for muskrats occurring in human-dominated landscapes[3] (i.e. central Illinois; 91% of landscape devoted to row-crop agriculture [85%] and urban land use [6%][2]), we lack similar data for muskrats occurring in more intact ecosystems. Comparison of reference ranges from differing systems will allow us to infer the effect of landscape changes on muskrat health. Thus, our objectives were to establish baseline physiologic and hematologic reference ranges for a muskrat population occurring in a relatively undisturbed and intact ecosystem.

MATERIALS AND METHODS

This study was approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol #4098) and conducted alongside a muskrat translocation study occurring in the Greater Voyageurs Ecosystem near International Falls, Minnesota (48.4841°N, 92.8271°W). Voyageurs National Park includes the lower end of the 38,600-km² Rainy Lake Watershed[13] and <1% of the park has experienced anthropogenic disturbance since the park's establishment in 1975. Primary disturbances in the Rainy Lake region were timber harvests on public and private lands, while human settlement or development was minimal.[14] Parks and designated wilderness areas compose 25% of the Rainy Lake Watershed upstream of the Greater Voyageurs Ecosystem,[13] including the Boundary Water Canoe Area Wilderness (4,387 km²) in Minnesota and Quetico Provincial Park (4,788 km²) in Ontario, Canada.

During July 2018 and June 2019, we captured 73 adult muskrats (54 male [74%] and 19 female [26%]) using live traps, as described previously.[15] After capture, we transferred muskrats to a

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handling bag, weighed them, and induced anesthesia with an IM injection of 0.02–0.025 mg/kg dexmedetomidine (Pfizer Inc, New York, NY 10017, USA) and 1 mg/kg midazolam (Hospira, Inc, Lake Forest, IL 60045, USA). We measured rectal temperature immediately after injection using a digital thermometer. When righting reflexes diminished, we positioned muskrats in dorsal recumbency and administered 2% isoflurane (Piramal Enterprises Limited, 400070 Mumbai, India) and 0.6 L/m of oxygen via facemask, as previously described.[3] On general anesthesia, we performed a complete physical examination and measured heart and respiratory rates an average of 2 m (standard deviation [SD] = 2 m) after isoflurane administration. Prior to termination of anesthesia, we collected 1–1.8 ml whole blood from the cranial vena cava (25-ga needle on a 3-ml syringe) into heparinized tubes (Monoject™ Blood Collection Tube, Covidien™, Minneapolis, MN 55432, USA). We used heparin tubes because we anticipated small blood volumes and wanted flexibility to use the samples for other screening tests. We reversed dexmedetomidine and midazolam with 0.20–0.25 mg/kg atipamezole (Zoetis Inc, Kalamazoo, MI 49007, USA) and 0.05 mg/kg flumazenil (Hikma Pharmaceuticals, 2705-906 Terrugem, Portugal), respectively, and inoculated muskrats with 0.1 ml penicillin (AgriLabs, Peachtree City, GA 30269, USA) and 1 mg/kg meloxicam (Putney, Inc, Portland, ME 04101, USA).

For samples collected in 2019 ($n = 50$), we created blood smears immediately following collection. Within 4–6 h of collection (with refrigerated storage of whole blood), we partially filled and centrifuged a nonheparinized microhematocrit tube (J-544, Jorgensen Laboratories, Inc, Loveland, CO 80538, USA) to separate plasma from cellular solids. We measured packed cell volume digitally (HemataStat II, EKF Diagnostics, CF64 2EZ Penarth, UK) and plasma total protein using a manual refractometer (RHC 200ATC Refractometer, C&A Scientific, Sterling, VA 20166, USA). Within 2 d of collection (with refrigerated storage of whole blood), we used the Whi-pette Test Kit (Exotic Animal Solutions, Melbourne, FL 32941, USA), a unopette-like system, for manual white blood cell (WBC) and platelet counting with a hemocytometer, according to manufacturer instructions. Due to the time-intensive nature of the procedure, we performed platelet counts by hemocytometer for only a subset of samples ($n = 24$). We performed manual WBC and platelet estimates and WBC differentials on blood smears stained with a modified Wright-Giemsa stain (Aerospray 7120, Wescor, Inc, Logan, UT 84321, USA). We estimated WBC numbers by enumerating the number of WBC in 10 high-power fields (hpf) (×400), dividing the total by 10 and multiplying by 2,000.[7] We estimated platelets by counting the number of platelets in 10 hpf (×1,000, oil), averaging the fields, and multiplying by 15,000.[9] We performed WBC differentials by counting 100 WBC in the monolayer, categorizing them into basophils, eosinophils, monocytes, band neutrophils, segmented neutrophils, and lymphocytes.[19] The monolayer was defined as even distribution of all cells with minimal disturbance of cell distributions between the body and feathered edge. All slides were assessed for platelet and leukocyte clumping by scanning the feathered edge. No leukocyte clumping was noted, and most muskrats had mild (2–4 clumps on feathered edge) or moderate (>4 clumps on feathered edge) platelet clumping, with a few having marked clumping (>4 clumps on feathered edge as well as clumping in body of smear). The latter were excluded from platelet summary analysis. We recorded nucleated red blood cells (nRBC) but did not include them as part of the 100 WBC. If we counted more than five nRBC on any slide, we corrected the WBC count using the following formula: Corrected WBC estimate = WBC estimate (100/[nRBC + 100]).[7] We converted differential counts into absolute values by multiplying the percentage by the total WBC count estimated using the hemocytometer. We analyzed blood samples using manual methods, as automated methods were not feasible given the remote field setting. All the estimations and hemocytometer counts were performed by the same researcher (OA), and only one slide was evaluated per muskrat.

To estimate reference intervals, we followed guidelines and met criteria for generation of veterinary reference intervals according to American Society for Veterinary Clinical Pathology guidelines.[10] We examined data from each variable separately for outliers and symmetry, transformed as needed using the Box-Cox method, and derived 95% reference intervals using the robust method (as $n \geq 40$ but < 120), with 90% confidence intervals bootstrapped around the bounds.[10] We checked for outliers using histograms and Horn's algorithm before and after transformation.

Removal of outliers was assessed using clinical expertise. As these data were collected from wild-caught species, we chose to conservatively exclude values when a biological reason for an outlier was plausible. We excluded several outli-

Table 1. Physiologic parameters of anesthetized wild-caught muskrats (*Ondatra zibethicus*) from the Greater Voyageurs National Park Ecosystem, International Falls, Minnesota, in July 2018 and June 2019. N/A = not available.

Parameter	*n*[a]	Mean	SD	Range	Low[b] (90% CI)	High[b] (90% CI)
Weight (kg)	73	1.032	0.137	0.7–1.36	0.754 (0.702, 0.802)	1.30 (1.26, 1.35)
Temperature (°C), females[c]	19	36.56	0.96	34.33–37.89	N/A	N/A
Temperature (°C), males[c]	53	35.99	0.98	34.33–38.89	34.2[d] (33.9, 34.5)	37.6[d] (37.3, 37.9)
Heart rate[e] (beats/m)	73	153.1	30.0	78–208	87.3 (72.7, 99.2)	209 (201, 217)
Respiratory rate[e] (breaths/m)	72	51.0	16.4	11–96	22.1[f] (16.2, 27.6)	77.0[f] (72.8, 81.0)

[a] *n* includes outliers and differs by variable due to one missing temperature value and two missing respiratory rate values.

[b] Low and High represent the 95% lower and the upper range of the reference interval, respectively

[c] Significant differences in rectal temperature between sexes ($P = 0.02$).

[d] Two outliers removed.

[e] Parameter measurement collected on average 2 m (SD = 2 m) following onset of general anesthesia.

[f] Four outliers removed.

ers we considered to be due to clinical illness or anesthetic effects, including two elevated temperature values (38.50°C and 38.89°C, both male, possibly associated with infection or inflammation), one low packed cell volume (24, possibly anemia), and four respiratory rates (11, 12, 90, and 96, possibly due to the level of anesthesia when the measurements were taken).

Variable symmetry was assessed using histograms and the Shapiro-Wilk test for normality. We transformed all variables except temperature using the Box-Cox transformation. Temperature values were symmetric and passed the Shapiro-Wilk test, so, as the best Box-Cox transformation depends on the chosen scale (as there is no true zero on either the Celsius or the Fahrenheit scale), we chose not to transform this variable. Band neutrophils, monocytes, eosinophils, and nRBC could not be transformed to symmetry, as they had too many zero values. Additionally, total protein was nonsymmetric and had a large number of ties, and platelet counts and estimates did not have the recommended number of samples.

We estimated reference intervals from pooled sexes for all variables except temperature. For temperature, we computed reference intervals for males only, as we had identified evidence for a difference in temperatures by sex, and the sample size for females was not large enough to derive a separate interval. We performed statistical tests using R version 4.0.2.[16]

RESULTS

For physiological parameter estimates, we report data from both years (Table 1), whereas we report hematologic parameter estimates for 2019 only (Table 2). Average rectal temperature was the only physiological parameter that varied between males (35.99°C, SD = 0.98, $n = 53$; one missing) and females (36.56°C, SD = 0.96; $n = 19$, $P = 0.02$). Erythrocyte morphology changes included anisocytosis ($n = 1$), codocytes ($n = 29$), echinocytes ($n = 1$), and stomatocytes ($n = 4$). Most muskrats demonstrated mild (3–8 polychromatophils/hpf; $n = 23$) or moderate (9–16 polychromatophils/hpf; $n = 19$) levels of polychromasia, with some having trace (<3 polychromatophils/hpf; $n = 6$) or marked (>16 polychromatophils/hpf; $n = 11$) polychromasia of erythrocytes. Polychromasia ranges were adapted from canine semiquantitative erythrocyte morphology changes.[11,20] No hemoparasites were observed.

WBC estimates (mean of 1.64×10^3 cells/ul) were an underestimate compared to WBC counts (mean of 7.47×10^3 cells/ul) in the same animal with an estimated average estimate : count ratio of 0.18 (95% confidence interval [CI]: 0.15, 0.23) and a 95% prediction interval of 0.04–0.92. Conversely, platelet estimates (mean of $1{,}333 \times 10^3$ platelets/ul) were on average overestimated compared to platelet counts (mean 556×10^3 platelets/ul) in the same animal, with an estimated average estimate : count ratio of 2.47 (95% CI: 1.75, 3.48) and a prediction interval of 0.53–11.55.

DISCUSSION

Our results represent the first attempt to categorize physiologic and hematologic parameters from wild-caught muskrats occurring in a near-pristine ecosystem. In comparison to Ahlers et al,[3] we observed lower total WBC and neutrophil counts. Similar to Ahlers et al[3] and in contrast to other rodents, our samples were primarily

Table 2. Hematologic parameters of wild-caught muskrats (*Ondatra zibethicus*) from the Greater Voyageurs National Park Ecosystem, International Falls, Minnesota, in June 2019. N/A = not available.

Parameter	*n*[a]	Mean	SD	Proportion zero[b]	Range	Low (90% CI)	High (90% CI)
Total protein (g/dl)	50	5.60	0.48	N/A	4.4–6.8	N/A	N/A
PCV (%)	50	36.00	3.35	N/A	24–43	29.9[c] (28.4, 31.2)	41.8[c] (40.8, 43.0)
WBC count (10^3 cells/ul)	50	7.47	2.95	N/A	2.37–14.3	2.31 (1.62, 2.97)	14.3 (13.0, 15.7)
WBC estimate (10^3 cells/ul)[d]	50	1.64	1.17	N/A	0.2–6	0.195 (0.104, 0.357)	4.95 (4.18, 6.08)
Platelet count (10^3 cells/ul)	19	556	250	N/A	151.5–1,051	N/A	N/A
Platelet estimate (10^3 cells/ul)[e]	37	1333	1092	N/A	51–4,801.5	N/A	N/A
Segmented neutrophils (10^3 cells/ul)	50	5.48	2.49	N/A	1.44–10.83	1.47 (1.04, 1.94)	11.7 (10.3, 13.2)
Band cells (10^3 cells/ul)	50	0.016	N/A	0.80	0–0.22	N/A	N/A
Lymphocytes (10^3 cells/ul)	50	1.78	1.00	N/A	0.53–4.42	0.487 (0.398, 0.592)	4.84 (3.99, 6.22)
Monocytes (10^3 cells/ul)	50	0.142	N/A	0.18	0–0.51	N/A	N/A
Eosinophils (10^3 cells/ul)	50	0.052	N/A	0.62	0–0.31	N/A	N/A
Basophils (10^3 cells/ul)	50	0	0	1.00	0	0	0
Nucleated RBC (per 100 WBC)[f]	50	0.069	N/A	0.74	0–1.47	N/A	N/A
Neutrophil : lymphocyte ratio	50	3.81	2.13	N/A	0.56–9.44	0.706 (0.439, 1.02)	9.40 (8.04, 11.1)

[a] *n* includes outliers.

[b] For parameters with a substantial number of measurements of zero, the proportion that was zero is reported instead of the standard deviation.

[c] One outlier removed.

[d] We estimated WBC by enumerating the number of white blood cells in 10 hpf (×400), dividing the total by 10, and multiplying by 2,000.[7]

[e] We estimated platelets as the number of platelets in 10 hpf (×1,000), averaging the fields, and multiplying by 15,000.[9]

[f] This value was from the blood smear.

neutrophilic,[5] likely attributed to capture and handling stress.[3,18] Differing WBC counts between studies suggests that muskrats from our population may be healthier and a more representative reference for baseline muskrat health. Further support is demonstrated by differences in pathogen exposure in these two populations. Previous literature reported 60% seroprevalence to *Toxoplasma gondii* in the muskrat population from a human-dominated ecosystem,[2] while we observed no evidence of *T. gondii* exposure in our muskrat population.[4] Collectively, these findings suggest that reference values produced from this study may be an optimal baseline for comparison of future muskrat studies.

The difference in WBC and platelet estimates versus counts is likely related to methodology. The hemocytometer is considered a more accurate measurement for determining the WBC total over WBC estimation. The Whi-pette Test Kit uses a dilutional technique with a specific blood volume that lyses all RBC, allowing for enumeration of all WBC and platelets that fall within the Neubauer hemocytometer counting chamber. In contrast, the WBC estimate derives the WBC and platelet concentrations from averages of cells counted in randomly reviewed regions of the monolayer. This methodology, while still often used in fieldwork, is discouraged because of inaccuracy secondary to blood film preparation technique, slight variations in whole blood volume with each blood smear preparation, and potential reviewer bias when selecting counting regions within the monolayer.[8] No studies have linked differences between muskrat samples stored at room temperature or refrigeration; however, in cattle, pigs, and goats, there is no effect on WBC concentration for samples stored up to 120 h at either 30°C or 5°C when using a hemocytometer to estimate WBC. Thus, we have no reason to suspect that a discrepancy was related to sample refrigeration or delay in processing.[12] Given our wide range of prediction intervals, we conclude that estimation methods for leukocyte and platelet concentrations are inadequate substitutes for standardized enumeration methods, such as the hemocytometer or, ideally, automated methods.

The high degree of platelet clumping precluded estimation of accurate reference intervals. Our results (Table 2) should be considered minimum platelet values, as no muskrats had overt evidence of bleeding disorders during anesthetized physical examination (e.g. petechia, ecchymosis, excessive bruising, or bleeding at the site of the blood draw), and all recovered uneventfully. Future research should provide accurate reference ranges, ideally using automated methodology, as there are currently no studies addressing platelets in muskrats.

Muskrat populations appear to be declining across North America,[1,17] and our results can be used to inform future research concerning the effects of landscape change on muskrat health. These data provide useful baseline measurements by which to compare other muskrat populations occurring in human-dominated ecosystems. By using our data from a pristine environment, the effects of landscape change on this species can be more accurately evaluated. This could be important in understanding and mitigating observed widespread declines in muskrat populations.

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Assessing translocation effects on the spatial ecology and survival of muskrats Ondatra zibethicus

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Assessing translocation effects on the spatial ecology and survival of muskrats *Ondatra zibethicus*

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Muskrats *Ondatra zibethicus* are semiaquatic herbivores experiencing long-term and widespread population declines across North America. Translocation may be a viable tool to bolster or reestablish local populations; however, subsequent effects of translocation on muskrats are unknown. We live-trapped and translocated radiomarked muskrats ($n = 65$) during the summers of 2018–2019 in Voyageurs National Park, MN, USA and assessed post-translocation effects on weekly survival probabilities and space-use patterns. We did not observe homing behavior, though individuals moved an average of 2.2 km ($SE = 0.30$ km) from release sites and established home ranges within ~8 days ($SE = 1.16$ days) post-translocation. Weekly post-translocation survival probabilities (0.95, $SE = 0.001$) and average home-range sizes (2.52 ha, $SE = 0.44$ ha) were similar to other studies of non-translocated muskrats. Our most-supported known-fate survival model revealed muskrats using beaver *Castor canadensis* lodges had greater weekly survival probabilities. Additionally, weekly muskrat survival varied between years suggesting a positive response to a novel soft-release technique applied in 2019. Our study provides the first empirical assessment of translocation effects on muskrats and suggests translocation may be effective for establishing or enhancing local muskrat populations. Additionally, our study suggests beaver lodges may confer fitness benefits to sympatric muskrats particularly during dispersal.

Keywords: beaver, *Castor canadensis*, dispersal, home range, lodge, muskrat, *Ondatra zibethicus*, survival, Voyageurs National Park

Wildlife translocation is an important conservation tool used to alter population abundances and distributions or enhance population viability for at-risk species (Jachowski et al. 2016, Berger-Tal et al. 2019). These efforts are generally focused on reintroducing or bolstering local populations (Olsson et al. 2007, Paul 2009, Werdel et al. 2019), restoring imperiled species (Jachowski and Lockhart 2009), or providing an alternative to lethal removal (Germano et al. 2015, Lehrer et al. 2016). Additionally, translocation can be used to restore native landscapes by reestablishing populations of ecosystem engineers (e.g. American beaver *Castor canadensis* and Eurasian beaver *Castor fiber*; Law et al. 2017). Regardless of management goals, practitioners should rigorously evaluate post-translocation metrics (e.g. survival, space use) to assess the effectiveness of their efforts (Jachowski et al. 2016, Lehrer et al. 2016, Werdel et al. 2018, Berger-Tal et al. 2019).

Muskrats *Ondatra zibethicus* are small (0.7–1.8 kg; Willner et al. 1980) semiaquatic herbivores experiencing long-term and widespread population declines across North America (Roberts and Crimmins 2010, Ahlers and Heske 2017, Greggory et al. 2019). Muskrats are an economically important species (Erb and Perry 2003, Ahlers et al. 2016), culturally significant in North America (Brietzke 2015, Straka et al. 2018, Turner et al. 2018), and possibly ecosystem engineers in wetland ecosystems (Bomske and Ahlers 2021). For instance, muskrat herbivory is positively associated with wetland vegetation species richness (Nyman et al. 1993, Tyndall 2011) and occurrence of open-water habitats (Bansal et al. 2019). Additionally, muskrat huts provide nesting structures for birds (Kiviat 1978) and increased abundances of aquatic macroinvertebrates (de Szalay and Cassidy 2001, Nummi et al. 2006). Because of their cultural significance in North America, declining population trends

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and importance to wetland ecosystems (Bhattacharjee et al. 2007, Ahlers and Heske 2017, Bomske and Ahlers 2021), translocation efforts focused on restoring or enhancing muskrat populations are timely and warranted.

Historically, muskrats were translocated to muskrat-absent wetlands to provide increased opportunities for fur trappers (Storer 1937, O'Neil 1949, Idaho Fish and Game 2015). However, these efforts were not rigorously evaluated (e.g. population persistence, individual survival) leaving the efficacy of these population-management actions unknown. Translocating individual muskrats has potential to influence their subsequent space use and survival, which may impact overall management goals. The effects of translocation on wildlife populations is difficult to generalize, however, as changes in key population demographics can be taxa-specific (Tetzlaff et al. 2019). McKinstry and Anderson (2002) reported greater emigration rates and lower survival rates for post-translocated American beavers while Van Vuren et al. (1997) reported similar emigration patterns along with increased homing rates in translocated California ground squirrel *Ostospermophilus beecheyi* populations. Larger male northern river otters *Lontra canadensis* had greater post-translocation survival rates than females and smaller individuals (Day et al. 2013). Lehrer et al. (2016) did not find evidence for homing behavior in translocated woodchucks *Marmota monax* and reported translocated individuals had similar survival rates as residents. Soft-release techniques (structures and release methods intended to acclimate translocated animals to a novel environment) are recommended by practitioners, in addition to release sites with relatively low predation risk, to enhance survival and site fidelity of individuals (Truett et al. 2001, Lehrer et al. 2016). When compared to hard-releases, animals translocated using soft-releases had greater survival rates and were more likely to establish territories at their new location (Tetzlaff et al. 2019).

We assessed weekly survival rates and the post-translocation movements of muskrats as part of a larger study investigating the potential for translocated muskrats to serve as a biocontrol of non-native invasive hybrid cattail (*Typha* × *glauca*; Brulliard 2018). We hypothesized that translocated muskrats would not exhibit homing behavior as translocation distances likely exceeded their perceptual ranges and known movement capabilities. Similar to other translocated species, we expected prospecting behaviors (searching for habitat in novel landscapes prior to establishing a home range) of muskrats to negatively influence weekly survival probabilities (Calvete and Estrada 2004, Lehrer et al. 2016). We expected post-translocation movements to remain within or close to release sites given the relative impermeability of surrounding upland landscapes and fetch impacts present in open water habitats (Larreur et al. 2020). Muskrats in North America are sympatric with American beavers and will often use active or inactive beaver lodges (Leighton 1933, Rosell et al. 2005, Mott et al. 2013, Windels 2017). It is plausible that beaver lodges could provide muskrats refugia from predation or adverse weather, and use of beaver lodges while prospecting in unfamiliar landscapes may confer increased fitness benefits such as increased survival probabilities (Rosell et al. 2005). Thus, we expected a positive association in weekly survival probabilities and beaver lodge use. Finally, we expected individuals translocated using soft-release techniques would have greater weekly survival probabilities than those translocated using hard-release methods.

Methods

Study area

Our study occurred in the Greater Voyageurs Ecosystem located in and around Voyageurs National Park (VNP; ~88 220 ha) near International Falls, Minnesota, USA (48°29′N, −92°49′W; Fig. 1). VNP comprises parts of five lakes, of which Rainy (58 065 ha) and Kabetogama (9726 ha), both located within the Rainy Lake watershed (Fig. 1), were the focus of our research. Areas outside VNP involved in our study included the Black Bay portions of Rainy Lake and Rat Root Lake, a tributary of Rainy Lake (Fig. 1). Water levels within Rainy and Kabetogama Lakes are artificially managed through dams at the Rainy River in International Falls, MN and the Kettle Falls and Squirrel Falls dams at the outlet of Namakan Lake. Water-level management regimes were modified in Rainy Lake in late 2018 to replicate natural fluctuations in the lake system prior to dam construction. These changes did not differ between our field seasons and were implemented partially in response to poor over-winter survival of muskrats within the lake system (Thurber et al. 1991, IJC 2018).

Rainy and Kabetogama Lakes are characterized by scattered islands and a mix of rocky and muddy shorelines. Wetland vegetation consisted of non-native cattails *Typha* × *glauca*, softstem bulrush *Schoenoplectus tabernaemontani*, wild rice *Zizania palustris* and sedges *Carex* spp. Upland areas adjacent to wetlands include shallow soils and bedrock dominated by conifers (white pine *Pinus strobus*, jack pine *Pinus banksiana* and balsam fir *Abies balsamea*) and deciduous trees (quaking aspen *Populus tremuloides* and paper birch *Betula papyrifera*). Beaver densities in VNP are the greatest reported in the USA and beaver lodges in the study area were ubiquitous (Johnston and Windels 2015). Potential muskrat predators included American mink *Neovison vison*, bald eagle *Haliaeetus leucocephalus*, raccoon *Procyon lotor*, red fox *Vulpes vulpes*, fisher *Martes pennanti* and great horned owl *Bubo virginianus*. Average annual temperature and precipitation was 3°C (range = 9.3°C to −3.3°C) and 242 cm (62 cm of rain and 180 cm of snow), respectively.

Captures and transmitter implantation

We captured and translocated muskrats from wetlands occurring in the Rainy Lake and Lake Kabetogama watersheds (Fig. 1) from 2–6 July 2018 and 1–7 June 2019 using double- and single-door live traps (Table 1; Tomahawk 202). We attached traps to 122 × 61 × 4-cm floating rafts (modified track boards; Reynolds et al. 2004, Schooley et al. 2012, Larreur et al. 2020) tethered to sturdy vegetation or wood laths (122 × 4 × 1-cm) anchored into the substrate or muskrat huts. We baited traps with apple and commercial trapping lures, and focused our efforts on or near muskrat huts or feeding platforms. We covered all traps in vegetation to make them appear more natural and provide cover from adverse weather and direct sunlight. Traps were checked

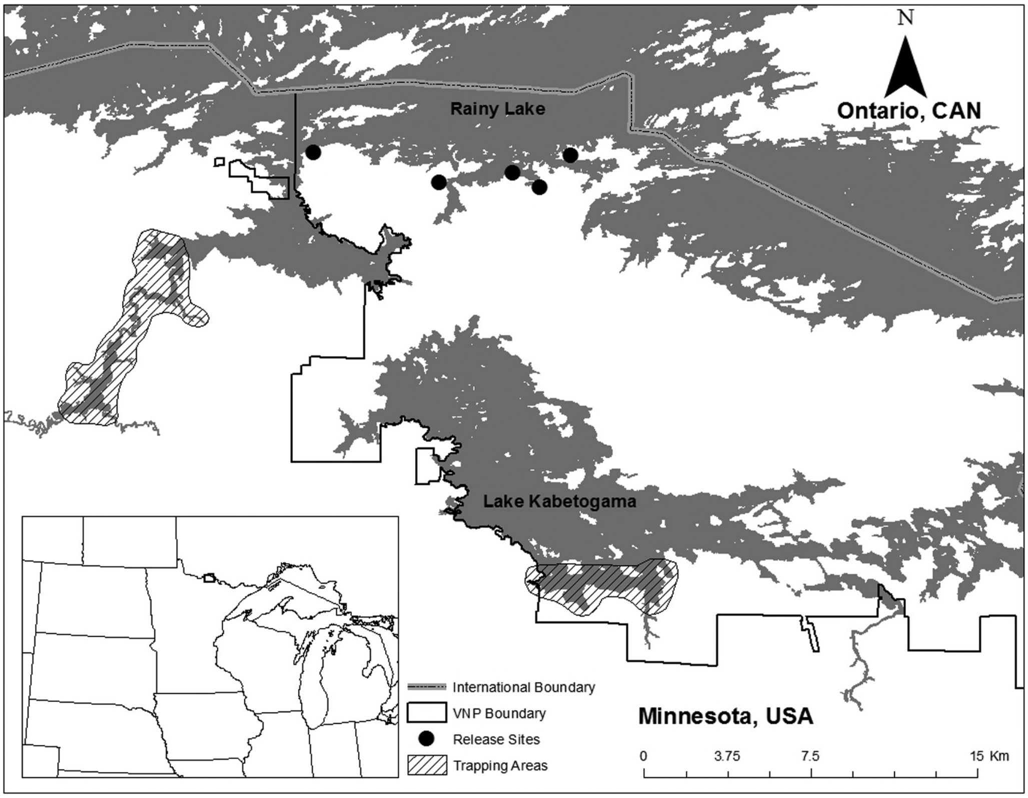

Figure 1. Spatial distribution of muskrat *Ondatra zibethicus* live-trapping areas and translocation wetlands (black circles; n = 5) for muskrats in Voyageurs National Park near International Falls, MN, USA during summers of 2018 and 2019.

every morning and captured muskrats (adults $\geq$ 700 g) were immediately transported to a surgery suite for implantation of internal, very-high-frequency (VHF) transmitters (13-g ATS model F1215, Advanced Telemetry Systems). Based on previous studies, we assumed internal transmitters would not negatively affect survival and were unlikely to be expelled from individuals (Davis et al. 1984, Ahlers et al. 2010a, b, Smith et al. 2016).

We transferred captured muskrats to a handling bag, weighed them and administered sedation (dexmedetomidine [0.020–0.025 mg kg^{-1}], midazolam [1 mg kg^{-1}]) via intramuscular injection. When individuals displayed reduced righting reflex, we induced surgical anesthesia using isoflurane (1–5%) via face mask. Once anesthetized, we recorded sex and conducted a basic health assessment. We implanted transmitters following Ahlers et al. (2010a, b); muskrats were maintained on 2.0–2.5% isoflurane at an oxygen flow rate of 0.6 l min^{-1} during the entire procedure (20–30 min) and heart and respiratory rates were monitored. We reversed dexmedetomidine and midazolam with atipamizole (0.20–0.25 mg kg^{-1}) and flumazenil (0.05 mg kg^{-1}), respectively, followed by inoculation of muskrats with penicillin (0.1 ml) and meloxicam (1 mg kg^{-1}). We marked individuals with passive integrated transponder tags (Ahlers et al. 2010a) and individual ear-tags. Prior to recovery, we collected 1.5 ml blood from individuals' cranial vena cava using a 25-ga needle attached to a 3-ml syringe (Ahlers et al. 2011, 2020). Additionally, we recorded four morphometric tail measurements from each individual (length, base-width, mid-width and end-width). We allowed individuals $\geq$ 2 h to recover post-surgery prior to translocating them to their assigned wetland.

Table 1. Summary of effort to translocate muskrats *Ondatra zibethicus* into Voyageurs National Park, MN, USA, during summers 2018 and 2019. The number of male and female muskrats used to assess translocation effects are reported for each year and translocation release type (hard release, soft release).

Year	Muskrats	Hard release	Soft release	Male	Female
2018	23	23	0	18	5
2019	42	0	42	30	12

We selected five lacustrine wetlands in Rainy Lake (VNP) to receive translocated muskrats and randomly assigned individuals to their respective wetlands (Fig. 1). Additionally, we translocated 111 non-radiomarked muskrats (2018 = 92, 2019 = 19) to wetlands as part of our broader study investigating muskrats as a potential biocontrol of *T.* × *glauca*. Prospective wetlands were representative of traditional muskrat habitat (shallow to deep marsh) and vegetation communities were dominated by *T.* × *glauca*. Wetlands averaged 1.42 ha in size (range = 1.09–1.78 ha) and were separated by $\geq$ 1.3 km ($\bar{x}$ = 5.7 km, range = 1.3–11.6 km). We did not quantify muskrat abundances in wetlands prior to muskrat translocations; however, observations during pre-study assessments (e.g. number of muskrat huts, clippings and scat) indicated low-to-zero muskrat abundances in those areas. Average translocation distance (Euclidian) from site of capture for all radio-marked muskrats (n = 65) was 18.1 km (range 4.7–25.5 km).

In 2018, we translocated muskrats using hard-release methods where we released an individual onto natural structures within their assigned wetland. We revised our translocation techniques in 2019 by applying soft release techniques (i.e. temporary shelters) to better acclimate them to their release area (Fig. 2). Shelters were constructed using a 76 × 51 × 44-cm (114 liter) plastic tote (with removable lid) affixed to 122 × 61 × 4-cm floating rafts (for detailed descriptions of floating rafts, Reynolds et al. 2004, Schooley et al. 2012 and Larreur et al. 2020). We cut a 15-cm diameter opening in the plastic tote and partially filled structures with vegetation collected at the release site. Individuals released into structures were able to freely leave or return through the opening (Fig. 2). We placed two structures in each release wetland (~10 m apart) to reduce potential for competition between translocated muskrats, and only one muskrat was released per structure at a time. Structures were placed in ~1 m of water and spatially positioned within wetlands to reduce exposure to wave action. We broadly assessed the potential for persistent use of structures by muskrats (> 24 h) with motion triggered video cameras (Browning, BTC-5HDPX). Cameras were attached to 2.5 m wooden stakes (5.08 × 2.04 cm) positioned 1.5–2.0 m away from structures, secured ~30 cm above the water surface, and oriented towards the structure opening. We programmed cameras to record 10 s videos when infrared sensors were triggered. All trapping, handling, marking techniques and release locations were consistent with no appreciable differences in environmental or climactic conditions between years.

Movements and survival

We used a boat or aircraft-mounted, four-element fixed Yagi antennae in conjunction with an ATS R4000 receiver (Advanced Telemetry Systems) to initially search for muskrats. Once general locations of muskrats were identified, we used a single handheld telemetry receiver (Communication Specialist R-1000) and a three-element folding Yagi antennae to home in to exact individual locations. We attempted to locate individuals at least once every 48 h and only during daylight or twilight, due to logistical constraints with operating watercraft at night. Muskrats are generally crepuscular and our sampling timeframe likely underestimated the spatial extent of actual muskrat home ranges. Once located, we recorded locations of individuals using a handheld GPS (Garmin GPSMAP 64), documented mortality status (alive or dead) and identified structure use (i.e. beaver lodges/dams and muskrat huts). We attempted to retrieve and assess cause-specific mortality as soon as possible when a mortality sensor was activated. Muskrats suspected to have died from translocation-related stress were included in our analyses (n = 4). This information was important to assess the feasibility of translocation efforts and censoring those data would potentially bias our results and inference.

Analyses

Prospecting period and home range estimation

Similar to Woodford et al. (2013), we determined the end of an individual's prospecting period and subsequent establishment of a home range when four consecutive locations occurred within the approximate size of the average muskrat home range (2.9 ha, Marinelli and Messier 1993). We used space-use data from individuals tracked consistently throughout their respective prospecting period to calculate average duration of prospecting (n = 28; 2018 = 6 [5 male, 1 female], 2019 = 22 [14 male, 8 female]). Movements during a prospecting period generally do not reflect normal habitat-use decisions (Villasenor et al. 2013, Lehrer et al. 2016, Berger-Tal et al. 2019). Thus, we did not include locations collected during individuals' prospecting period in home-range size estimations. We estimated home-range sizes for all translocated muskrats with ≥ 20 post-prospecting period locations (n = 26; male = 17, female = 9, Ahlers et al. 2010a). Due to small per capita sample sizes for locations in 2018 ($\bar{x} = 12.4$ locations, range = 5–19 locations), we only used data from muskrats in 2019 to estimate home-range sizes. We estimated 95% home-range sizes from kernel density estimates (KDE) using an Epanechnikov kernel and individual reference bandwidths with package 'adehabitatHR' in

Figure 2. Soft-release shelter used to release translocated muskrats *Ondatra zibethicus* into wetlands in Voyageurs National Park near International Falls, MN, USA during summer 2019. Shelters included a detachable lid (a) and a 15 cm hole cut on the side (b) so muskrats could move freely in and out of the shelter. Shelters were affixed to floating rafts (c) and tethered to emergent vegetation (d). We partially filled shelters with local vegetation prior to releasing a muskrat inside.

R ver. 3.6.2 (Calenge 2006). We tested for sex-specific differences in home-range sizes using a t-test and the duration of prospecting time using a Mann–Whitney U-test in R base package (Zar 2010, Woodford et al. 2013). We established an a priori cutoff for significant effects at $p = 0.05$.

Homing analysis

We investigated if post-translocation movement trajectories oriented back to initial capture locations (i.e. homing behavior). We used all individuals with ≥ 5 locations (n = 42; 2018 = 10, 2019 = 32) to calculate average post-translocation movement trajectories from release sites to individual's home ranges or last known location. We measured travel routes of individuals using the point-to-line tool and then fitting a line to the route using the linear-directional-mean tool in ArcMAP. We plotted all muskrat trajectories respective to their capture location (Lehrer et al. 2016), where 0° represented individual capture locations (as opposed to north). We used a V-test (Oriana ver. 4.02) to test if there was a difference in mean movement trajectories away from 0° (original capture location) and calculated the r vector (scaled from 0 to 1) to measure concentration of all trajectories (n = 42) around their mean (Landler et al. 2018).

Post-translocation movement analysis

To quantify distances traveled during prospecting periods, we measured Euclidian distance (km) from individuals' release sites to the center of their 95% home range. If a home range was not established for an individual (either died or was lost during the prospecting period), we measured this distance from their release site to last known location. If an individual established a home range, but lacked sufficient locations for home-range estimation (< 20 locations), we measured the Euclidian distance to the geographic center of the post-prospecting period location cluster. Assuming that movement routes of muskrats followed a Euclidian trajectory is likely unrealistic (i.e. requiring them to move freely through upland landscape) so we also estimated a meandering distance using similar methods described above. Using the linear-measurement-tool in ArcMAP we measured the most parsimonious route for individuals assuming they would preferentially move (using the most direct route) through wetland habitats (Ahlers et al. 2010a, 2015). We estimated individual travel routes using satellite imagery, concentrating movements along shorelines and shallow to deep-marsh habitats, while maintaining the most direct route of travel. We used Mann–Whitney U-tests to investigate potential sex- and year-specific differences in both estimates of post-translocation movement distances.

Survival analysis

We used known-fate models with a staggered entry design to estimate weekly post-translocation survival probabilities (Program MARK ver. 9.0; White and Burnham 1999). We chose to report weekly survival estimates, rather than annual survival estimates, because we did not track muskrat survival in winter months, a known bottleneck period for muskrat populations (Errington 1963, Thurber et al. 1991). We structured models using five covariates hypothesized as important for muskrat survival including sex (male or female), year (2018 or 2019), tail index (TailID), beaver lodge-use (Lodge) and prospecting status (Prosp). Muskrats store fat reserves within their tails, thus tail size may be an indicator of overall body condition (Aleksiuk 1970, Hickman 1979, Smith and Jenkins 1997). We derived a muskrat 'tail index' by modifying a similar index developed for beavers (Smith and Jenkins 1997). We first calculated tail size, X, for the ith individual as:

$$X_i = \frac{\bar{X}_w}{L}$$

where $\bar{X}_w$ = the mean horizontal width (mm) of the tail derived from three measurements evenly spaced along the length (base, middle and 1 cm from the tip); and L = the length (mm) of the tail (base to tip). We then derived a tail index, Z, for the ith individual as:

$$Z_i = \frac{\left(X_i - \bar{X}\right)}{S}$$

where $\bar{X}$ = mean tail size for all muskrats (n = 65); and S = standard deviation of $\bar{X}$.

We developed a time-varying covariate representing an individual's use of a beaver lodge at least once during a given week (Lodge; 1 = ≥ 1 location recorded in a beaver lodge during a given week, 0 = no locations recorded in a beaver lodge during a given week). We determined an individual was located in a beaver lodge when we recorded their exact location using homing techniques. Three muskrats used beaver dams during a portion of our study and we categorized their use of these structures as lodge use. We developed an additional time-varying covariate representing if an individual exhibited prospecting behavior during a given week (Prosp; 1 = muskrat located during prospecting period, 0 = muskrat located after establishing a home range). We acknowledge these are coarse estimates of beaver-lodge use and prospecting behavior, and location data on a finer temporal scale would likely reveal more precise activity patterns and their subsequent effects on survival.

We estimated survival over a 69 week period (2 July 2018–24 October 2019) as a single muskrat marked in 2018 was relocated in 2019. We only monitored muskrats from July–November 2018 and June–October 2019; therefore weekly survival estimates only reflect survival during those two periods. Individuals that we were unable to relocate due to transmitter failure or movement outside of the study area were censored from the analyses. We created 11 a priori models to estimate weekly survival of translocated muskrats. To prevent over-parameterization of models we restricted the maximum number of parameters per model to ≤ 4 (Burnham and Anderson 2002). Models included single effects (Year; Lodge; Prosp; Sex; TailID), additive effects (Lodge + Year; Lodge + Prosp + Year; Prosp + Year; Lodge + Prosp), potential interactions between beaver-lodge use and prospecting behavior (Lodge + Prosp + Lodge × Prosp), and a null model (intercept only). We used a logit-link function to express weekly survival probability as a continuous function of our covariates. We assessed support for models using Akaike's information criterion corrected for small sample sizes (AIC_c) and based all inferences on our most-supported model.

We considered models with $\Delta \mathrm{AIC}_c$ of ≤ 2.00 as competitive (Burnham and Anderson 2002). Covariates that failed to improve model fit (ΔDeviance) when included in a model were considered uninformative (Burnham and Anderson 2002, Arnold 2010). We used our most-supported model to derive estimates of weekly survival probabilities in Program MARK.

Results

We marked and translocated 65 adult muskrats (2018 = 23, 2019 = 42), of which 48 were male (2018 = 18, 2019 = 30) and 17 were female (2018 = 5, 2019 = 12). We relocated post-translocated muskrats with VHF telemetry 1451 times, yielding an average of 22.3 locations per individual (SE = 2.23). We tracked each muskrat an average of 73 days (2018 = July 2–November 5; 2019 June 1–October 24) and 17 individuals retained active transmitters by the end of our yearly monitoring periods (2018 = 3, 2019 = 14). The average duration of prospecting period was 8.4 days (SE = 1.16 days). There was no difference in duration of prospecting period between males ($\bar{x}$ = 9.3 days, SE = 1.58 days) and females ($\bar{x}$ = 6.4 days, SE = 1.29; U = 62, p = 0.34) or between years (2018 = 8.5, SE = 2.25 days; 2019 = 8.4, SE = 1.37 days; U = 69.5, p = 0.72). Through our remote camera surveys and telemetry efforts we observed muskrats frequently using soft-release structures immediately after release but none were observed using the structures > 24 h post-translocation.

Most muskrats did not exhibit post-translocation homing behavior (r vector = 0.18, U = 1.32, p = 0.09; Fig. 3) although only ~15% of muskrats (n = 10) remained within their assigned release wetlands for the duration of the study. Mean post-translocation Euclidean and meandering movement distance was 2.17 km (SE = 0.30 km) and 2.69 km (SE = 0.37 km), respectively. Post-translocation movement distances did not differ between males (Euclidean = 2.31 km, SE = 0.38 km; meandering = 2.85 km, SE = 0.47 km) and females (Euclidean = 1.74 km, SE = 0.31 km; meandering = 2.16 km, SE = 0.39 km; U = 154, p = 0.87 and U = 156.5, p = 0.93, respectively, for Euclidean and meandering distances). Post-translocation movement distances for pooled sexes differed between years for both Euclidean (2018 = 1.14 km, SE = 0.33 km; 2019 = 2.50 km, SE = 0.37 km; U = 86, p = 0.02; Fig. 4a) and meandering distance metrics (2018 = 1.42 km, SE = 0.49 km; 2019 = 3.09, SE = 0.44 km; U = 84, p = 0.03; Fig. 4b).

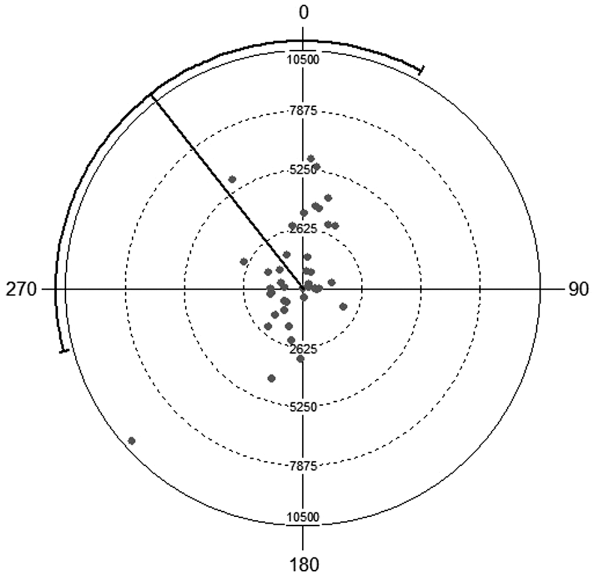

Figure 3. Post-translocation movement distances (m) and trajectories (0–360°) for radiomarked muskrats *Ondatra zibethicus* (n = 42) scaled to their individual capture locations (0°). Muskrats were live-trapped and translocated into wetlands in Voyageurs National Park near International Falls, MN, USA during summers of 2018 and 2019. The center of the figure represents individual release locations, grey circles represent individual travel distances (m) and trajectory (°), bold lines represent the mean trajectory for all individuals along with the 95% confidence interval.

We estimated post-translocation home-range sizes for 26 muskrats translocated in 2019 (average 37 locations per muskrat; SE = 1.53). Average home-range size was 2.52 ha (SE = 0.44 ha). There was no statistical difference between male ($\bar{x}$ = 2.53 ha, SE = 0.58 ha) and female ($\bar{x}$ = 2.50 ha, SE = 0.71 ha, t = −0.03, p = 0.98) post-translocation home-range sizes.

We observed 23 mortalities (2018 = 11, 2019 = 12), of which four were predation events (American mink [n = 3] and bald eagle [n = 1]). We recovered four additional carcasses without obvious signs of predation, trauma or disease and subsequent necropsy results were inconclusive. For the remaining 15 mortalities, we only recovered transmitters with minimal evidence at the site that limited our ability to characterize cause of mortality. We were unable to successfully relocate nine individuals > 1 time after release (2018 = 4, 2019 = 5) despite extensive searching-likely because transmitters failed or were submerged in deep water after the mortality occurred. Our top ranked and most-supported model (Lodge + Year), indicated that muskrats that used beaver lodges were 7.69 times more likely to survive (S = 0.99, SE = 0.01) than those that did not (S = 0.95, SE = 0.01; β = 2.04, SE = 1.03; Fig. 5a). Additionally, muskrats tracked in 2019 had 4.18 greater odds of survival (S = 0.97, SE = 0.01) than in 2018 (S = 0.88, SE = 0.03; β = 1.43, SE = 0.44; Fig. 5b). Weekly survival probabilities were greater if muskrats used beaver lodges (2018, S = 0.98 [SE = 0.02]; 2019, S = 0.99 [SE = 0.004]) than if they did not (2018, S = 0.88 [SE = 0.03]; 2019, S = 0.97 [SE = 0.01]). Our second-ranked model included the covariate 'Prosp' (Table 2). However, the inclusion of 'Prosp' did little to improve model fit (ΔDeviance between models = 0.24) suggesting this effect was spurious.

Discussion

Translocated muskrats moved relatively long distances in the hydrologically-connected lacustrine ecosystems of our study area. Although translocation is not biologically similar to dispersal, it is plausible that individual movement decisions during post-translocation prospecting periods may be similar to movement decisions during dispersal. Errington (1940, 1963) reported long-distance movements (5–30 km) by muskrats between isolated wetland complexes in

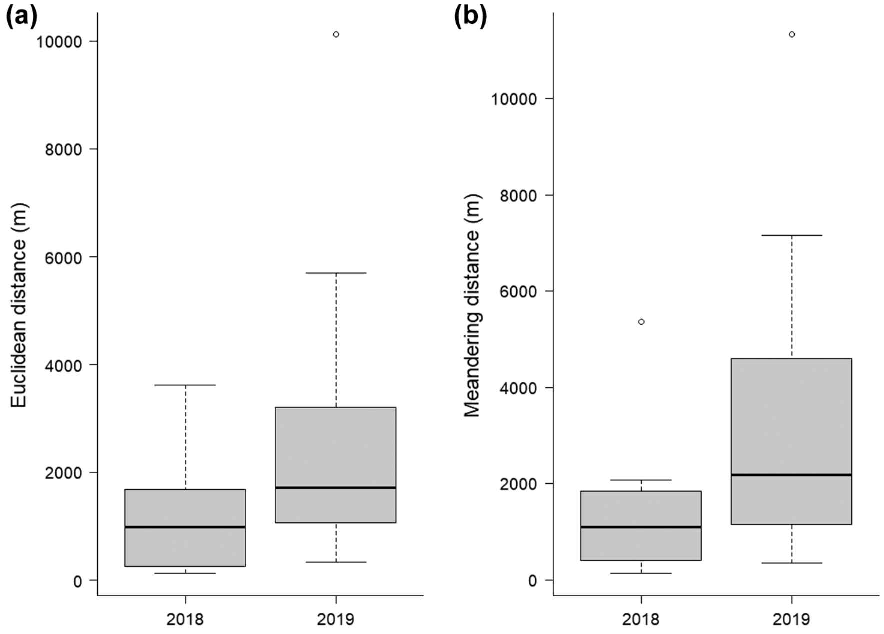

Figure 4. Annual differences in median post-translocation Euclidean (a) and meandering (b) distances moved by radiomarked muskrats *Ondatra zibethicus* (n = 42). Muskrats were live-trapped and translocated into wetlands in Voyageurs National Park near International Falls, MN, USA during summers of 2018 and 2019. Bold lines represent median values, boxes represent the interquartile range, whiskers represent minimum and maximum values exclusive of outliers, and circles represent outliers.

agroecosystems. Laurence et al. (2013) found genetic connectivity of muskrat populations in a boreal ecosystem was negatively influenced by open landscapes and forests in uplands surrounding wetland environments. While we did detect muskrats moving to interior wetlands hydrologically connected to the main lake, we did not observe individuals colonizing hydrologically isolated, interior wetlands likely due to impermeability of surrounding upland landscapes. We did observe translocated muskrats swimming across wind-exposed, deep-lake habitats (> 5 m depth), to establish home ranges. Recent evidence, however, suggests site colonization by muskrats was negatively influenced by greater amounts of fetch present in lacustrine wetlands (Larreur et al. 2020). We recommend future research use molecular tools to empirically assess the relative permeability of fetch-affected waterscapes for dispersing muskrats.

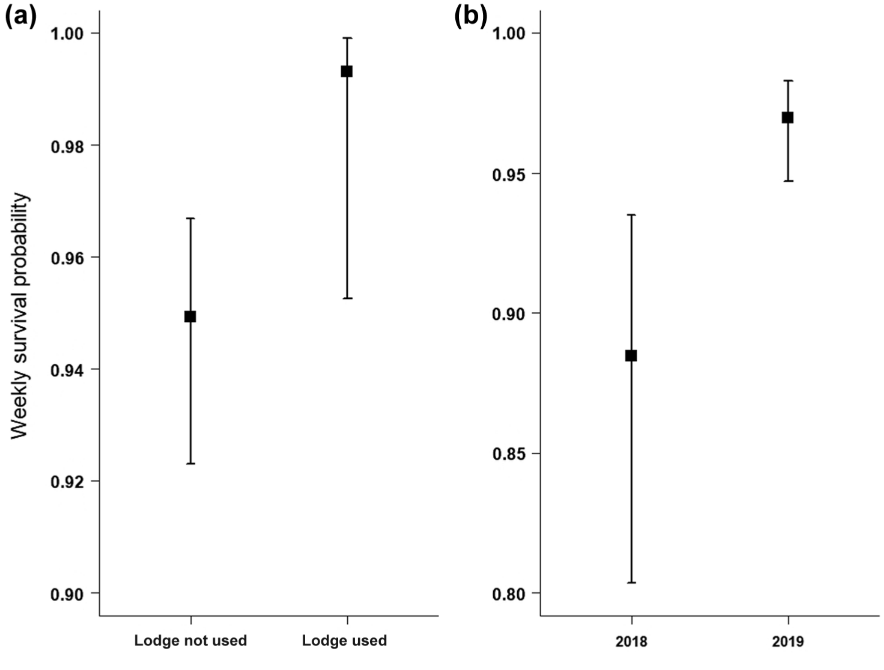

Figure 5. Post-translocation known-fate weekly survival probabilities (and 95% CIs) for adult muskrats *Ondatra zibethicus* (n = 65) derived from the top-ranked model including beaver *Castor canadensis* lodge use (a) and year (b). Muskrats were live-trapped and translocated to wetlands in Voyageurs National Park near International Falls, MN, USA during summers of 2018 and 2019.

Table 2. Known-fate model selection results describing post-translocation weekly survival of muskrats *Ondatra zibethicus* (n = 65) in Voyageurs National Park, MN, USA, during summers 2018 and 2019. Models were ranked by differences in Akaike's information criterion corrected for small sample sizes (ΔAIC_c). *w* = model weight, K = number of parameters within the model, Deviance = −2log ([$\log_e$ likelihood of the model] − [$\log_e$ likelihood of the saturated model]). Explanatory variables include Lodge (time-varying covariate indicating if a muskrat was located in a beaver *Castor canadensis* lodge during a given week), Year (2018 or 2019) and Prosp (time-varying covariate indicating that an individual was prospecting during a given week). We only present models with $\Delta AIC_c \leq 2.00$ along with the null model for comparison.

Model	ΔAIC_c	ω	K	Deviance
Lodge + Year	0.00	0.63	3	178.41
Lodge + Year + Prosp	1.79	0.26	4	178.17
Year	5.10	0.05	2	185.53
Year + Prosp	6.28	0.03	3	184.69
Lodge	7.90	0.01	2	188.33
Lodge × Prosp	8.69	0.01	4	187.10
Lodge + Prosp	8.81	0.01	4	187.23
Prosp	15.51	0.00	2	195.93
Null	16.66	0.00	1	199.10
Sex	18.45	0.00	2	198.88
TailID	18.60	0.00	2	199.03

Translocated muskrats did not exhibit homing behavior though most did not remain in their initial release site. Significant variation in post-translocation movement trajectories supports our hypothesis that muskrat movements would not orient back to their original capture locations. Although the 95% confidence interval of our v-test encompassed 0°, a low r-vector value (0.18) and wide confidence intervals were likely a result of significantly dispersed movement trajectories (i.e. mean trajectories were not directional; Landler et al. 2018). In these cases, Landler et al. (2018) cautioned against relying on confidence intervals to draw inference. Additionally, muskrats moved longer distances than we anticipated given their size and surrounding landscapes. Animals translocated using soft release techniques generally move short distances post-translocation and are more likely to establish territories at their release sites (Tetzlaff et al. 2019). We observed significantly larger movement distances in 2019 that may reflect our larger sample size in that year or unnoticed changes in muskrat abundances near the release sites. Errington (1963) reported muskrats moving longer distances (up to 34 km) in response to adverse conditions such as freezing, drought and high population densities.

Past studies used widely different estimation techniques to characterize muskrat home ranges (Errington 1939, Sather 1958, MacArthur 1978, 1980, Proulx and Gilbert 1983, Ahlers et al. 2010a, Ganoe et al. 2021) making direct comparisons to our results difficult. However, our home-range size estimates of post-translocated muskrats were similar to those of muskrats in a Saskatchewan prairie marsh estimated using minimum convex polygons (Marinelli and Messier 1993). Anecdotally, average home-range size of translocated muskrats was similar to that of three resident muskrats (muskrats radiomarked in our study area but not translocated; $\bar{x} = 3.66$ ha, SE = 2.99) in our study system. We acknowledge that our home-range size estimates were likely underestimated as we only relocated muskrats during daylight and crepuscular hours when muskrats are more likely to be resting and less likely to be active (O'Neil 1949). Muskrats established home ranges ~8 days after translocation though this estimate was likely overestimated as we only relocated individuals every ~48 h and our methodology required four consecutive locations within a 2.9 ha area to define home-range establishment. Because muskrat densities appeared relatively low in release wetlands, translocated muskrats likely located and established home ranges in a relatively short amount of time. We observed translocated muskrats constructing huts and improving unoccupied beaver lodges soon after establishing home ranges. These observations underscore muskrats' plasticity to adapt and establish populations in novel environments. Due to the limited battery life of transmitters (~180 days) and seasonal weather constraints in our study area, we were unable to assess long-term muskrat home-range dynamics and structure use.

Survival probabilities of post-translocated muskrats were similar to other studies of resident muskrat populations (Proulx and Gilbert 1983, Clark 1987, Clark and Kroeker 1993, Kanda and Fuller 2004, Ahlers et al. 2010b, Ganoe et al. 2021). Weekly muskrat survival was greater in 2019, suggesting soft-release techniques (only used in 2019) enhanced post-translocation survival probabilities. We acknowledge, however, that since soft-release techniques were only implemented in 2019 we cannot separate this effect from other unmeasured or confounding effects that may have occurred between years. Further, we observed increased use of beaver lodges by muskrats from 2018 (n = 3 [~13%]) to 2019 (n = 18 [~43%]) which may have contributed to yearly differences in survival. Nonetheless, soft-release techniques can improve species' survival and enhance individuals' acclimation to novel areas (Teztlaff et al. 2019). Additionally, the use of soft-release structures are common for species that use burrows (Jachowski and Lockhart 2009) or cavities (Woodford et al. 2013). Soft-release structures mimic natural dwellings and, in some cases, serve as long-term surrogates in the absence of natural dwellings (McComb and Noble 1981, Truett et al. 2001), thereby increasing establishment success in novel environments. Subsequent muskrat translocation efforts may benefit from incorporating similar soft-release techniques into management plans, though additional research is needed to assess this specific effect.

As expected, translocated muskrats that used beaver lodges had greater weekly survival probabilities. Moving through unfamiliar landscapes is inherently risky due to predation risk, competition with conspecifics and lack of refugia (Waser 1985, Yoder et al. 2004, Berger-Tal et al. 2019). Muskrats rely on huts and burrows for shelter (Errington 1963, Hazard 1982) and granite bedrock shorelines in VNP preclude burrow construction. Muskrats without shelter will likely rest in exposed areas or search until a shelter is located or constructed, exposing them to increased predation risk. Beavers, and beaver lodges, are ubiquitous throughout the Greater Voyageurs Ecosystem as VNP hosts the greatest beaver densities in the United States (Johnston and Windels 2015). Beaver lodges likely serve as temporary refugia for muskrats during their prospecting periods and may provide stepping-stone resources during dispersal. Although muskrat use of beaver lodges is well documented (Leighton 1933, Rosell et al. 2005, Mott et al. 2013, Windels 2017), ours is the first study to reveal the fitness benefits conferred to individual muskrats using these structures. Although we used a coarse estimate of beaver-lodge use by muskrats, the effect was large enough for us to detect in our survival analyses. Nonetheless, our results enhance the evidence that beavers provide critical ecosystem benefits for sympatric wetland fauna (Nummi and Holopainen 2014, Pollock et al 2014, Law et al. 2016, 2017, Windels 2017). We encourage additional research to evaluate the relative contribution of beaver lodges to muskrat population growth in wetlands with dynamic water levels or in regions with extreme winter temperatures.

The long-term and widespread decline of muskrat populations necessitates active management efforts, such as translocations, to restore and enhance population abundances across their native range. Our research suggests that survival and spatial ecology of translocated muskrats are similar to resident muskrat populations (Clark 1987, Clark and Kroeker 1993, Kanda and Fuller 2004, Ahlers et al. 2010b, Ganoe et al. 2021). However, assuming that translocated muskrats will remain in discrete target wetlands in hydrologically-connected systems was unrealistic. For muskrat translocation efforts to be successful in lacustrine systems, we suggest managers designate larger geographic areas as targets for population restoration efforts rather than discrete, hydrologically connected wetlands. In addition, we recommend efforts focus on areas with established beaver populations, while using soft-release techniques, to improve post-translocation survival probabilities and increase the likelihood of population persistence. We also encourage future research regarding the feasibility of muskrat translocations focus on geographically isolated wetland complexes in other parts of their native range (i.e. prairie potholes, Nebraska sandhill wetlands and coastal plains ponds; Tiner 2003).

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Survey of Toxoplasma gondii Exposure in Muskrats in a Relatively Pristine Ecosystem

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SURVEY OF *TOXOPLASMA GONDII* EXPOSURE IN MUSKRATS IN A RELATIVELY PRISTINE ECOSYSTEM

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KEY WORDS

Muskrats
Toxoplasma gondii
Voyageurs National Park
Watershed Health
Wildlife Disease

ABSTRACT

Waterborne transmission of *Toxoplasma gondii* is assumed to be enhanced in areas with human-altered landscapes (e.g., urbanization, agriculture) and increased populations of non-native domestic and feral cats (*Felis catus*). However, little is known concerning *T. gondii* exposure risks in more natural watersheds (e.g., reduced human footprint, no domestic or feral cats) to establish a baseline for comparisons. In this study, muskrats (*Ondatra zibethicus*) were used as sentinels to assess baseline *T. gondii* exposure in a relatively pristine watershed in the Greater Voyageurs Ecosystem, northern Minnesota, during the summers of 2018–2019. *Toxoplasma gondii* antibodies were assayed in sera of live-trapped muskrats ($n = 70$) using a modified agglutination test. None of our samples were positive for *T. gondii* antibodies ($P = 0.00$, 95% Wald Score Confidence Interval = 0.00–0.05). This study establishes a baseline to compare *T. gondii* waterborne transmission risks in other human-modified watersheds.

Toxoplasma gondii is a protozoal parasite that poses human- and animal-health risks (Dubey, 2010; Hill and Dubey, 2013; Torrey and Yolken, 2013) although most *T. gondii* infections are subclinical. Infected humans can exhibit modified behaviors (Flegr, 2013) and have greater risks for neurological disorders (Kusbeci et al., 2011; Webster, 2013) and death (Mboera et al., 2019). *Toxoplasma gondii* infection in wildlife and domestic animals can result in clinical disease (Calero-Bernal and Gennari, 2019) and mortality (e.g., Kreuder et al., 2003; Kumar et al., 2019). The only definitive hosts of *T. gondii* are felids (Family: Felidae), who can introduce *T. gondii* into the environment via oocysts in their feces. Subsequent infection in humans, wildlife, and domestic animals can occur by incidental ingestion of *T. gondii* oocysts or by consuming tissue stages occurring in a host.

Transportation of *T. gondii* oocysts from terrestrial areas to aquatic habitats is a growing concern (Miller et al., 2002; Conrad et al., 2005; Jones and Dubey, 2010; Shapiro et al., 2019). Contaminated water runoff has been linked to some *T. gondii* infection in humans (Bowie et al., 1997; de Moura et al., 2006; Palanisamy et al., 2006) and reduced survival of southern sea otters (*Enhydra lutris nereis*; Kreuder et al., 2003). Sea otters with *T. gondii* encephalitis were 3 times more likely to be killed by sharks and were also more likely to die of cardiac disease (Kreuder et al., 2003). Semiaquatic mammals, including muskrats (*Ondatra zibethicus*), likely encounter *T. gondii* oocysts from contaminated runoff entering the watershed (Ahlers et al., 2015b). Wetland loss and degradation, intensive agriculture, and urbanization can facilitate the transport of *T. gondii* oocysts from terrestrial to aquatic areas (Shapiro et al., 2010; Ahlers et al., 2015b). Additionally, the presence and abundance of non-native domestic and feral cats can increase infection risks in wildlife species occurring in natural areas (Fredebaugh et al., 2010).

Although studies have linked environmental changes to higher prevalence of *T. gondii* exposure in aquatic habitats (Shapiro et al., 2010; Ahlers et al., 2015b), it remains unclear what baseline *T. gondii* exposure risks are in more natural watersheds (e.g., watersheds not exposed to agriculture, urbanization, non-native felids). Thus, to understand the magnitude of how environmental change can influence *T. gondii* exposure in aquatic systems it is necessary to first establish baseline exposure levels in areas devoid of contemporary landscape changes. Moreover, it is important to assess baseline *T. gondii* exposure in areas with no (or limited) occurrence of domestic cats. To this end, our objective was to assess baseline *T. gondii* exposure in a wetland ecosystem relatively unaffected by landscape change and devoid of domestic cats. Muskrats can be sentinels for waterborne *T. gondii* exposure because they are a wetland obligate species that rarely use upland habitats (Ahlers et al., 2010, 2015a). Muskrats are short-lived (1–3

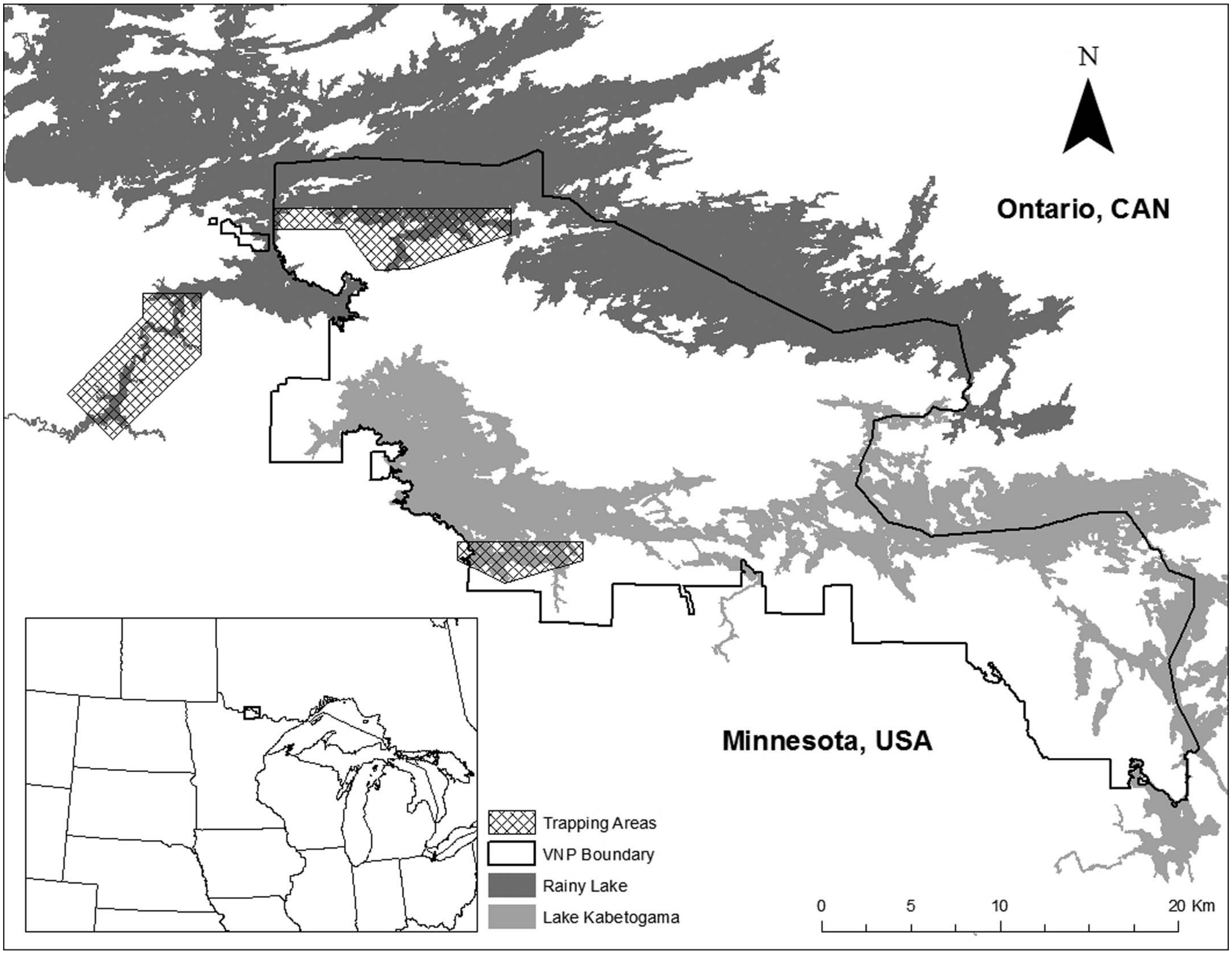

Figure 1. Location of muskrat (*Ondatra zibethicus*) trapping sites within the Rainy Lake and Kabetogama watersheds in and around Voyageurs National Park, International Falls, Minnesota.

yr), and published estimates of *T. gondii* prevalence in muskrats range from 9.1 to 60.0% (Nezval and Literák, 1994 [South Moravia, Czech Republic]; Smith and Frenkel, 1995 [Kansas, United States]; Hejlíček et al., 1997 [Strakonice district, Czech Republic]; Ahlers et al., 2015b [Illinois, United States). Like sea otters, another semiaquatic mammal considered sentinels, *T. gondii* infection in muskrats likely occurs via waterborne transmission (Ahlers et al., 2015b).

This study occurred in the Greater Voyageurs Ecosystem located in and around Voyageurs National Park (VNP; 88,220 ha; 48°30′01″N, 92°50′01″W), Minnesota, during the summers of 2018–2019 (Fig. 1). Voyageurs National Park is located at the lower end of the 38,600 km^2 Rainy Lake Watershed and is a relatively pristine ecosystem, and <1% of the park has been affected by anthropogenic disturbance since the park's establishment in 1975 (Kallemeyn et al., 2003). Timber harvest occurs in public and private lands outside of VNP along with minimal human settlement or development (Kirschbaum and Gafvert, 2017). Parks and designated wilderness areas make up 25% of the Rainy Lake Watershed upstream of VNP (Kallemeyn et al., 2003), including the Boundary Water Canoe Area Wilderness (4,387 km^2) in Minnesota and Quetico Provincial Park (4,788 km^2) in Ontario, Canada. Domestic cats were not observed in the VNP area despite >22,000 trap-nights of remote camera monitoring from 2007 to 2017 (0.0% of 2,839 detections of carnivores; S. Windels, Voyageurs National Park, unpubl. data). Native felids (potential definitive hosts for *T. gondii*) occurring within VNP included bobcat (*Lynx rufus*; 0.4% of total detections) and Canada lynx (*Lynx canadensis*; 0.2% of total detections). There are no published estimates of *T. gondii* prevalence in native felids within our study area. However, Verma et al. (2016) detected *T. gondii* antibodies in 29 of 50 bobcats that were harvested in northern Minnesota.

We leveraged samples collected from muskrats used in a concurrent study in the region and who were candidates for internal VHF radio-transmitter implants. Because our sample sizes were constrained by the number of adult muskrats needed for that study, and this particular study was designed as a baseline survey, we did not calculate the minimum sample sizes needed for statistical inference a priori. Muskrats were live-trapped in lacustrine wetlands positioned in the Rainy Lake and Lake Kabetogama watersheds (Fig. 1) using baited traps (Tomahawk® 202, Hazelhurst, Wisconsin) attached to floating platforms. Muskrats are multiple central-place foragers and concentrate their space-use in and around feeding platforms and huts (Ahlers et al., 2010). Thus, we focused all trapping efforts around and near areas with fresh muskrat signs (e.g., huts, clippings). Traps were checked every morning, and we immediately transported captured muskrats to a surgical laboratory (~1–2 hr). Muskrats were sedated with a combination of dexmedetomidine (0.02–0.025 mg/kg; Pfizer, New York, New York) and midazolam (1 mg/kg; Hospira, Lake Forest, Illinois) and maintained on surgical anesthesia using isoflurane (2%, Piramal Enterprises, Mumbai, India) gas anesthesia via a mask (for detailed immobilization methods, see Ahlers et al., 2011). Individual muskrats were monitored throughout all procedures by trained veterinarians (T. Wolf and O. Aarrestad). Once anesthetized, we collected blood (1.5 ml) via the cranial vena cavae (25-ga needle affixed to a 3-ml syringe). We implanted radio transmitters (13 g), allowed muskrats to recover from anesthesia (3–6 hr), and released them back into wetlands in VNP. We sampled 70 adult muskrats (male = 51, female = 19) during 2–6 July 2018 (n = 20) and 1–7 June 2019 (n = 50). We sampled only adults because they were the target age group for the concurrent study and because they were the age group most likely infected (Ahlers et al., 2015b).

A modified agglutination test (MAT) was used to identify *T. gondii* antibodies in muskrat serum samples. Although test sensitivity and specificity have not been estimated for muskrats, multiple methods have been used to characterize test performance, with sensitivity estimated to range 80.9–83.6% and specificity 89.3–91.9% (Gardner et al., 2010). Assessing MAT across many species suggests that a titer of 25 indicates exposure to *T. gondii* (Dubey, 2010), and MAT has been used to establish *T. gondii* exposure in muskrats occurring in human-modified ecosystems (Ahlers et al., 2015b). We used a 1:25 dilution, similar to Ahlers et al. (2015b), and considered reactive sera positive for *T. gondii* antibodies (Dubey, 2010). *Toxoplasma gondii* antibodies were not detected in any of our samples ($P = 0.00$, 95% CI = 0.00–0.05).

These results concur with past research and suggest that *T. gondii* exposure risks for semiaquatic mammals may be reduced in relatively pristine watersheds (e.g., devoid of agriculture, urbanization, non-native felids). Additionally, even when considering the upper ranges of our 95% confidence interval ($P = 0.00$, 95% CI = 0.00–0.05), this study provides the lowest published estimates of *T. gondii* prevalence in muskrats. This is likely because (1) wetlands and riparian areas within VNP naturally filter *T. gondii* oocysts before reaching the watershed or (2) low densities of feral cats resulted in reduced *T. gondii* oocyst burdens in VNP. Because this study occurred in a region largely unaffected by large-scale landscape changes and with low densities of non-native felids, these results can provide a useful baseline by which to compare *T. gondii* prevalence rates in other aquatic systems.

Potential caveats with this baseline study include that muskrats were not sampled uniformly across VNP, and we did not compare our results from VNP with samples from muskrats occurring in more modified landscapes. Although site-specific (e.g., pristine vs. modified) comparisons were not made, past research suggests that *T. gondii* exposure in muskrats is elevated in human-modified landscapes. Ahlers et al. (2015b) reported the highest known seroprevalence in live-caught muskrats (60%) in a highly modified agroecosystem. They posited that alterations to the landscape (e.g., tile drainage, agriculture) likely facilitated the movement of *T. gondii* oocysts from terrestrial areas, with high densities of domestic cats, to riparian habitats were muskrats occurred. Additionally, Nezval and Literák (1994) found differences in prevalence rates for muskrats occurring in sites polluted with municipal waste (47%) and in slightly polluted sites (9%). Although our moderate sample size and convenience sampling regime used in this correlative study limit our inference, these results provide a meaningful baseline by which to compare *T. gondii* exposure in less-pristine watersheds. Future research should differentiate the relative contributions of domestic cat densities and landscape modification to increased *T. gondii* exposure in aquatic ecosystems.

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RESEARCH ARTICLE

Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species

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Abstract

Context Landscape configuration and composition can influence the spatial distribution of species. Cross-scale interactions may exist when multiscale effects interplay to shape species' distribution patterns.

Objectives We investigated how the spatial distribution of a semiaquatic mammal, muskrat (*Ondatra zibethicus*), is influenced by local-scale resource characteristics. We also assessed how fetch, the unobstructed distance wind can travel across water, influences fine-scale habitat use by muskrats.

Methods We used 2 years of presence-absence surveys (2015–2016) at 71 wetland sites to evaluate the spatial distribution of muskrats in a lacustrine system in Minnesota, USA. We expected site occupancy and colonization to be positively associated with the amount of *Typha x glauca* (a rapidly establishing invasive hybrid cattail species) at sites, and negatively associated with fetch impact, water depths, and open water areas.

Results As expected, sites with greater coverage of *T. x glauca*, shallower water depths, and less open water had greater initial occupancy probabilities. Muskrats were more likely to colonize fetch-impacted sites if there were also greater coverages of *T. x glauca* present.

Conclusion The distribution and intensity of fetch, dictated by the watershed-scale configuration of upland landscapes, influenced site colonization by muskrats. Our results suggest that this landscape-scale effect is mediated by the amount of *T. x glauca* present at much finer scales. This cross-scale interaction may facilitate distribution expansions of wetland-obligate species into otherwise unsuitable habitats.

Keywords Fetch · Habitat use · Invasive species · Muskrat · *Ondatra zibethicus* · *Typha x glauca* · Wetlands

Introduction

Landscape pattern can influence ecological processes (Turner 1989) and their effects can be scale-dependent (Wiens et al. 1987; Turner et al. 1989; Levin 1992). Cross-scale interactions can exist when broad-scale drivers (e.g., regional scale effects) interact among other drivers to shape ecological patterns at much finer spatial or temporal scales (Peters et al. 2007; Heffernan et al. 2014; Soranno et al. 2014). For instance, regional-scale land-use change (i.e., agriculture) can

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mediate the influence that wetlands have on phosphorous concentrations in watershed lakes (Soranno et al. 2014). To better manage complex ecological issues, such as mitigating the landscape-scale effects of invasive species on native biodiversity, practitioners must understand these relationships (Miller et al. 2004).

Wind impact in coastal areas, or 'fetch' (Finlayson 2005; Rohweder et al. 2008), is determined by the unobstructed distance that wind can travel over a landscape. The severity of fetch on a discrete area of coastline is greater where wind can travel longer distances without obstruction. Thus, the configuration of landscapes at large spatial scales can influence fetch impacts at much smaller scales. For instance, the spatial position of islands in the Bearing Sea mediate the effects of wind and structure the distribution of both predators and prey at local scales. Female northern fur seals (*Callorhinus ursinus*) avoid areas exposed to greater wind impacts because prey species in these areas occur deeper in the water column (Mackas et al. 2005; Sterling et al. 2014). Instead, they will utilize areas shielded from greater wind impacts (dictated by the spatial position of marine islands) where prey occur at reasonable foraging depths (Sterling et al. 2014). It is plausible that fetch may affect fine-scale habitat use of wetland-obligate species by disrupting feeding activities, destroying nests or lodges, or precluding movement between resources or suitable habitat patches. However, the influence of this effect on structuring ecological patterns is not well understood.

An invasive hybrid cattail species (*Typha x glauca*; hereafter '*T. x glauca*') has rapidly expanded into wetland ecosystems across the upper Midwest, USA, displacing native vegetation (including native broadleaf cattails, *Typha latifolia*) and reduced the presence and extent of open-water areas (Frieswyk and Zedler 2006; Travis et al. 2010). *T. x glauca* is a hybrid of native broadleaf cattail and invasive narrowleaf cattail (*Typha angustifolia*) and exhibits characteristic attributes of hybrid vigor (e.g., rapidly establishing, can expand into areas typically unsuitable for native species). Areas dominated by *T. x glauca* undergo biotic homogenization and typically have lower macroinvertebrate biomass (Lawrence et al. 2016) and native plant diversity (Lishawa et al. 2010) and increased amounts of organic plant litter (Mitchell et al. 2011). *T. x glauca* can form floating mats and expand into areas where native emergent vegetation cannot typically establish (e.g., deep-water habitats, rocky bottom). The relationship between *T. x glauca* expansions and wetland-obligate species, however, remains unclear.

Our objectives were to understand how the spatial distribution of muskrats (*Ondatra zibethicus*), a freshwater semiaquatic mammal, is influenced by landscape pattern, composition, and local-scale resources. Additionally, we wanted to explore potential cross-scale interactions between fetch and fine-scale habitat use by muskrats. Muskrats are small (1.0–1.5 kg) rodents obligately associated with wetlands. Space use by muskrats is generally restricted to the water or shoreline and movements in terrestrial areas are rare (Ahlers et al. 2010, 2015). They are considered multiple central-place foragers (Ahlers et al. 2010) with regular movements up to 260 m from burrows or huts (Errington 1939; MacArthur 1978, 1980). Muskrats primarily feed on and construct huts (small mounds of vegetation that extend above the waterline where family groups live) with local vegetation (e.g., cattails [Typha spp.] Clark 1994), and occur in wetlands with relatively shallow water depths that can support wetland vegetation growth (Errington 1963). Recent studies focused on muskrat distributions have occurred in riparian habitats in human-dominated landscapes (e.g., Cotner and Schooley 2011; Ahlers et al. 2015; Holland et al. 2019) and may not reflect patterns occurring in lacustrine systems. Muskrat populations appear to be declining across North America (Roberts and Crimmins 2010; Ahlers and Heske 2018) necessitating contemporary investigations of potential distributional constraints across their native range (Ahlers and Heske 2018).

We used 2 years of presence/absence data and a multi-season occupancy modeling approach to assess how the spatial distribution of muskrats is influenced by local and landscape context and also by potential interactions across these scales. Since cattails are important resources for muskrats, we expected site occupancy probabilities and colonization rates would be greater in areas with more *T. x glauca*. We expected that 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. Wetlands positioned in areas exposed to greater fetch impacts may be unfavorable for muskrats due to the negative impacts of wind and wave intensity. We predicted sites exposed to greater fetch impacts would have lower muskrat occupancy probabilities and colonization rates. Additionally, we investigated how the spatial coverage of *T. x glauca* at wetland sites may mediate any potential effects of fetch in these areas.

Methods

Study area

We conducted our study in and around Voyageurs National Park (VNP; 88,220 ha) located near International Falls, Minnesota, USA (48.51896° N, − 92.91938° E; Fig. 1a). This area occurs at the southern edge of the boreal forest region and is characterized by forests (conifer and hardwood) and both lentic and lotic habitats. Annual precipitation averages 66 cm and average temperatures range from − 3.3° to 9.3 °C. We centered our sampling in the Rainy and Kabetogama Lake watersheds which contain ~ 230,000 ha of open water areas (Fig. 1a). This region also has hundreds of small islands and irregular shorelines that influence the distribution and intensity of fetch in wetland areas (Fig. 1a). *T. x glauca* populations have expanded in this region and displaced nearly all native cattail populations (Travis et al. 2011; Windels et al. 2013). The dominant wetland vegetation in our study area was *T. x glauca* but also consisted of wild rice (*Zizania* spp.), common water reed (*Phragmites australis*), arrowhead (*Sagittaria* sp.), water lilies (*Nymphaea* spp. and *Nuphar* spp.), bulrush (*Schohenoplectus acutus*), reed canary grass (*Phalaris arundinacea*), submerged vegetation (*Ceratophyllum demersum*, *Potamogeton* spp., *Myriophyllum* spp.), and various species of sedges (*Carex* sp.).

Sampling design

We used ArcMap 10.5 (ESRI 2017) and a digitized vegetation map (30 m raster; adapted from the National Vegetation Classification System; Faber-Langendoen et al. 2007) to identify lacustrine wetland areas in VNP. We randomly selected 71 points within these wetlands and delineated our sampling sites (100 m × 200 m; 2 ha) centered on these points (Fig. 1a). Sampling sites were smaller than average muskrat home ranges (MacArthur 1978, 1980) and reflect local-scale habitat use. Sites were separated by an average Euclidian distance of 1247 m (SD = 377 m) and considered spatially independent. Water depths varied among sites (mean = 0.54 m: 2016 range 0.03–3 m: 2017 range 0.05–2.06 m).

We surveyed for the presence/absence of muskrats at 71 sites from 07 June to 12 August 2016 and at 69 sites from 05 June to 28 July 2017. We employed two survey methods (walking surveys and floating raft surveys) to assess site occupancy by muskrats. For walking surveys, two observers systematically searched the area within the boundaries of each site for muskrat sign (e.g., tracks, scat, huts, clippings, or animal). Each site was visited twice each year and observers used a combined survey effort during each site visit. Thus, we considered each site visit one independent survey (two surveys per year). We conducted both site visits within seven days to ensure population closure (MacKenzie et al. 2017). Three observers conducted walking surveys between 2016 and 2017, and 1 observer (ML) participated in all surveys. Average survey time at each site was ~ 30 min.

In conjunction with walking surveys, we conducted floating raft surveys (hereafter ‘rafts’). Rafts use a clay/sand tracking medium to capture tracks of animals walking across them and have been used to document habitat use by American mink (*Neovison vison*) in North America and Europe (Reynolds et al. 2004; Schooley et al. 2012). We constructed rafts by securing 6-mm, rectangle plywood sheets (122 cm × 61 cm) to the top and bottom of a 32-mm polystyrene sheet (122 cm × 61 cm) with six evenly spaced carriage bolts. We positioned a plastic basket (27 cm × 20 cm × 4 cm) filled with floral foam into a cut-out portion in the center of the raft such that the top of the basket was flush with the surface of the raft. We 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 and maintained a viable clay/sand tracking surface. We covered the tracking surface with a 3-pannel, plywood tunnel to prevent clay from washing away via rain or waves. For a detailed description of raft construction, see Reynolds et al. (2004). We camouflaged unbaited rafts with local vegetation and tethered with a nylon rope to nearby cattails or other sturdy vegetation.

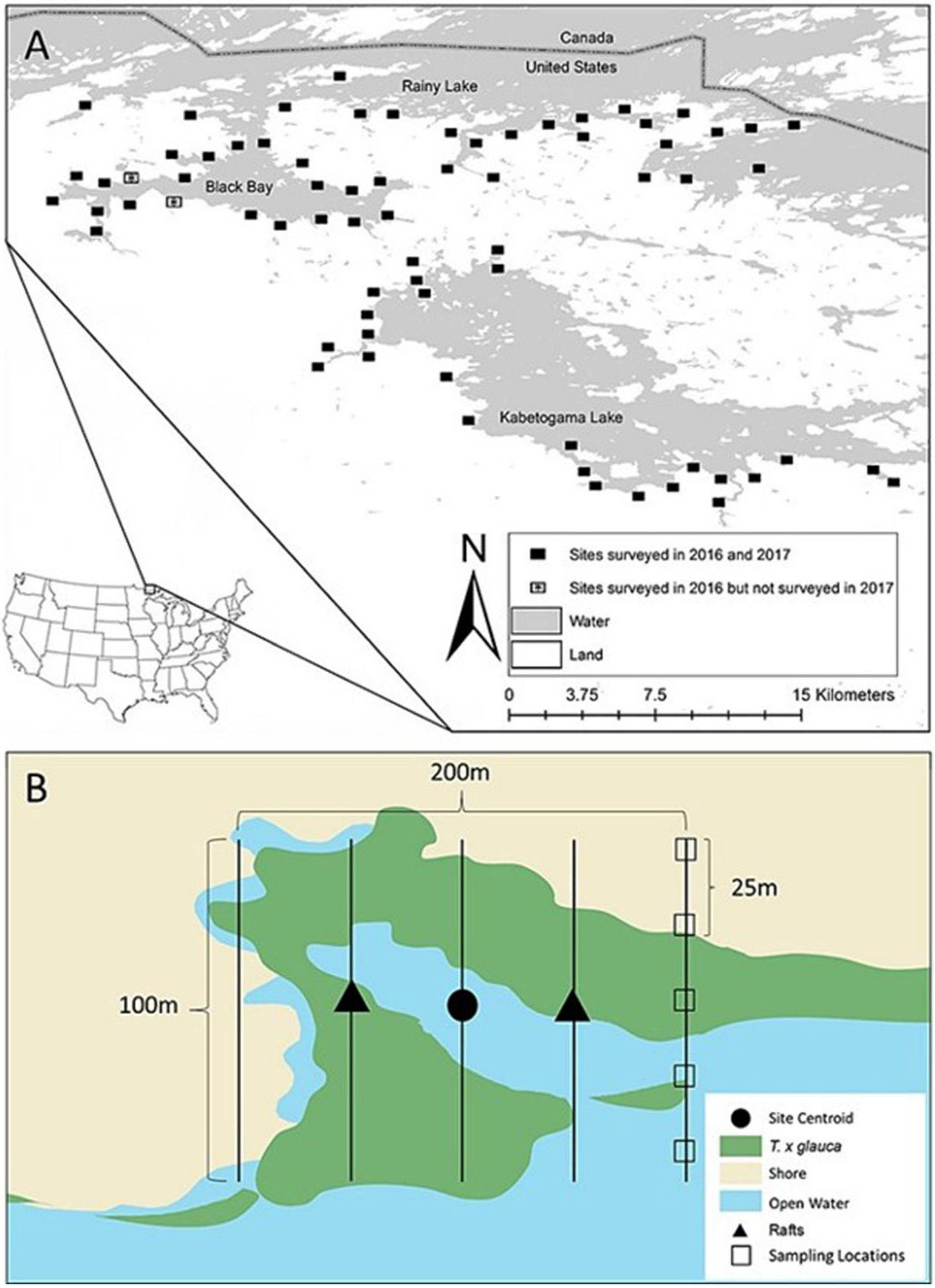

Fig. 1 Distribution of wetland sites (n = 71) used to assess site occupancy by muskrats (*Ondatra zibethicus*) within Voyageurs National Park in International Falls, MN during summers of 2016–2017 (**a**). Schematic of our sampling sites (200 m × 100 m) including transects (vertical lines), habitat-sampling points (open squares), and position of floating rafts (black triangles) (**b**)

We positioned two rafts 100-m apart and centered them within each site (Fig. 1b). We checked rafts for muskrat sign (e.g., scat, clippings, feeding stations, tracks) 7 days after securing them at a site (1st survey). We rechecked rafts after an additional 7 days (2nd survey) resulting in two primary surveys for each site. Both primary surveys for rafts occurred during the same weeks as walking surveys. For each site, our detection histories included two independent walking surveys and two independent raft surveys per year. We considered a site occupied by muskrats during a given year if we found muskrat sign on at least 1 raft or during at least 1 site visit.

Wetland characteristics

We measured habitat characteristics at each site immediately following the first site visit each year. At each site, we established five parallel transects spaced 50-m apart and measured habitat characteristics at five evenly spaced positions along each transect (Fig. 1b). We estimated the percent *T. x glauca* coverage (Typha), open water, and emergent vegetation (Total Emergent) at each position along transects using a 1 m × 1 m Daubenmire frame. At each position, we also measured water depth (m). We 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 we used a principal components analysis (PCA: SAS Institute Inc. 2017) to construct a composite variable (water depths and open water) using the first eigenvector (Water).

We used the Fetch Analysis Tool in ArcMap 10.5 (ESRI 2017) to quantify the impact of wave fetch (m) in VNP based on the United States Army Corps of Engineers Shore Protection Manual (SPM; USACE 1984; Finlayson 2005; Rohweder et al. 2008). We obtained wind distribution and direction data from the International Falls, MN weather station recorded during ice free months (May–November) from 1992 to 2016 (NOAA 2017). We calculated the percentage of wind from 36 compass directions at 10° angular increments. The Fetch Analysis Tool function created 36 fetch raster layers each representing unobstructed travel distance (m) from the center of every water raster cell to the nearest land raster cell in all 36 wind directions. Each fetch measurement is the average distance of nine radials (3° angular increments) centered on each wind direction to better account for long narrow fetches (Smith 1991). Finally, a single fetch impact landscape raster (10 m × 10 m raster cells) was created which represents the average of all fetch values from the 36 wind fetch exposure layers, weighted by the distribution of wind in each direction (Fig. 2). To quantify the endpoint impact of fetch at each site, we averaged fetch values from all raster cells within a 200 m circular buffer centered on each site.

Analysis

We used multi-season occupancy models (Program PRESENCE, Version 12.7) to estimate site occupancy and turnover dynamics of muskrats. Due to model convergence issues likely resulting from the low number of observed site extinctions (see "Results"), we did not model extinction rates. We evaluated three 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). We predicted that detection probabilities for muskrats 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, we summed the total precipitation 7-days prior to each survey using data from the NOAA weather station located on Kabetogama Lake (Precip). To account for variation between our two sampling techniques (walking surveys vs. rafts), we also included 'Methods' as a covariate.

Our candidate set of detection models (n = 8) included the single or additive effects of our covariates along with a constant model (DOY; Method; Precip; DOY + Method; DOY + Precip; Precip + Method; DOY + Precip + Method; *Constant*). We considered candidate sets of initial occupancy (n = 13) and colonization models (n = 13) that were structured identically 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*). We also considered the potential for a cross-scale interaction between the proportion of Typha and Fetch at sites (Typha + Fetch + Typha * Fetch).

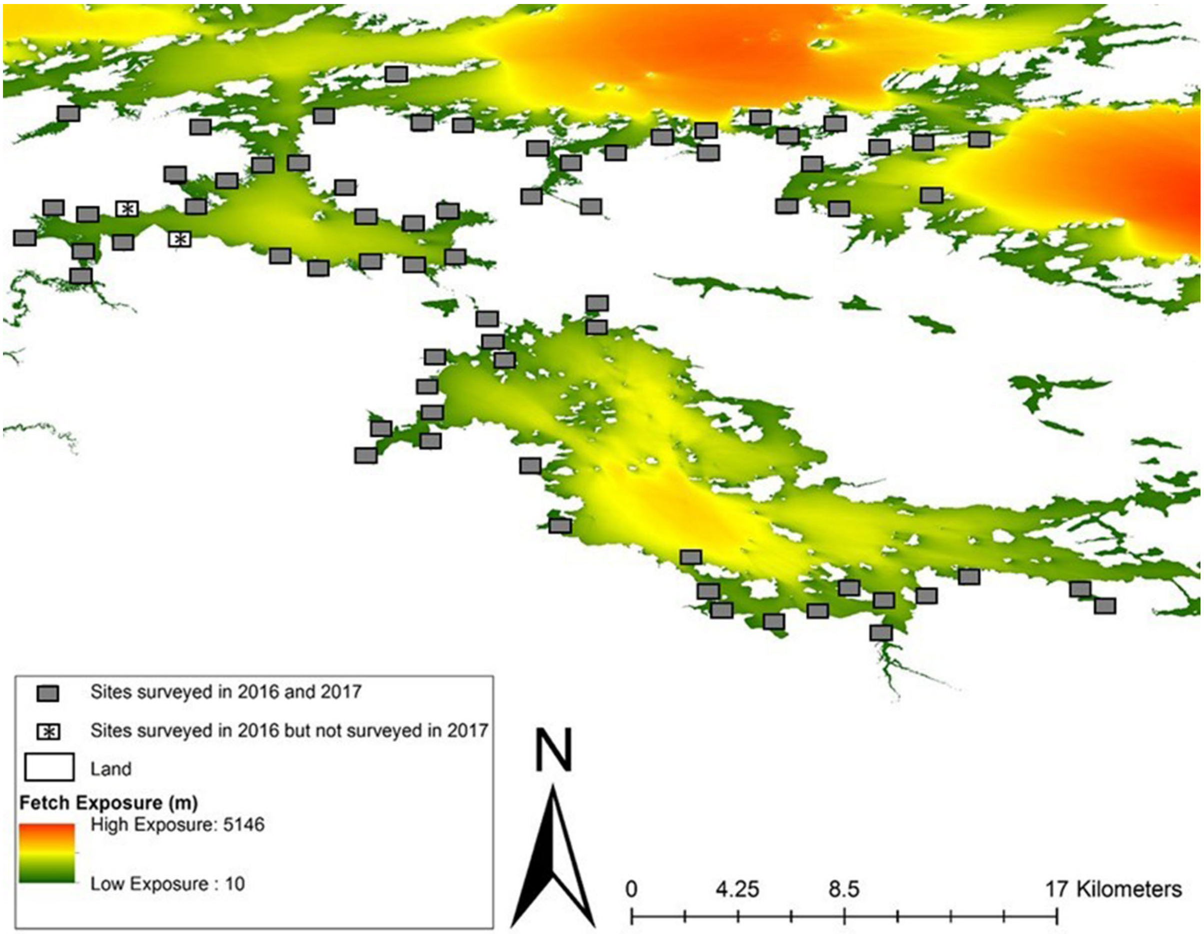

Fig. 2 Fetch exposure map of Voyageurs National Park (VNP) located in International Falls, Minnesota, USA. We quantified discrete fetch impacts across VNP water habitats with the color ramp indicating areas of greater and reduced fetch

We 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. We did not include highly correlated covariates ($|r| \geq 0.70$) in the same model. We used an information-theoretic approach to select the most-supported model from each candidate set (Burnham and Anderson 2002; Arnold 2010). We used model-averaging for all parameter estimates (derived from all models included in the $\Sigma\omega = 0.95$) to reduce biases that may have existed due to model-selection uncertainty (Burnham and Anderson 2002).

Results

We conducted 560 independent surveys for muskrats from 2016 to 2017 (284 in 2016 [walking = 142, rafts = 142], 276 in 2017 [walking = 138, rafts = 138]). Naïve site occupancy estimates for muskrats varied by year (2016 = 0.69, 2017 = 0.77) and by survey method (2016: walking = 0.58, rafts = 0.45; 2017: walking = 0.57, rafts = 0.65). We did not detect muskrat sign at 10 sites and always detected muskrat sign at 43 sites. We documented 12 colonization and 4 extinction events between 2016 and 2017.

Our constant model of detection indicated that per-survey detection probability was moderate (0.53, SE = 0.03). Our top detection model indicated that day of year (DOY) and survey method (Method)

Table 1 Multiseason occupancy models used to assess detection, initial site occupancy, and colonization by muskrats (*Ondatra zibethicus*) at wetland sites (n = 71) in Voyageurs National Park, Minnesota, USA during the summers of 2016 and 2017

Model	ΔAIC_c	ω	*k*	Deviance
Detection				
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				
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				
Typha + Fetch + Typha*Fetch	0.00	0.41	11	678.90
Constant	4.42	0.11	8	689.32

We ranked models by descending ΔAIC_c values and included all models with a $\Delta AIC_c \leq 2.00$ as well as the null 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 on each site), and a *Constant* (intercept model). *k* = number of parameters in each model; ω = model weight; Deviance = − 2Log(Likelihood)

influenced our ability to detect muskrats (Table 1). Detection probabilities diminished later in the year (DOY; β = − 0.015, SE = 0.001) and were greater using raft surveys (Method; β = − 0.360, SE = 0.194). We 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 0.74 (SE = 0.06) and colonization rate was 0.52 (SE = 0.13).

Our 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 = 0.046, SE = 0.001) and at sites with shallower water depths and less open water (Water; β = − 0.047, SE = 0.001; Fig. 3). Two other models including the negative effect of 'Fetch' were also competitive (Table 1). We subsequently modeled colonization rates with our most parsimonious initial occupancy model (Typha + Water). Our only supported colonization model (ω = 0.41) included the positive interaction (β = 0.004, SE = 0.002) between Typha (β = 0.095, SE = 0.017) and Fetch (β = − 0.003, SE = 0.001; Fig. 4; Table 1). Muskrats were more likely to colonize greater fetch-exposed sites if those sites also had greater coverage of *T. x glauca* (Fig. 4).

Discussion

Our results suggest the spatial distribution of muskrats is affected by both resource availability within wetlands and fetch. As predicted, muskrats occupied sites with greater coverage of *T. x glauca*, an aggressive invasive hybrid species, and also with shallower water depths and less open water. Our findings also revealed a cross-scale interaction suggesting that muskrats will colonize wetlands with greater fetch impacts, dictated by the landscape configuration of upland areas, if there are also greater coverages of *T. x glauca* present at the local scale.

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 suitable areas for foraging and hut construction and maintenance. Muskrats generally construct huts in 43–101 cm of water (Sather 1958) and experience population growth in areas with ∼ 85 cm of water (Messier et al. 1990).

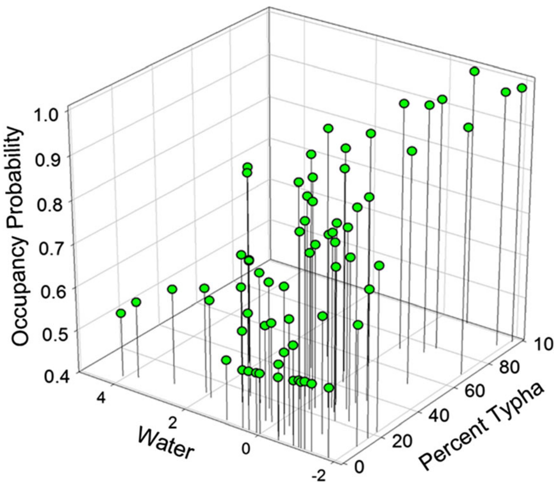

Fig. 3 Local-scale initial site occupancy probabilities by muskrats (*Ondatra zibethicus*) at 71 wetland sites in Voyageurs National Park, International Falls, MN during summers 2016 and 2017. Our most-supported model indicated that the percentage of *T. x glauca* at sites (Typha) and water depths and amount of open water at sites (Water) influenced initial site occupancy probabilities

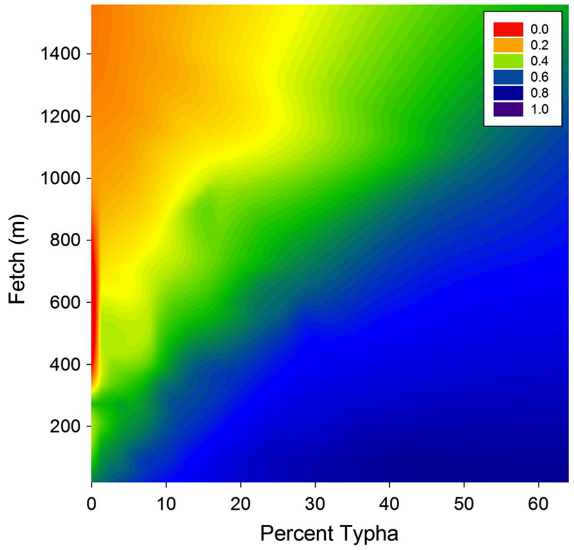

Fig. 4 Site colonization rates by muskrats (*Ondatra zibethicus*) at 71 wetland sites in Voyageurs National Park, International Falls, MN during 2016 and 2017. Colonization rates were best predicted by a cross-scale interaction representing the percentage of *T. x glauca* coverage at sites and fetch impacts

Water depths can influence availability of emergent vegetation while also mediating predation risks for muskrats (Messier et al. 1990; Clark 1994; Virgin and Messier 1997; Ahlers et al. 2015). Muskrat populations are sensitive to fluctuating water depths (Ahlers et al. 2015) but can persist in stable areas with sufficient food resources (Messier et al. 1990; Thurber et al. 1991; Messier and Virgl 1992; Toner et al. 2010). In lacustrine systems, wetlands with suitable water depths are isolated by large areas characterized by deep, open-water habitats. Identifying factors influencing muskrat movements between suitable wetlands will help uncover macroscale distribution constraints present in lacustrine watersheds.

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 (Takos 1947) and our results suggest that *T. x glauca* may also be an important resource. *T. x glauca* has similar nutritional qualities as other native wetland plants along with greater nitrogen content (Campbell and MacArthur 1994). Muskrats occurring in areas with *T. x glauca* have greater body-mass gains and increased winter survival probabilities and these areas can be important for hut construction and maintenance (Clark 1994). Because floating *T. x glauca* mats extend into areas unsuitable for native wetland vegetation (e.g., deep water, rocky substrate), they may provide additional resources for muskrats in these areas. Thus, it is plausible that floating *T. x glauca* mats may enhance the functional connectivity of isolated bays or wetlands in lacustrine systems. Future work should evaluate the relative importance of *T. x glauca* populations at enhancing muskrat dispersal rates between suitable wetland habitats and for facilitating muskrat distribution expansions.

Muskrats were less likely to colonize sites exposed to greater fetch impacts unless those sites also had greater coverage by *T. x glauca*. This suggests that *T. x glauca* may mediate the negative effects of fetch and allow muskrats to colonize otherwise unsuitable areas. Greater wind speeds and wave heights likely affect muskrat movements in open water and degrade or destroy muskrat huts more quickly. Additionally, movement of ice sheets during the winter and spring (mediated by wind and wave action) can also destroy established muskrat huts (Errington 1939). Although suitable muskrat habitats may not appear isolated because they are connected by open water, fetch-exposed areas likely represent matrix habitats with reduced functional connectivity benefits for muskrats and other wetland-obligate species. Site colonization by muskrats is influenced by a cross-scale interaction between landscape-dictated fetch effects and contemporary expansions of invasive hybrid cattail species. Thus, our results suggest that historic constraints on muskrat distributions in lacustrine systems may be relaxed by the presence of expanding invasive hybrid *T. x glauca* populations. However, there is likely a threshold response to increasing *T. x glauca* coverage at wetlands as muskrats cannot likely persist in wetlands devoid of open-water habitats. Future research is needed to elucidate subsequent population-level effects for muskrats occurring in these areas.

Our study highlights how biotic and abiotic effects can interplay across scales (landscape to local) and habitats (upland to wetland) to structure distributions of wetland-obligate species. Additionally, we revealed a potential positive influence of an aggressively establishing invasive hybrid species at expanding distributions of semiaquatic herbivores. Future research should focus on community-level responses to *T. x glauca* expansions and how individual species' population-level demographics (e.g., fecundity, recruitment, population growth) are influenced by *T. x glauca* expansions in wetland ecosystems.

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Post-translocation spatial ecology and survival of muskrats (*Ondatra zibethicus*) in lacustrine wetlands.

by

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Abstract

Translocation is a common wildlife management tool though managers often lack follow-up information regarding overall effectiveness of these efforts. Muskrats (*Ondatra zibethicus*) are native semi-aquatic herbivores with a rich cultural and economic history in North America. Muskrats have been positively associated with increased species richness within wetlands and can act as drivers of disturbance through intense herbivory at high population densities. Currently, muskrats are experiencing long-term and widespread population declines across their native range. Translocations may hold potential for muskrats to restore local populations and mitigate declines. However, it is unclear how translocating muskrats will affect their survival, post-translocation movements, and space use – all critical to effective translocation efforts. I live-trapped muskrats (n = 65) during the summers of 2018-2019 in Voyageurs National Park, MN, USA and assessed the effects of translocation on weekly survival rates and space use patterns. I implanted muskrats with internal VHF transmitters, moved them to treatment wetlands, and tracked space use, survival, and cause-specific mortality. On average, individuals traveled 2.2 km (0.12-10.11 km) from release sites and established a home range within 8 days post-translocation. There was no evidence of homing behavior (i.e., returning to their previous home range). Weekly survival rate was low (0.95, SE = 0.001) and my top known-fate survival model indicated that beaver lodge use and year of release (likely a function of the difference in release techniques between years) had the most influence on post-translocated muskrats. My study provides the first empirical assessment of translocation effects on muskrats and establishes a methodological technique to assess future efforts to use muskrats as a native biocontrol of *T. x glauca*.

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Figure 2.2 Soft-release shelter used to release translocated muskrats (*Ondatra zibethicus*) into wetland habitats in Voyageurs National Park near International Falls, MN, during summer 2019. Shelters were constructed using a 114-l plastic tote with a secured detachable lid (A) with a 15-cm hole cut on the side (B) so muskrats could move freely in and out of the shelter. Shelters were affixed to 122 x 61 x 4-cm floating rafts (C) and tethered to emergent vegetation (D). I partially filled shelters with local vegetation prior to releasing a muskrat inside. Note recently translocated muskrat on a soft-release shelter feeding on invasive cattail (*Typha x glauca*). 26

Figure 2.3 Post-translocation movement distances (m) and trajectories (0 - 360º) for radiomarked muskrats (*Ondatra zibethicus*, n = 42) scaled to their individual capture locations (0°). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019.The center of the figure represents individual release locations, grey circles represent individual travel distances (m) and trajectory (º), bold lines represent the mean trajectory for all individuals along with the 95% confidence interval. 27

Figure 2.4 Annual differences in median post-translocation Euclidean (A) and least-cost path (B) distances moved by radiomarked muskrats (*Ondatra zibethicus*, n =42). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019. Bold lines represent median values, boxes represent the interquartile range, whiskers represent minimum and maximum values exclusive of outliers, and circles represent outliers. 28

Figure 2.5 Weekly muskrat (*Ondatra zibethicus*, n = 65) survival probabilities (and 95% confidence intervals) derived from my top-ranked known-fate model. Muskrats were radiomarked and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019. Translocated muskrats that used beaver (*Castor canadensis*) lodges had greater weekly survival probabilities (A). Translocated muskrats also had greater weekly survival probabilities in 2019 (B), likely a result of using a soft-release method for translocation that year. 29

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Table 2.1 Known-fate model selection results describing survival of translocated muskrats (*Ondatra zibethicus*; n = 65) in lacustrine wetlands in Voyageurs National Park, MN, during summers 2018 and 2019. Models were ranked by differences in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c). *w* = model weight, K = number of parameters within the model, deviance = -2log ([$\log_e$ likelihood of the model)-($\log_e$ likelihood of the saturated model)]. Explanatory variables include Lodge (time-varying covariate indicating if a muskrat was located in a beaver (*Castor canadensis*) lodge during a given week), Year (2018 or 2019), and Prosp (time-varying covariate indicating that an individual was prospecting during a given week). I only present models with $\Delta AIC_c \leq 2.00$ along with the null model for comparison. 24

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I want to thank Steve Windels, Bryce Olson, and Reid Plumb for their expertise, support, and comic relief throughout the two field seasons in Voyageurs National Park. Their innate knowledge of the park, field methods, and sage advice was crucial in completing this research. Working with these three was an experience I will not soon forget. In addition I want to thank Dr. Tiffany Wolf for taking the time to perform muskrat surgeries in the midst of conducting her own research and raising her family.

I want thank Drew Ricketts and Dave Haukos for serving on my committee and sharing their knowledge of wildlife research and analytics. I feel as though my graduate career would not have been complete without the classes provided by these two. The amount of personal insight shared through their courses was invaluable and helped me to grow professionally and expand my understanding of the natural world.

I would also like to thank all of my fellow graduate students for their knowledge and support, from assistance with coding and analytics to providing additional support during muskrat captures and surgeries. Enough cannot be said about the support system provided through their diversity of knowledge and willingness to help. To have been able to attend graduate school with these peers was tremendous.

Finally, I want to thank the numerous technicians, interns, and volunteers from the National Park Service and Kansas State University who took part in this project. This project was very labor intensive and without their hard work and persistence it would not have been what it is today.

Dedication

To my mother and father, Therese and Robert, for their continued encouragement and support throughout my various endeavors.

Chapter 1 - Introduction

Muskrats (*Ondatra zibethicus*) are wetland-obligate rodents native throughout much of North America and invasive in Europe, Asia, and South America (Hazard 1982, Anderson et al. 2006). Similar to beavers (*Castor canadensis*), muskrat populations are considered ecosystem engineers (Bomske and Ahlers *In Revision*). Because of intense herbivory, hut construction, and disturbance of aquatic soils, muskrat populations are positively associated with greater wetland vegetation species richness (Nyman et al. 1993, Tyndall 2011). The disturbance muskrats create in wetlands can reduce dominant emergent wetland vegetation (e.g., cattails [*Typha* spp.], *Phragmites australis*), create open water habitat, and enhance diversity of forage for other wetland fauna (Tyndall 2011, Bansal et al. 2019). Huts constructed by muskrats also provide nesting structures for waterfowl and are positively associated with abundances of aquatic invertebrates (Kiviat 1978, de Szalay and Cassidy 2001, Nummi et al. 2006). Muskrats also contribute to a rich cultural history in indigenous cultures and provides a valuable resource for subsistence communities (Brietzke 2015, Straka et al. 2018, Turner et al. 2018). Muskrats have been a vital component of the North American fur industry since the 1800s (Erb and Perry 2003, Ahlers et al. 2016), being one of the most accessible and widely trapped furbearing species (White et al. 2015).

Using historic fur-harvest data, Ahlers and Heske (2017) noted widespread declines of muskrat populations throughout the United States. Other research has demonstrated similar patterns of decline throughout North America (Roberts and Crimmins 2010, White et al. 2015, Greggory et al. 2019). Specific causes for these declines are unknown, but reduced water quality, loss of wetlands, and diminishing habitat quality through anthropomorphic land change and invasive species encroachment are believed to be major drivers (Ahlers and Heske 2017).

Changes in water regimes, particularly winter draw-downs, due to damming and implementation of water-control structures are also a noted cause of muskrat declines (Hazard 1973, Thurber et al. 1991). These findings, along with the realized importance of muskrats to the overall health of native wetlands, have fostered a renewed interest in muskrat management.

Translocation, the act of taking an animal and moving it to a novel area, is a commonly used technique in wildlife management and conservation. This technique has been implemented to restore and reintroduce native game species (Olson 2007, Paul 2009, Werdel et al. 2019), endangered species (Jachowski and Lockhart 2009), and keystone species to restore ecological stability (Law et al. 2017). Translocations are also common practice in nuisance wildlife management as an alternative to lethal removal (Craven et al. 1998, Lehrer et al. 2016). Various methods are used in translocations, much of which are dependent on actual management goals. Release methods are likely the most varied aspect of the translocation process ranging from 'hard-releases' wherein an animal is released without additional human aid, to 'soft-releases' involving intricate acclimation pens to habituate the translocated animals to their new environment over a span of several weeks. Generally, animals translocated using soft-releases had greater survival rates and were more likely to establish themselves in their new environment (Berger-Tal et al. 2019).

Historically, translocations have been used to expand the range of muskrats and increase opportunity for fur harvesters (Storer 1937, O'Neil 1949). Records of these translocations are inconsistent and their success is relatively unknown. Our understanding of their successes rely on mostly anecdotal accounts and emphasizes the need for in-depth analyses of translocation success. Translocation techniques have become more refined, and studies analyzing these methods have provided valuable insight regarding keys to successful implementation and the post-translocation ecology of various species (Van Vuren et al. 1997). Post-translocation survival is an immediate indicator of success and provides key information regarding the feasibility and methods used in the translocation effort (Massei et al. 2010). Behaviors expressed post-translocation may be analogous to behaviors and decisions expressed during natural dispersal events (Van Vuren et al. 1997). Analysis of these behaviors may identify key resources for the species and expand our knowledge of the species, leading to more informed management decisions and increased translocation success.

My thesis research focuses on the post-translocation ecology of muskrats in a large lacustrine system as a means of exploring the feasibility of translocating muskrats as a large-scale non-native cattail (*Typha x glauca*) management technique. Using muskrats equipped with surgically implanted very-high-frequency (VHF) transmitters, I investigated post-translocation movements by calculating movement distances from release sites, quantifying the duration of prospecting periods and subsequent home range establishment, and investigating for potential homing behaviors. In addition, I used known-fate models to investigate post-translocation survival and determine factors most likely to predict weekly survival of translocated muskrats. Empirically assessing post-translocation spatial ecology and survival of muskrats will help inform about potentially important local resources for managers interested in restoring muskrat populations. To my knowledge this is the first in-depth analyses of translocation efforts involving muskrats and one of the most comprehensive ecological studies of muskrat populations occurring in a large lacustrine ecosystem.

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Chapter 2 - Post-translocation spatial ecology and survival of muskrats (*Ondatra zibethicus*) in lacustrine wetlands.

Introduction

Wildlife translocation is an important conservation tool used to alter population abundances and distributions or enhance population viability for at-risk species (Berger-Tal et al. 2019). These efforts include translocations of charismatic species to reintroduce or bolster local populations (Olson 2007, Paul 2009, Werdel et al 2019), and restoration of imperiled species (Jachowski and Lockhart 2009). Translocations have also served as an alternative to lethal removal of individuals to mitigate negative human-wildlife interactions (Germano et al. 2015, Lehrer et al. 2016). Additionally, these efforts can restore native landscapes by reestablishing ecosystem engineers (i.e., American beaver [*Castor canadensis*] and Eurasian beaver [*Castor fiber*]; Law et al. 2017). Regardless of management goals, practitioners should rigorously evaluate post-translocation metrics (e.g., survival, space use) to assess the effectiveness of their efforts (Lehrer et al. 2016, Werdel et al 2018, Berger-Tal et al. 2019).

Muskrats (*Ondatra zibethicus*) are small (0.7-1.8 kg; Willner et al. 1980) semiaquatic herbivores experiencing long-term and widespread population declines across North America (Roberts and Crimmins 2010, Ahlers and Heske 2017, Greggory et al. 2019). Because of their cultural significance in North America (Brietzke 2015, Straka et al. 2018; Turner et al. 2018) and importance to wetland ecosystems (Bhattacharjee et al. 2007, Bomske and Ahlers *In Revision*), translocation efforts focused on restoring or enhancing muskrat populations are timely and warranted. Muskrats are an economically important species (Erb and Perry 2003, Ahlers et al. 2016), invasive to Europe, Asia, and South America (Hazard 1982, Anderson et al. 2006), and considered ecosystem engineers in wetland habitats (Bomske and Ahlers *In Revision*). Muskrat herbivory is positively associated with wetland vegetation species richness (Nyman et al. 1993, Tyndall 2011) and occurrence of open-water habitats (Bansal et al. 2019). Additionally, muskrat huts provide nesting structures for birds (Kiviat 1978) and increased abundance of aquatic macroinvertebrates (de Szalay and Cassidy 2001, Nummi et al. 2006).

Historically, muskrats were translocated to muskrat-absent wetlands primarily to provide increased opportunities for fur harvest (Storer 1937, O'Neil 1949, Idaho Fish and Game 2015). However, these efforts were poorly evaluated, if at all, leaving many questions about the efficacy of muskrat translocation. Translocations have the potential to influence muskrat space use and survival, which may impact overall management goals, although, available evidence for post-translocation related effects is contradictory and generally species-specific (Berger-Tal et al. 2019). Increased emigration rates and low survival rates were observed in post-translocated American beavers (McKinstry and Anderson 2002), while similar emigration patterns, in addition to high homing rates, were noted in translocated California ground squirrel (*Ostospermophilus beecheyi*) populations (Van Vuren et al. 1997). In northern river otters (*Lontra canadensis*) it was found that males and larger individuals had greater post-translocation survival rates than females and smaller individuals (Day et al. 2013). Lehrer et al. (2016) did not find evidence for homing behavior in translocated woodchucks (*Marmota monax*) and reported that translocated woodchucks had similar survival rates as residents. Moreover, Lehrer et al. (2016) recommended practitioners use soft-release techniques and also choose release sites with relatively low predation risks to enhance translocation success. Increased survival and site fidelity of post-translocated prairie dogs (*Cynomys parvidens* and *C. ludovicianus*) was observed when using soft-release methods (Truett et al. 2001).

Muskrats are primarily restricted to aquatic habitats (Ahlers et al. 2010a, 2015), highlighting the relative impermeability of upland landscapes to muskrats (Schooley and Branch 2006, Cooney et al. 2015). With longer translocation distances, muskrat homing behavior may diminish because of the limited permeability of upland landscapes (Schooley and Branch 2006, Laurence et al. 2013), limited perceptual range (Zollner and Lima 1997, Villasenor et al. 2013), and small size. Similar to other translocated species (Calvete and Estrada 2004, Lehrer et al. 2016), I expect prospecting behaviors (searching for habitat in novel landscapes prior to establishing a home range) of muskrats immediately following translocation to be linked to reduced survival rates. Muskrats in North America are sympatric with American beavers and will often use active or inactive beaver lodges (Leighton 1933, Rosell et al. 2005, Mott et al. 2013, Windels 2017). It is plausible that beaver lodges could provide muskrats refugia from predation or adverse weather, and use of beaver lodges while prospecting in unfamiliar landscapes may confer increased fitness benefits such as increased survival probabilities (Rosell et al. 2005).

I translocated radiomarked muskrats to lacustrine wetlands to investigate their subsequent spatial ecology and survival. This study was concurrently evaluating the long-term feasibility of using the same translocated muskrats as a biocontrol of a non-native cattail species (*Typha x glauca*; Brulliard 2018), but that study is beyond the scope of this thesis. Here, I focus on identifying how translocation efforts subsequently affect muskrat survival and movements. I expected that translocated muskrats would not exhibit homing behavior as translocation distances exceeded their perceptual ranges and published movement capabilities. Similarly, I expected post-translocation movements to remain within or close to release sites given the relative impermeability of surrounding upland landscapes, fetch impacts of open water habitats (Larreur et al. 2020), and limited dispersal capabilities of muskrats. Because beaver lodges may provide refugia for muskrats in novel areas, I expected a positive association in weekly survival and beaver lodge use. Finally, there is evidence that soft-release techniques may improve survival rates of translocated species; therefore, I expected muskrats translocated using soft-release techniques would have greater weekly survival rates.

Methods

Study Area

My study occurred in and around Voyageurs National Park (VNP; ~88,220 ha) near International Falls, Minnesota, USA and Fort Francis, Ontario, Canada (48°29’ N, -92°49’ W; Fig. 2.1). VNP comprises parts of five large lakes, of which Rainy (58,065 ha) and Kabetogama (9,726 ha), both located within the Rainy Lake watershed (Fig. 2.1), were the focus of my research. Areas outside the park involved in my study included the Black Bay portion of Rainy Lake and Rat Root Lake, a tributary of Rainy Lake. Water levels within Rainy and Kabetogama Lakes are artificially managed through dams at the Rainy River in International Falls, MN and the Kettle Falls and Squirrel Falls dams at the outlet of Namakan Lake. Rainy and Kabetogama Lakes are classified as oligotrophic and mesotrophic-eutrophic, respectively (Christensen and Maki 2014) and are characterized by scattered islands and a mix of rocky and muddy shorelines. Vegetated shorelines consisting of non-native cattails (*Typha x glauca*), softstem bulrush (*Schoenoplectus tabernaemontani*), wild rice (*Zizania palustris*), and sedges (*Carex* spp.) occur primarily within areas adjacent to the main lake. Upland areas adjacent to wetlands were characterized by shallow soils and bedrock dominated by conifers (white pine [*Pinus strobus*], jack pine [*Pinus banksiana*], and balsam fir [*Abies balsamea*]) and northern deciduous trees (quaking aspen [*Populus tremuloides*] and paper birch [*Betula papyrifera*]). Average annual temperature and precipitation for the area is 3°C (range = 9.3 - -3.3°C) and 242 cm (62 cm of rain and 180 cm of snow), respectively. For my study the average temperature in 2018 was 2.1°C (range = 19.2 - -17.5°C) and 1.34°C in 2019 (range = 18.9 - -18.9°C). Total precipitation for 2018 was 218 cm (61 cm rain and 157 cm snow) and 285 cm in 2019 (78 cm of rain and 207 cm of snow).

Captures and Transmitter Implantation

From 2-6 July, 2018 and 1-7 June, 2019, I captured muskrats in western Black Bay, Rat Root Lake, and the Mud Bay, Irwin Bay, and Daley Bay portion of Lake Kabetogama (Fig. 2.1) using double- and single-door live traps (Tomahawk® 202, Tomahawk, WI, USA). I attached traps to 122 x 61 x 4-cm floating rafts (modified track boards; see Reynolds et al. 2004, Schooley et al. 2012, Larreur et al. 2020) tethered to sturdy vegetation or wood laths (120 x 4 x 1-cm) anchored into substrate or muskrat huts. I baited traps with apple and commercial trapping lures, and focused my efforts on or near muskrat huts or feeding platforms. I covered all traps with vegetation to make them more natural and provide trapped muskrats cover from adverse weather and direct sunlight. Traps were checked every morning and I immediately transported captured muskrats (adults ≥700 g) to a surgery suite to implant internal very-high-frequency (VHF) transmitters (13 g, ATS model F1215, Advanced Telemetry Systems, Isanti, MN, USA). Based on previous literature, I assumed the transmitters would not negatively affect survival and were unlikely to be expelled from the muskrats (Davis et al. 1984, Ahlers et al. 2010a, b, Smith et al. 2016).

I transferred captured muskrats to a handling bag and weighed them. An attending veterinarian administered sedation (dexmedetomidine [0.025 mg/kg], midazolam [1 mg/kg]) via intramuscular injection. When individuals displayed reduced righting reflex, the veterinarian induced surgical anesthesia using isoflurane (1-5%) via face mask. Once anesthetized, I assessed sex and conducted a basic health assessment. The veterinarian implanted transmitters following Ahlers et al. (2010a, b); muskrats were maintained on oxygen (0.6 L/min) during the entire procedure (20-30 min) and heart rate and breathing trends were constantly monitored. Sedation was reversed with atipamizole (0.25 mg/kg) and flumazenil (0.05 mg/kg) followed by inoculation of muskrats with penicillin (0.1 mL) and meloxicam (1 mg/kg). I marked all muskrats with passive integrated transponder tags (Ahlers et al. 2010a) and individual ear-tags. Prior to recovery, 1.5 mL blood was collected from individuals' cranial vena cava using a 25-ga needle attached to a 3-mL syringe (Ahlers et al. 2011; Ahlers et al. 2020 *In Press*) and four morphometric tail measurements were recorded (length, base-width, mid-width, and end-width). I allowed muskrats ≥2 hrs to recover post-surgery prior to translocating them. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (Protocol #4098) and followed guidelines established by the American Society of Mammologists (Sikes et al. 2016).

I selected five lacustrine wetlands from a suite of prospective sites to receive translocated muskrats and randomly assigned individuals to their respective wetlands prior to translocation (Fig. 2.1). Prospective wetlands were representative of traditional muskrat habitat (shallow to deep marsh). Wetlands selected as translocation sites were selected based on size (in hectares) and the distance to neighboring translocation sites. Wetlands averaged 1.42 ha (range = 1.09-1.78ha), were separated by ≥1.3 km ($\bar{x}$ = 5.7 km, range = 1.3-11.6 km), and supported diverse emergent vegetation communities (cattail, bulrush, wild rice, sweet flag [*Acorus calamus*], and giant bur-reed [*Sparganium eurycarpum*]) and floating vegetation (white water lily [*Nymphaea* *odorata*], common bladderwort [*Utricularia macrorhiza*], and floating-leaf pondweed [*Potamogeton natans*]). Wetlands were not geographically isolated as they were all hydrologically connected to Rainy Lake (Fig. 2.1). I did not quantify muskrat abundance in wetlands prior to muskrat translocations; however, observations during pre-study assessments (e.g., number of muskrat huts, clippings, and scat) indicated low-to-zero muskrat abundances in those areas. Average translocation distance (Euclidian) from site of capture for all muskrats (n = 65) was 18.13 km (range of 4.68-25.46 km).

In 2018, I translocated muskrats using a hard-release technique where I released an individual from their trap onto natural structures within their assigned wetland (e.g., floating cattail mat, beaver lodge, shoreline structure). In an effort to reduce possible translocation related stress and boost survival of the translocated muskrats, I implemented a novel soft-release technique in 2019. This included releasing muskrats directly into temporary shelters to better acclimate them to their release site (Fig. 2.2). Shelters were constructed using a 76 x 51 x 44-cm (114 liter) plastic tote (with removable lid) affixed to 122 x 61 x 4-cm floating rafts (for detailed descriptions of floating rafts, see Reynolds et al. [2004], Schooley et al. [2012], and Larreur et al. [2020]). I cut a 15-cm diameter opening in the plastic tote and partially filled structures with local vegetation. I released individuals directly into structures and they had the ability to freely leave or return through the opening (Fig. 2.2). Two structures were placed in each release wetland (~10 m apart) to reduce potential for competition between translocated muskrats, and I only released one muskrat per structure at a time. Structures were placed in ~1 m of water and spatially positioned within wetlands to reduce exposure to wave action.

Movements and Survival

I used a boat or aircraft-mounted, four-element fixed Yagi antenna in conjunction with an ATS R4000 receiver (Advanced Telemetry Systems, Isanti, MN, USA) to initially search for muskrats. Once the general locations of muskrats were identified, I used a single handheld telemetry receiver (Communication Specialist R-1000; Communication Specialist Inc. Orange, CA, USDA) and three-element folding Yagi to home in on exact locations of muskrats. I attempted to find muskrats once every 48 hrs and only during daylight or twilight. Muskrats are generally crepuscular and my sampling timeframe likely underestimated the spatial extent of actual muskrat home ranges. Once located, I recorded locations of individuals using a handheld GPS (Garmin GPSMAP® 64; Garmin Ltd, Olathe, KS, USA), documented mortality status (alive or dead), and identified structure use (i.e., beaver lodge/dam, muskrat huts). I attempted to locate and physically retrieve all mortalities as soon as they were detected to characterize cause of mortality.

Analyses

Similar to Woodford et al. (2013), I determined the end of an individual’s prospecting period and subsequent establishment of a home range when four consecutive locations occurred within the approximate size of an average home range of a muskrat (2.9 ha, Marinelli 1993). I used space-use data from individuals tracked consistently throughout the prospecting period to calculate average duration of prospecting (n = 28; 2018 = 6 [5 male, 1 female], 2019 = 22 [14 male, 8 female]).

Translocated individuals search for new areas to settle immediately after release and movements during this prospecting period generally do not reflect normal habitat-use decisions

(Vilasenor et al. 2012, Lehrer et al. 2016, Berger-Tal et al. 2019). Thus, I did not include locations collected during an individual's prospecting period in home range size estimations. Based off of Ahlers et al. (2010a) I calculated individual home range size for muskrats with ≥20 locations post-prospecting period (n = 26, 17 males and 9 females). Due to small per capita sample sizes of locations in 2018 ($\overline{x}$ = 12.4 locations, range = 5-19 locations), I only used data collected from muskrats in 2019 to estimate home range sizes. I estimated 95% home range sizes from kernel density estimates (KDE) using an Epanechnikov kernel and individual reference bandwidths with package 'adehabitatHR' in R (Calenge 2019). I tested for sex-specific differences in home range sizes using a *t*-test and the duration of prospecting time using a Mann-Whitney *U*-test in R base package (Zar 2010, Woodford et al. 2013). I established an *a priori* cutoff for significant effects at $\alpha = 0.05$.

I investigated if individual post-translocation movement trajectories oriented back to initial capture locations (i.e., homing). Using individuals with ≥5 locations (n = 42, 10 in 2018 and 32 in 2019) I calculated average post-translocation movement trajectories by plotting the travel route of each muskrat using the Point-To-Line tool and then fitting a line to the route using the Linear-Directional-Mean tool in ArcMAP (Esri Corporation, Redlands, CA, USA). I plotted all muskrat trajectories respective to their capture location (Lehrer 2016), this way 0° would represent capture locations as opposed to North. I then ran a *V*-test of 0° (Oriana version 4.02, Kovach Computing Services, Anglesey, Wales, UK) to assess if there was a difference in mean movement trajectories and capture locations (i.e., homing) and calculated the *r* vector to measure the concentration of the trajectories around their mean (Landler et al. 2018).

To assess total distances traveled during prospecting periods, I measured Euclidian distance (km) from an individual's release site to the center of their 95% home range. If a home range was not established for an individual muskrat (either died or was lost during the prospecting period), I measured the Euclidean distance from their release site to last known location. If a muskrat established a home range, but lacked sufficient locations for home range estimation (< 20 locations), I measured the Euclidian distance to the geographic center of the post-prospecting period location cluster. Assuming that movement routes of muskrats followed a Euclidian trajectory is likely unrealistic (e.g., requiring them to move freely through upland landscape), so I also estimated a modified least-cost path using similar methods described above. As opposed to using a straight-line distance measurement, I manually measured the most parsimonious route (km) using the Linear Measurement Tool in ArcMAP for each muskrat assuming individuals would remain in water (Ahlers et al. 2010a). I used Mann-Whitney *U*-tests to investigate potential sex- and year-specific differences in both estimates of post-translocation movement distances.

I used known-fate models with a staggered entry design to estimate weekly post-translocation survival (Program MARK version 9.0; Cooch and White 2008). I structured models using six covariates hypothesized as important for muskrat survival including sex (male or female), year (2018 or 2019), tail index (TailID), beaver lodge-use (Lodge) and prospecting status (Prosp). Muskrats store fat reserves within their tails, thus tail size may be an indicator of overall body condition (Aleuksiuk 1970, Hickman 1979, Smith and Jenkins 1997). I derived a muskrat ‘tail index’ by modifying a similar index developed for beavers (Smith and Jenkins 1997). I first calculated tail size, X, for the i^{th} individual as:

$$X_i = \frac{\bar{X}_w}{L}$$

where $\bar{X}_w$ = the mean horizontal width (mm) of the tail derived from three measurements evenly spaced along the length (base, middle, and 1cm from the tip); and L = the length (mm) of the tail (base to tip). I then derived a tail index, Z, for the i^{th} individual as:

$$Z_i = \frac{(X_i - \bar{X})}{S}$$

where $\bar{X}$ = mean tail size for all muskrats (n = 65); and S = standard deviation of $\bar{X}$.

Beaver lodges can be important structures for muskrats as they provide refugia from predation and adverse weather conditions (Mott et al. 2013). I developed a time-varying covariate that represented an individual's use of a beaver lodge at least once during a given week (Lodge; 1 = ≥1 location recorded in a beaver lodge during a given week, 0 = no locations recorded in a beaver lodge during a given week). I determined a muskrat to be located in a beaver lodge by homing in to the exact location of the beaver lodge. I developed an additional time-varying covariate representing if an individual was exhibiting prospecting behavior (i.e., movements prior to establishing a home range) during a given week (Prosp; 1 = muskrat located during prospecting period, 0 = muskrat located after establishing a home range).

Because a single marked muskrat was relocated in both 2018 and 2019, my detection history spanned 69 weeks (2 July 2018- 24 October 2019). I only monitored muskrats from July – November 2018 and June – October 2019; therefore, weekly survival estimates only reflect survival during that period. I created a suite of models (n = 11) to estimate weekly survival of 65 muskrats (48 males [2018 = 18, 2019 = 30] and 17 females [2018 = 5, 2019 = 12]. To prevent over-parameterization of models while preserving overall model parsimony, I restricted the maximum number of parameters per model to ≤4 (Burnham and Anderson 2002). Models included single effects (Year; Lodge; Prosp; Sex; TailID), additive effects (Lodge + Year; Lodge + Prosp + Year; Prosp + Year; Lodge + Prosp), potential interaction between beaver lodge use and prospecting behavior (Lodge + Prosp + Lodge*Prosp), and a null model. I used a logit-link function to express weekly survival probability as a continuous function of selected covariates. I assessed support for models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and based all inferences on model rankings. I considered models with ΔAIC_c of $\leq$ 2.00 as competitive (Burnham and Anderson 2002).

Results

I marked and translocated 65 adult muskrats (2018 = 23, 2019 = 42), of which 48 were male (2018 = 18, 2019 = 30) and 17 were female (2018 = 5, 2019 = 12). I relocated post-translocated muskrats with VHF telemetry 1,451 times, yielding ~22 locations per individual (range = 1-48). I tracked each muskrat an average of 73 days (2018 = July 2 - November 5; 2019 June 1 - October 24) and 17 known individuals retained active transmitters by the end of the field seasons (2018 = 3, 2019 = 14). The average duration of prospecting period was 8.4 days (range = 2-32 days). There was no difference in duration of prospecting period between males ($\bar{x}$ = 9.3 days, range = 2-32 days) and females ($\bar{x}$ = 6.4 days, range = 1-12 days; *U* = 62, *p* = 0.34) or years (2018 = 8.5, range = 2-17 days; 2019 = 8.4, range = 2-32 days; *U* = 69.5, *p* = 0.72). I did not observe evidence of long-term use (>24 hrs) of soft-release structures by muskrats.

Muskrats did not exhibit post-translocation homing behavior (Fig 2.3, *r* vector = 0.18, *p* = 0.09); although, only ~15% of muskrats (n = 10) remained within their assigned release wetlands after translocation. Mean post-translocation Euclidean and least-cost path movement distance was 2.17 km (range = 0.12-10.11 km) and 2.69 km (range = 0.12-11.32 km), respectively. Post-translocation movement distances between males (Euclidean = 2.31 km, range = 0.12-10.11 km; least-cost path = 2.85 km, range = 0.12-11.32 km) and females (Euclidean = 1.74 km, range =

0.57-3.57 km; least-cost path = 2.16 km, range = 0.71-4.57 km), were not significantly different (U = 154, p = 0.87 and U = 156.5, p = 0.93, respectively). Post-translocation movement distances for pooled sexes differed between years for both Euclidean (2018 = 1.14 km, range = 0.12-3.63 km; 2019 = 2.50 km, range = 0.34-10.11 km; U = 86, p = 0.02; Fig. 2.4A) and least-cost path metrics (2018 = 1.42 km, range = 0.12-5.36 km; 2019 = 3.09, range = 0.36-11.32; U = 84, p = 0.03; Fig. 2.4B).

For muskrats with sufficient data to model post-translocation home range area (n = 26) the mean number of locations per muskrat was 37.4 (range = 23-47). Average 95% home range area was 2.52 ha (range = 0.05-9.67 ha). There was no statistical difference between male ($\bar{x}$ = 2.53 ha, range = 0.06-9.67 ha) and female ($\bar{x}$ = 2.50 ha, range = 0.05-6.79 ha, t[18.1] = -0.03, p = 0.98) post-translocation home range sizes.

I recorded 23 mortalities (2018 = 11, 2019 = 12) and I attributed four to predation (American mink [*Neovison vison*, n = 3] and bald eagles [*Haliaeetus leucocephalus*, n = 1]) and four unknown (no obvious signs of predation, trauma, or disease). For the remaining 15 mortalities, I only recovered transmitters with little or no obvious signs of predation preventing characterization of cause of mortality. I was unable to relocate 9 individuals post-translocation (2018 = 4, 2019 = 5). My top ranked and most-supported model (Lodge + Year; Table 2.1), indicated muskrats using beaver lodges had greater weekly survival rates (0.99, SE = 0.01) than those that did not (0.95, SE = 0.01; β = 2.04, SE = 1.03, $\Sigma\omega_{\text{Lodge}}$= 0.92; Fig. 2.5A). Additionally, muskrats had greater weekly survival rates in 2019 (0.97, SE = 0.01) than in 2018 (0.88, SE = 0.03) (β = 1.43, SE = 0.44, $\Sigma\omega_{\text{Year}}$= 0.97, Fig 2.5B). Overall weekly survival rates based on my top-ranked model were 0.95 (SE = 0.001). My second-ranked model included the covariate

‘Prosp’ (Lodge + Year + Prosp; Table 2.1). However, inclusion of ‘Prosp’ did little to improve model fit (ΔDeviance between models = 0.24; Table 2.1) suggesting this effect was spurious.

Discussion

My results demonstrate that translocated muskrats are capable of moving relatively long distances in hydrologically connected lacustrine ecosystems. Although translocation is not biologically similar to dispersal, it is plausible that individual movement decisions during post-translocation prospecting periods may be similar to movement decisions during dispersal. Errington (1940, 1963) reported long-distance movements (5-30 km) by muskrats between isolated wetland complexes in agroecosystems. Laurence et al. (2013) found genetic connectivity of muskrat populations in a boreal ecosystem was influenced by landscape composition including negative associations with open landscapes and forests. While I did detect muskrats traveling through interior wetlands hydrologically connected to the main lake, I did not observe radiomarked muskrats colonizing hydrologically isolated interior wetlands likely due to the impermeability of surrounding upland landscapes (mostly conifer and deciduous forest landcover). I did observe translocated muskrats swimming across deep-lake habitats (>5 m depth) exposed to greater levels of wind and wave action (i.e., fetch) to establish home ranges in areas away from their release sites. Recent evidence, however, has suggested that site colonization by muskrats is negatively influenced by greater amounts of fetch present in lacustrine wetlands (Larreur et al. 2020). Similar to the methods described in Laurence et al. (2013), I recommend future research utilize molecular tools to empirically assess the relative permeability of fetch-impacted waterscapes and identify geographic barriers to the connectivity of muskrat populations in boreal ecosystems.

Although translocated muskrats did not orient movements towards their original capture sites, most did not remain in their respective release wetland. Although the 95% confidence intervals for the *v*-test did include 0º (the scaled trajectory towards capture location), Zar (2010) cautioned uniformly distributed trajectories may produce unreliable confidence estimates, as I observed in my dataset. Additionally, muskrats moved longer distances than I anticipated given their size and surrounding landscapes. Significantly larger movement distances in 2019 could reflect the larger sample size in that year or more likely a function of an increased abundance of muskrats near the release sites created by translocations in 2018.

Past studies have used widely different estimation techniques to characterize muskrat home ranges (e.g., Errington 1939, Sather 1958, MacArthur 1978, 1980, Ahlers et al. 2010a) making direct comparisons to my results difficult. However, my estimated home range size of post-translocated muskrats was similar to those of resident muskrats when estimated using minimum convex polygons (Marinelli 1993), though, with the caveat that I am comparing the results of two different methods of home range estimation. In addition, my results were also similar to the home ranges of three resident muskrats within my study area whose home ranges were estimated using the same methods. Due to the method of collecting locations during daylight hours the estimates for home ranges may be underestimated since this would be when muskrats are least active. Muskrats established home ranges ~8 days after translocation though this estimate is likely overestimated as I relocated individuals every ~48 hrs. Relatively low abundances of muskrats within and around release wetlands (and in VNP) likely resulted in increased available habitat, possibly reducing the time required to establish home ranges. I observed translocated muskrats constructing huts and improving existing structures (abandoned or dilapidated beaver lodges) soon after establishing home ranges. These observations underscore plasticity in muskrats' ability to adapt to novel environments or may be a function of available good-quality habitat within their newly established home ranges. Due to the limited battery life of the transmitters and seasonal weather constraints in the study area, I was unable to assess long-term muskrat home range dynamics and structure use. I recommend future research develop methods for remotely tracking the long-term spatial ecology of translocated muskrats in boreal ecosystems.

Survival rates of post-translocated muskrats were similar to other studies of resident muskrat populations (Clark 1987, Clark and Kroeker 1993, Kanda and Fuller 2004, Ahlers et al. 2010b, Ganoe et al. 2019). Weekly muskrat survival was greater in 2019, providing evidence that using soft-release techniques (only used in 2019) enhanced post-translocation survival probabilities. All trapping, handling, and marking techniques were consistent with no appreciable differences in environmental or climatic conditions between years. Soft-release techniques can improve species' survival and enhance acclimation of individuals to novel areas (Tezlaff et al. 2019). Additionally, the use of soft-release structures are common for species that use burrows (Jachowski and Lockhart 2014) or cavities (Woodford et al. 2013). Soft-release structures mimic natural dwellings and, in some cases, serve as long-term surrogates in the absence of natural dwellings (McComb and Noble 1981, Truett et al. 2001), thereby increasing establishment success in novel environments. Subsequent muskrat translocation efforts will likely benefit from incorporating similar soft-release techniques into management plans.

As expected, translocated muskrats that used available beaver lodges had greater weekly survival rates. Moving through unfamiliar landscapes is inherently risky due to predation risk, competition with conspecifics, and lack of shelter or refugia (Waser 1985, Yoder et al. 2004, Berger-Tal et al. 2019). Muskrats rely on huts and burrows for shelter (Errington 1963, Hazard

1982), but shorelines in VNP consisted of granite bedrock or shallow soils preventing the construction of burrows. Moreover, established muskrat huts are likely unavailable to translocated muskrats unless vacated by resident muskrats. Lack of shelter would likely force muskrats to rest in exposed areas or continuously travel until a shelter is located or constructed, exposing them to increased risk of predation. Beavers are ubiquitous throughout VNP hosting the highest reported beaver densities in the United States (Johnston and Windels 2015) creating an abundance of lodges throughout the study area. Beaver lodges likely serve as temporary refugia for muskrats during their prospecting periods and may provide stepping-stone resources during dispersal. Additionally, active lodges (those currently occupied by beavers) may provide predator deterrence. Although muskrat use of beaver lodges is well documented (Leighton 1933, Rosell et al. 2005, Mott et al. 2013), this is the first study to reveal the fitness benefits provided to muskrats using these structures. My results enhance the evidence that beavers can enhance biodiversity and provide critical ecosystem benefits for wetland flora and fauna (e.g., Nummi and Holopainen 2014, Pollock et al 2014, Law et al. 2016, 2017, Windels 2017).

The long-term and widespread decline of muskrat populations necessitates active management efforts, such as translocations, to restore and bolster populations across their native geographic range. My research suggests that survival and spatial ecology of translocated muskrats are similar to resident muskrat populations. However, assuming that translocated muskrats will remain in discrete target wetlands in hydrologically connected systems may be unrealistic. For muskrat translocation efforts to be successful in lacustrine systems, biologists should designate larger geographic areas as targets for population restoration efforts rather than discrete, hydrologically connected wetlands. In addition, I recommend using soft-release techniques to translocate muskrat populations into areas with established beaver populations to improve post-translocation muskrat survival and increase the likelihood of population persistence. Future research regarding the feasibility of muskrat translocations should focus on geographically isolated wetland complexes in other parts of their native range (i.e., prairie potholes, Nebraska sandhill wetlands, coastal plains ponds; Tiner 2003).

Table 2.1 Known-fate model selection results describing survival of translocated muskrats (*Ondatra zibethicus*; n = 65) in lacustrine wetlands in Voyageurs National Park, MN, during summers 2018 and 2019. Models were ranked by differences in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c). *w* = model weight, K = number of parameters within the model, deviance = -2log ([$\log_e$ likelihood of the model)-($\log_e$ likelihood of the saturated model)]. Explanatory variables include Lodge (time-varying covariate indicating if a muskrat was located in a beaver (*Castor canadensis*) lodge during a given week), Year (2018 or 2019), and Prosp (time-varying covariate indicating that an individual was prospecting during a given week). I only present models with $\Delta AIC_c \leq 2.00$ along with the null model for comparison.

Model	ΔAIC_c	*w*	K	Deviance
Lodge + Year	0.00	0.63	3	178.41
Lodge + Year + Prosp	1.79	0.26	4	178.17
Null	16.66	0.00	1	199.10

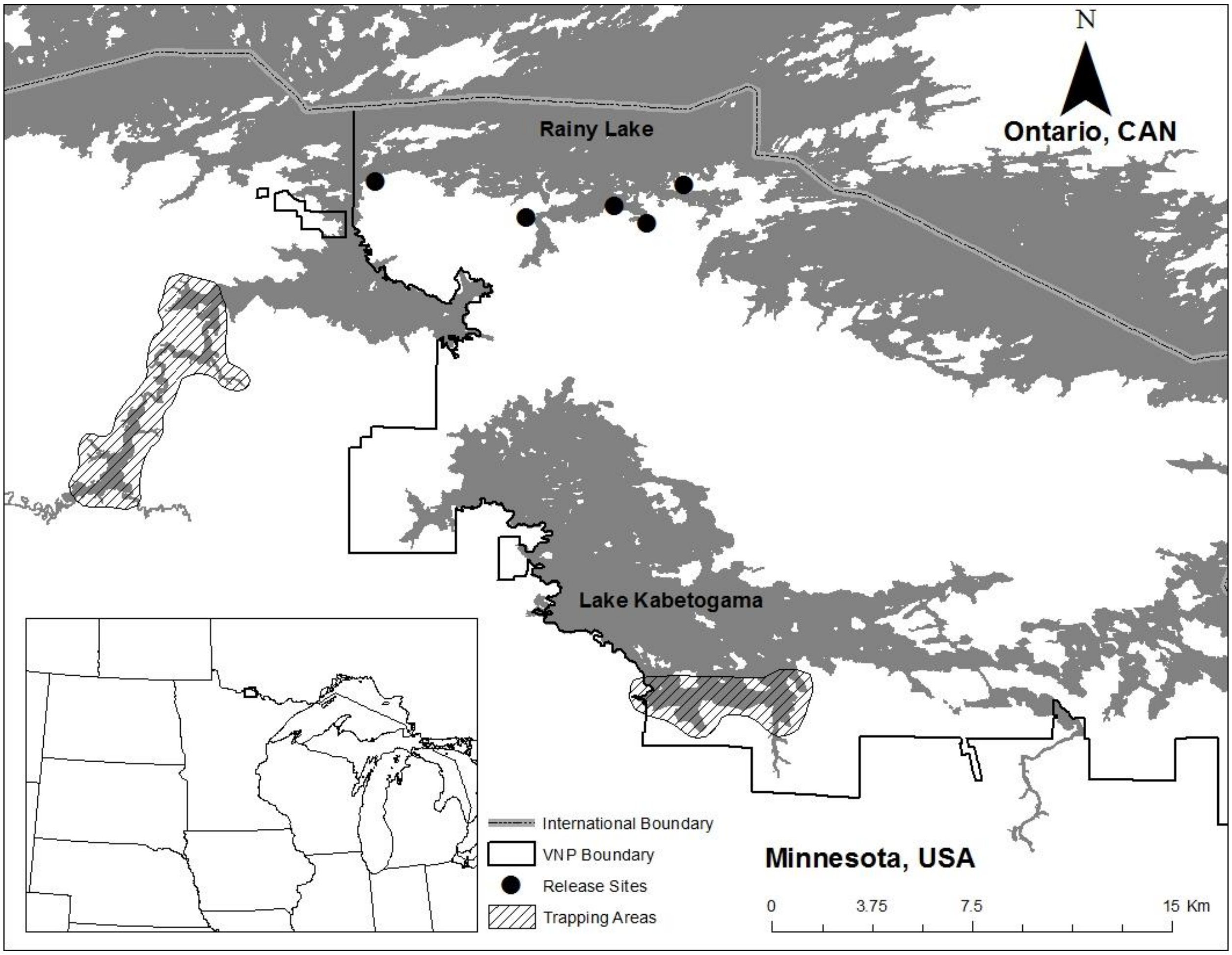

Figure 2.1 Spatial distribution of muskrat (*Ondatra zibethicus*) live-trapping areas and translocation sites (black circles; n = 5) for muskrats in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019**.** Trapping areas (represented by the cross-lined polygons) include the Mud Bay, Irwin Bay, and Daley Bay portion of Lake Kabetogama, the western end of the Black Bay portion of Rainy Lake, and Rat Root Lake, a tributary of Rainy Lake.

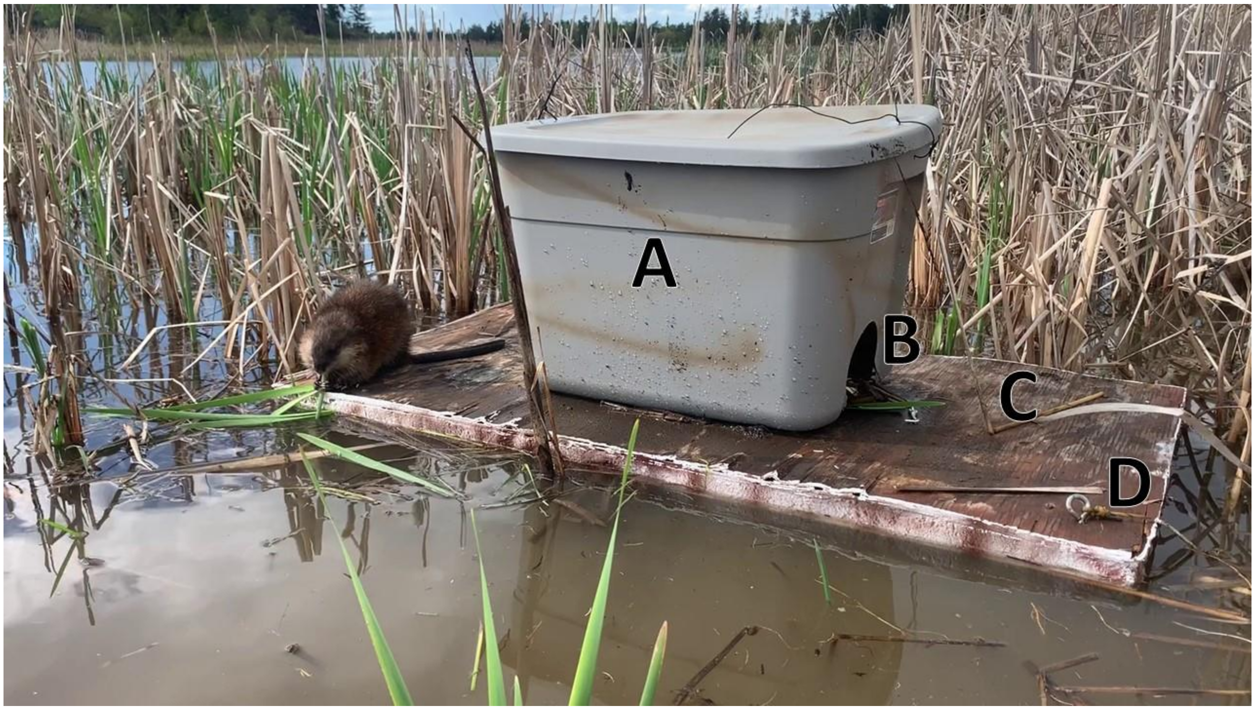

Figure 2.2 Soft-release shelter used to release translocated muskrats (*Ondatra zibethicus*) into wetland habitats in Voyageurs National Park near International Falls, MN, during summer 2019. Shelters were constructed using a 114-l plastic tote with a secured detachable lid (A) with a 15-cm hole cut on the side (B) so muskrats could move freely in and out of the shelter. Shelters were affixed to 122 x 61 x 4-cm floating rafts (C) and tethered to emergent vegetation (D). I partially filled shelters with local vegetation prior to releasing a muskrat inside. Note recently translocated muskrat on a soft-release shelter feeding on invasive cattail (*Typha x glauca*).

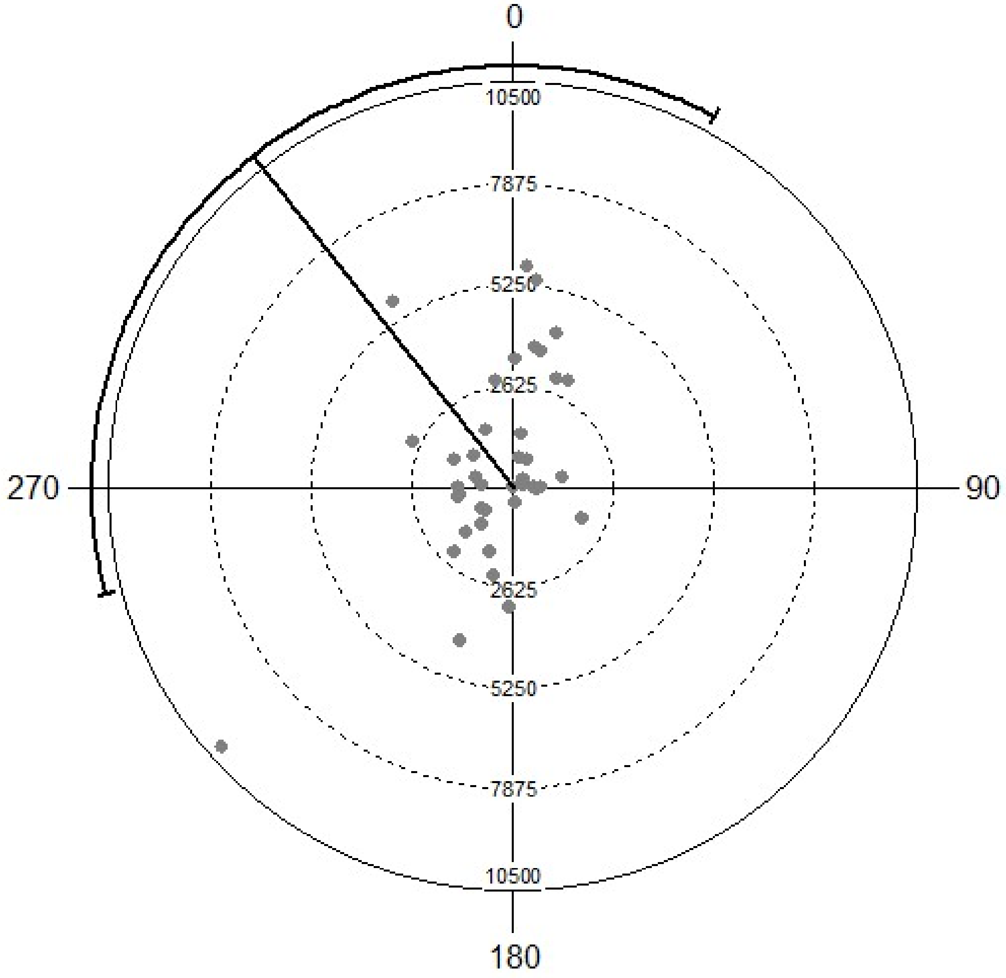

Figure 2.3 Post-translocation movement distances (m) and trajectories (0 - 360º) for radiomarked muskrats (*Ondatra zibethicus*, n = 42) scaled to their individual capture locations (0°). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019.The center of the figure represents individual release locations, grey circles represent individual travel distances (m) and trajectory (º), bold lines represent the mean trajectory for all individuals along with the 95% confidence interval.

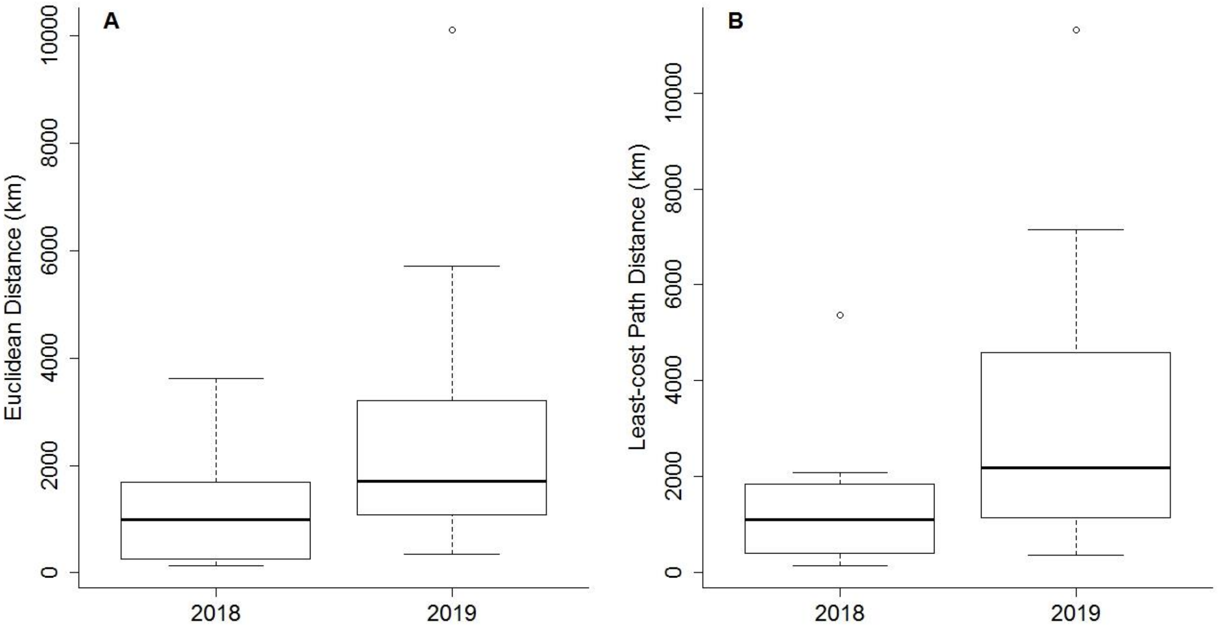

Figure 2.4 Annual differences in median post-translocation Euclidean (A) and least-cost path (B) distances moved by radiomarked muskrats (*Ondatra zibethicus*, n =42). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019. Bold lines represent median values, boxes represent the interquartile range, whiskers represent minimum and maximum values exclusive of outliers, and circles represent outliers.

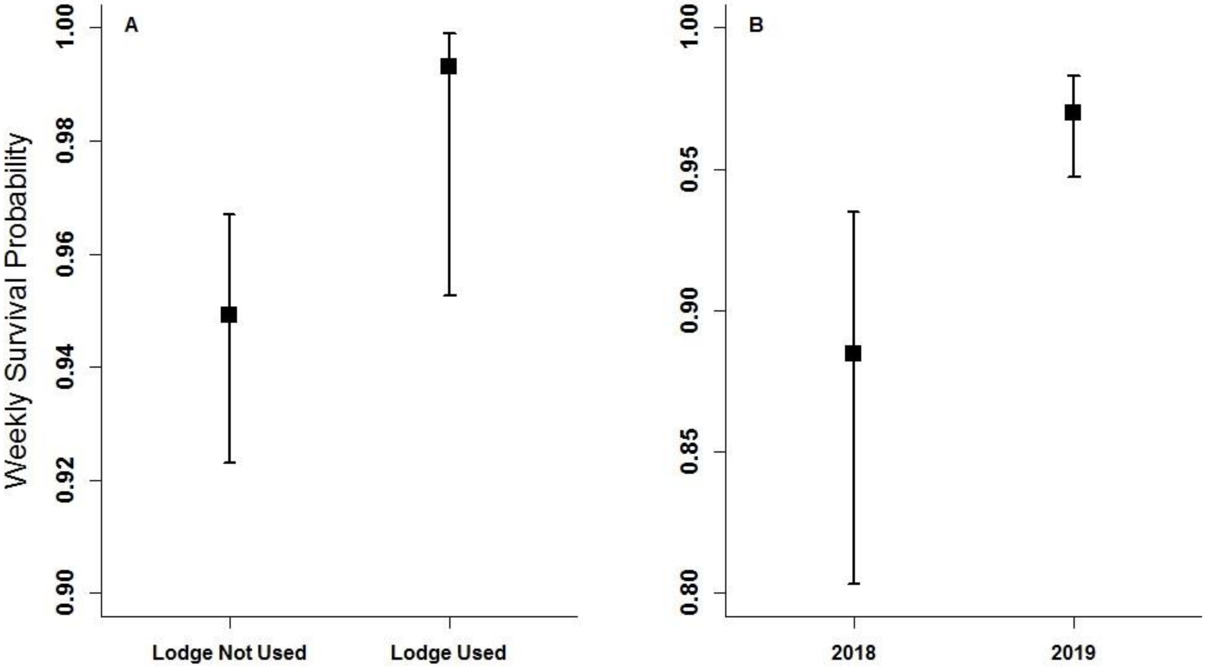

Figure 2.5 Weekly muskrat (*Ondatra zibethicus*, n = 65) survival probabilities (and 95% confidence intervals) derived from my top-ranked known-fate model. Muskrats were radiomarked and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019. Translocated muskrats that used beaver (*Castor canadensis*) lodges had greater weekly survival probabilities (A). Translocated muskrats also had greater weekly survival probabilities in 2019 (B), likely a result of using a soft-release method for translocation that year.

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Chapter 3 - Conclusion

Muskrat (*Ondatra zibethicus*) populations are declining throughout North America (Roberts and Crimmins 2010, Ahlers and Heske 2017, Greggory et al. 2019) with little evidence indicating why. Considered an ecosystem engineer (Bomske and Ahlers *In Revision*), muskrats populations can reduce wetland vegetative coverage and promote wetland species richness (Nyman et al. 1993). Structures created by muskrats provide habitat for aquatic invertebrates (de Szalay and Cassidy 2001, Nummi et al. 2006) and are often utilized as avian nest foundations (Kiviat 1978). Reductions in wetland habitat quality and access to one of the most widely trapped furbearers in North America (White et al. 2015) has sparked interest in active management of this ecologically and economically important furbearer. Historically, muskrat translocation efforts were implemented to expand the range of muskrats throughout North America with the explicit intention of providing increased opportunity for trappers (Storer 1937, O'Neil 1949). The success of these efforts, similar to other species' translocation efforts, is largely unknown. Contemporary translocation research emphasizes the need for scientifically rigorous studies to investigate the success and viability of translocation efforts, though information is still lacking for muskrats populations.

Invasive hybrid cattails (*Typha x glauca*) are a common invader in wetlands throughout the United States (Bansal et al. 2019). These cattails aggressively outcompete native vegetation through rapid rhizomal reproduction and formation of dense floating mats extending into open water habitats, effectively reducing the amount of available habitat to wetland flora and fauna (Bansal et al. 2019). My research was part of a larger study to investigate possible methods of control and reduction of *T. x glauca* (Brulliard 2018). Though the full scope that study was beyond the scope of my thesis research, an investigation into the feasibility of using translocated muskrats as a method of vegetation management was warranted to fully understand the realism of the ultimate management goals.

Using two years of survival and telemetry data from 65 translocated muskrats, I quantified post-translocation survival and spatial ecology of muskrats within a lacustrine ecosystem in Voyageurs National Park (VNP), Minnesota, USA. During the summers of 2018-2019, I collected 1,451 telemetry locations from post-translocated muskrats to quantify average prospecting period, distances traveled after release, subsequent home range sizes, and potential homing behaviors. I also quantified weekly survival of post-translocated muskrats and related these rates to intrinsic and biological covariates. I detected 23 mortalities, three of these from mink (*Neovison vison*) and one from a bald eagle (*Haliaeetus leucocephalus*). My results suggest that muskrats are capable of traveling greater distances than hypothesized (relative to their body size). Additionally, I detected no homing behaviors and found the average prospecting period comparable to similar species (Van Vuren 1997) and average home range size similar to those of resident muskrats (Marinelli 1993, Ahlers et al. 2010). Individuals that used beaver lodges and those released using soft-release structures had greater weekly survival rates than those that did not. Although previous research documented commensalism between muskrats and beavers (Leighton 1993, Rosell et al. 2005, Mott et al. 2013), mine was the first study to uncover the potential benefits to muskrats provided by beavers.

My research provided evidence that translocation of muskrats is a viable population recovery technique, although muskrats largely did not remain in the targeted wetlands. This evidence corroborates anecdotal accounts from historical translocation efforts (Storer 1937, O’Neil 1949, Idaho Game and Fish 2015) and provides a basis for modern efforts. Growing evidence supports muskrats as a vital component of healthy wetland ecosystems (Bomske and

Ahlers *In Revision*) and increased muskrat abundances can decrease cover of more aggressive vegetation within wetlands (e.g., *Typha* spp; Tyndall 2011, Bansal et al. 2019). Using telemetry data and known-fate analyses I uncovered landscape variables and translocation techniques that improve the weekly survival probability and success of translocated muskrats. Integration of these variables into management plans targeted towards muskrat recovery could help increase the potential for a successful effort. Future research focused on similar efforts in hydrologically isolated wetlands would provide additional needed information regarding the feasibility of muskrat translocations and the effects surrounding habitats may have.

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