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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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.

Literature Cited

Ahlers, A. A. et al. 2016. Influences on trapper participation and per capita harvest of muskrat. – J. Wildl. Manage. 40: 548-553.

Ahlers, A. A. and Heske, E. J. 2017. Empirical evidence for declines in muskrat populations across the United States. – J. Wildl. Manage. 81: 1408-1416.

Anderson, C. B. et al. 2006. Exotic vertebrate fauna in the remote and pristine sub-Antarctic Cape Horn archipelago, Chile. – Biodivers. Conserv. 15: 3295-3313.

Bansal, S. et al. 2019. *Typha* (cattail) invasion in North American wetlands: biology, regional problems, impacts, ecosystem services, and management. – Wetlands 39: 645-684.

Berger-Tal, O. et al. 2019. Conservation translocations: a review of common difficulties and promising directions. – Anim. Conserv. doi:10.1111/acv.12534

Bomske, C. M. and Ahlers, A. A. *In Revision*. How do muskrats influence ecosystems? A review of evidence. – Mammal Rev.

Brietzke, C. 2015. Muskrat ecology in the Mackenzie Delta: insights from local knowledge and ecological field surveys. – Arctic 68: 527-531.

Craven, S. et al. 1998. Toward a professional position on the translocation of problem wildlife. – Wildl. Soc. Bull. 26: 171-177.

Erb, J. E. and Perry Jr, H. R. 2003. Muskrats (*Ondatra zibethicus* and *Neofiber alleni*). Wild mammals of North America, biology, management, and conservation, Second Edition. – Johns Hopkins University Press.

Gregory, G. J. et al. 2019. Declines in muskrat (*Ondatra zibethicus*) population density on Prince Edward Island, CA. – Can. Wildl. Biol. Manage. 8: 46-60.

Hazard, E. B. 1982. The mammals of Minnesota. – University of Minnesota Press.

Jachowski, D. S. and Lockhart, J. M. 2009. Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. – Small Mammal Conserv. 41: 58-64.

Kiviat, E. 1978. Vertebrate use of muskrat lodges and burrows. – Estuaries 1: 196-200.

Law, A. et al. 2017. Using ecosystem engineers in habitat restoration and rewilding: beaver and wetlands. – Sci. Total Environ. 605-606: 1021-1030.

Lehrer, E. W. et al. 2016. Happily ever after? Fates of translocated nuisance woodchucks in the Chicago metropolitan area. – Urban Ecosyst. 19: 1389-1403.

Massei, G. et al. 2010. Can translocations be used to mitigate human-wildlife conflicts? – Wildlife Res. 27: 428-439.

Nummi, P. et al. 2006. Alien grazing: Indirect effects of muskrats on invertebrates. – Biol. Invasions 8: 993–999.

Nyman, J. A. et al. 1993. Some effects of herbivory and 30 years of weir management on emergent vegetation in Brackish Marsh. – Wetlands 13: 165-175.

Olson, P. M. O. et al. 2007. Movement and activity patterns of translocated elk (*Cervus elephus nelsoni*) on an active coal mine in Kentucky. – Wildl. Biol. Pract. 3: 1-8.

O'Neil, T. Muskrat in the Louisiana coastal marshes. – Louisiana Department of Wildlife and Fisheries. New Orleans, LA.

Paul, T. W. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. – Alaska Department of Fish and Game. Juneau, Alaska. 150pp.

Roberts, N. M. and Crimmins, S. M. 2010. Do trends in muskrat harvest indicate widespread population declines? – Northeast. Nat. 17: 229-238.

Straka, J. R. et al. 2018. "We used to say rats fell from the sky after a flood": temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta. – Arctic 71: 218-228.

Storer, T. I. 1937. The muskrat as a native and alien. – J. Mammal. 18: 443-460.

de Szalay, F. A. and Cassidy, W. 2001. Effects of muskrat (*Ondatra zibethicus*) lodge construction on invertebrate communities in a Great Lakes coastal wetland. – Am. Midl. Nat. 146: 300-310.

Thurber, J. M. et al. 1991. The effect of regulated lake levels on muskrats, *Ondatra zibethicus*, in Voyageurs National Park, Minnesota. – Can. Field-Nat. 105: 34-40.

Turner, C. K., et al. 2018. Springtime in the Delta: the socio-cultural importance of muskrats to Gwich'in and Inuvialuit trappers through periods of ecological and socioeconomic change. – Human Ecology 46: 601-611.

Tyndall, R. W. 2011. Long-term monitoring of two subpopulations of the federally threatened Aeschynomene virginica (sensitive joint-vetch) in Maryland. – Castanea 76: 20-27.

Van Vuren, D. et al. 1997. Translocations as a nonlethal alternative for managing California ground squirrels. – J. Wildl. Manage. 61: 351-359.

Werdel T. J. et al. 2019. Restoration of a bighorn sheep population impeded by *Mycoplasm ovipneumoniae* exposure. – Restor. Ecol. 28: 387-395.

White, H. B. et al. 2015. Trapping and furbearer management in North America wildlife conservation. – Int. 5: 756-769.

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, $\Sigma\omega_{Lodge}$= 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, $\Sigma\omega_{Year}$= 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

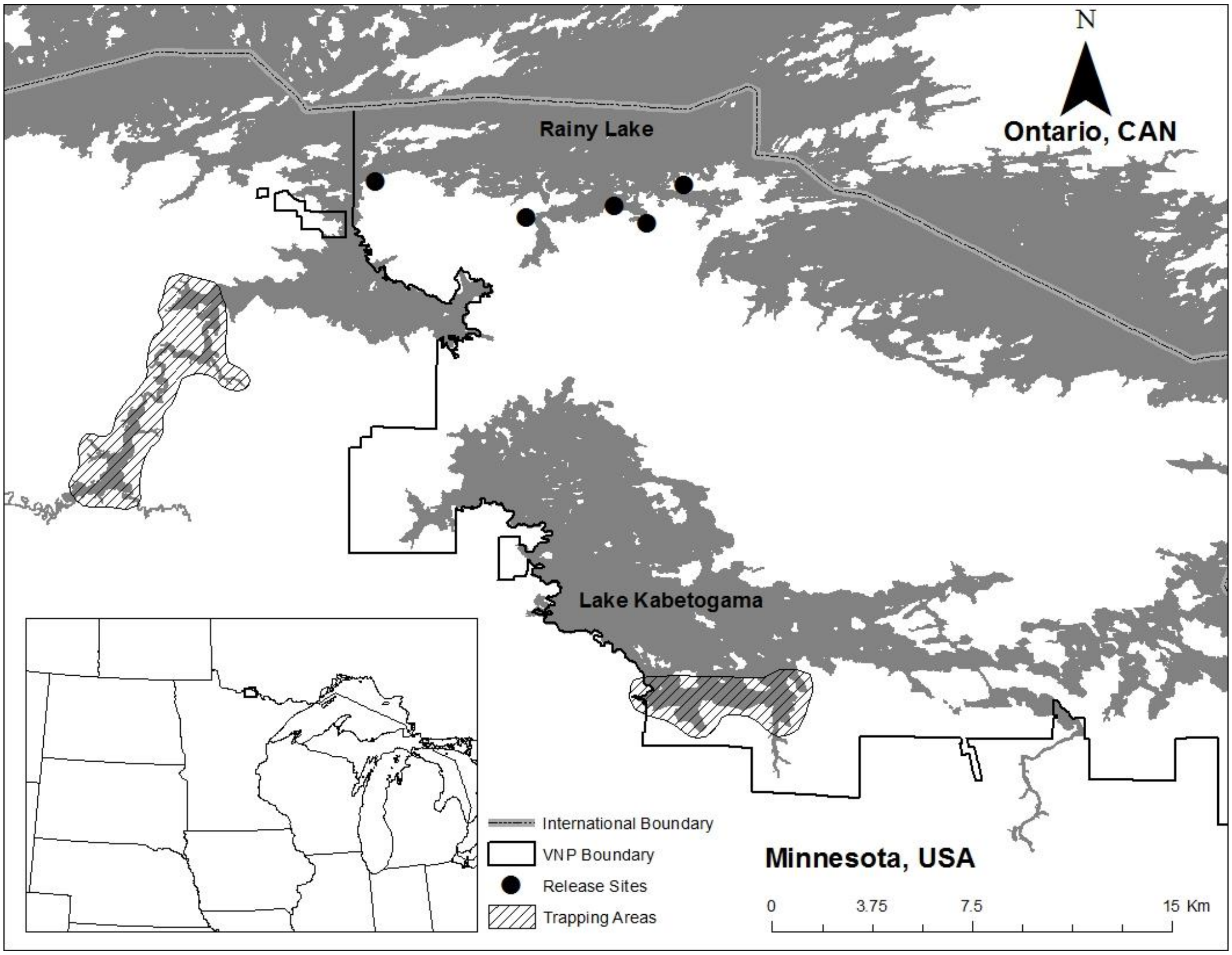

Figure 2.1 Spatial distribution of muskrat (*Ondatra zibethicus*) live-trapping areas and translocation sites (black circles; n = 5) for muskrats in Voyageurs National Park near International Falls, MN, during summers of 2018 and 2019**.** Trapping areas (represented by the cross-lined polygons) include 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.

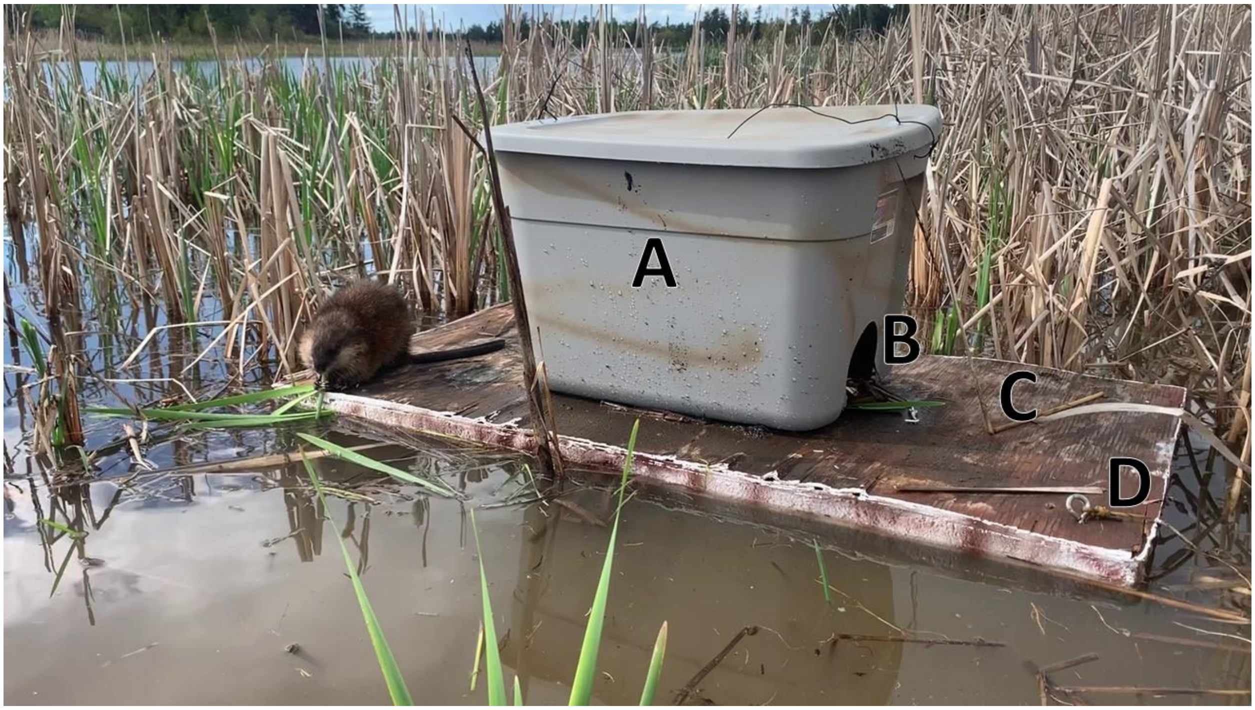

Figure 2.2 Soft-release shelter used to release translocated muskrats (*Ondatra zibethicus*) into wetland habitats in Voyageurs National Park near International Falls, MN, during summer 2019. Shelters were constructed using a 114-l plastic tote with a secured detachable lid (A) with a 15-cm hole cut 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*).

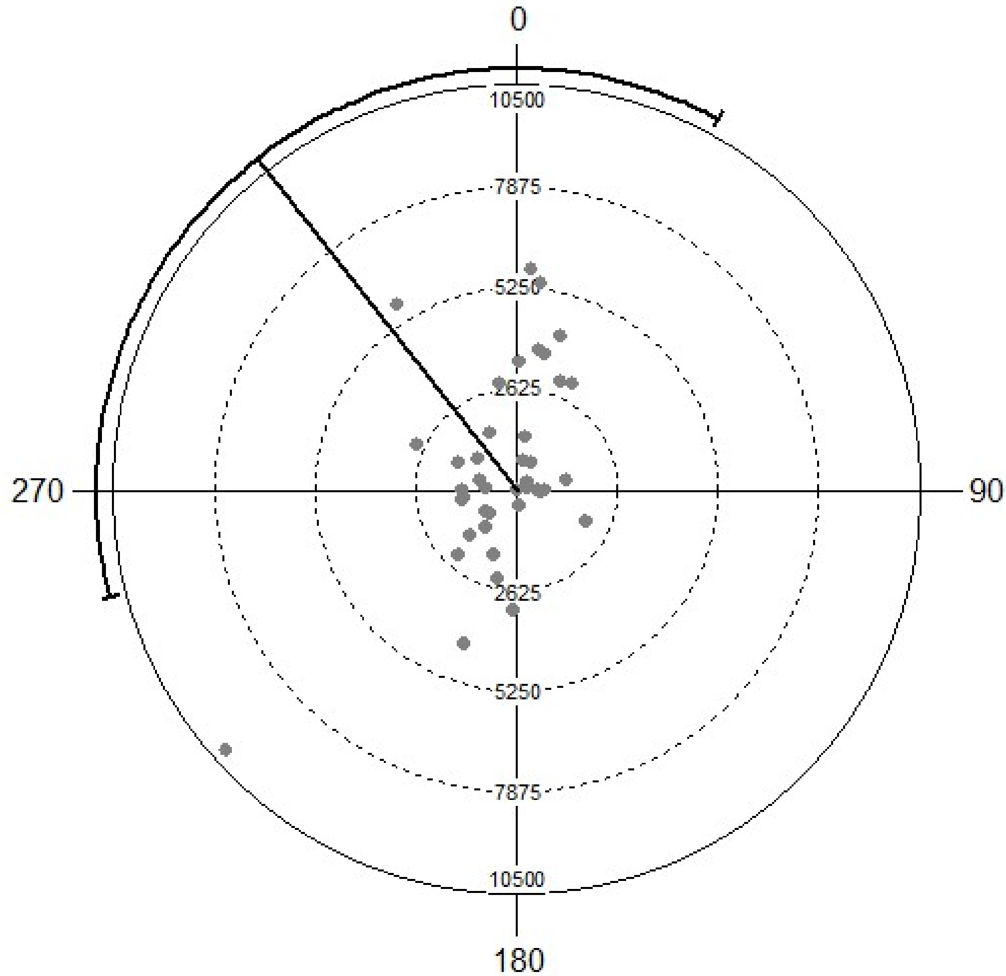

Figure 2.3 Post-translocation movement distances (m) and trajectories (0 - 360º) for radiomarked muskrats (*Ondatra zibethicus*, n = 42) scaled to their individual capture locations (0°). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International 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.

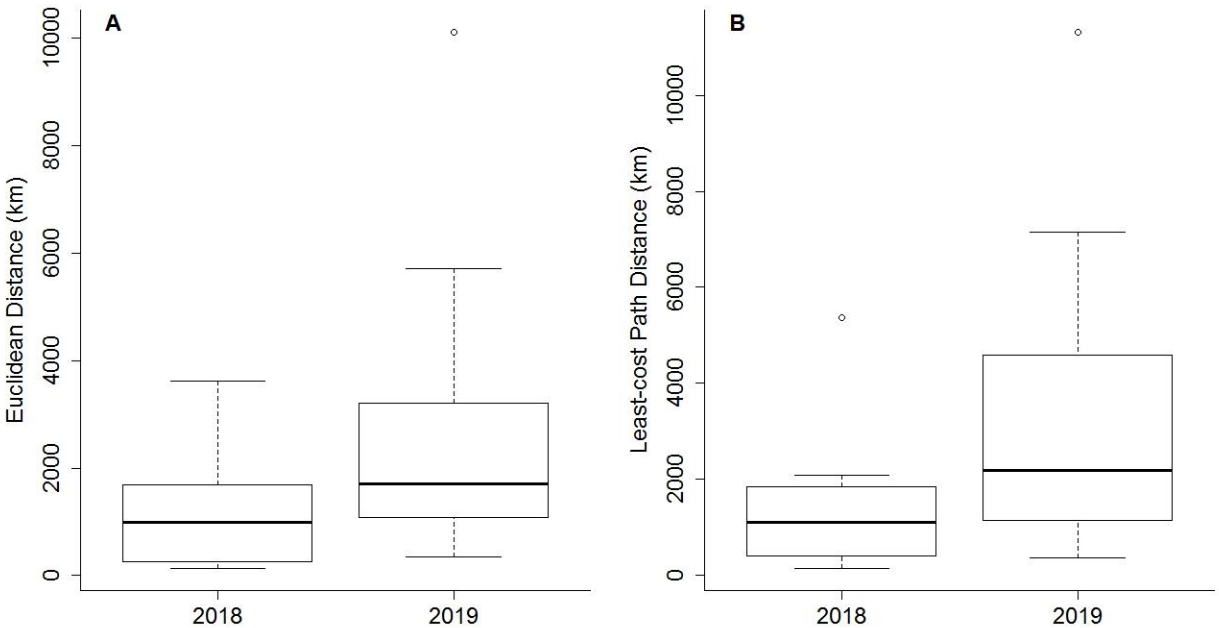

Figure 2.4 Annual differences in median post-translocation Euclidean (A) and least-cost path (B) distances moved by radiomarked muskrats (*Ondatra zibethicus*, n =42). Muskrats were live-trapped and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during 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.

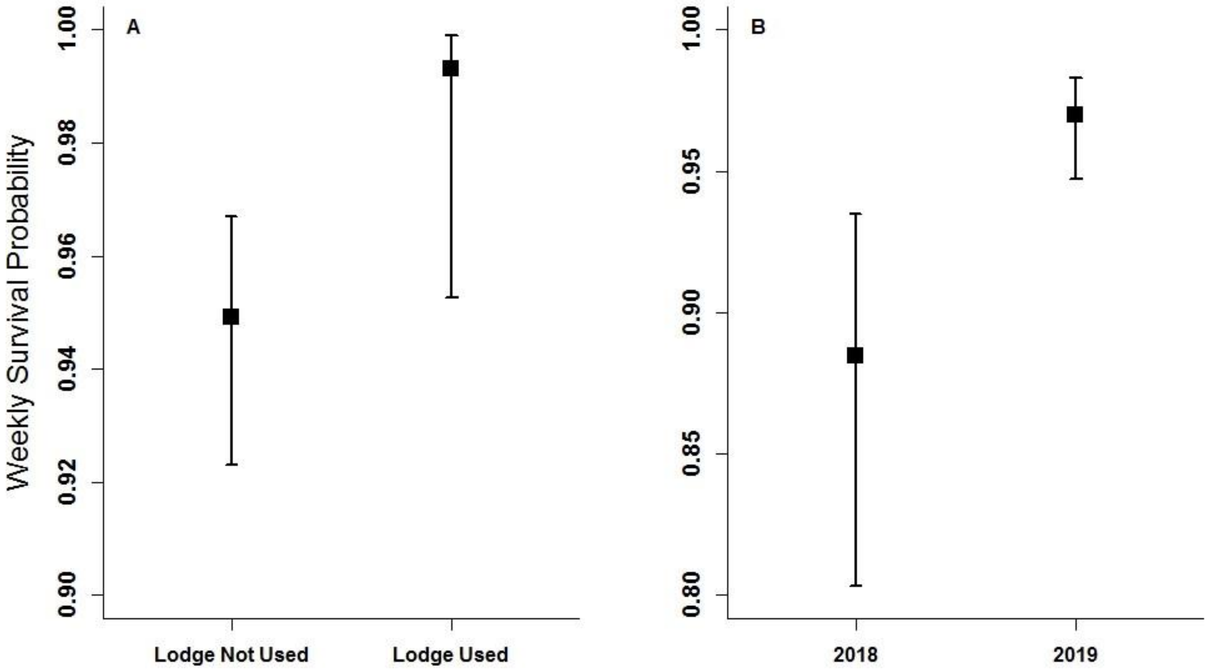

Figure 2.5 Weekly muskrat (*Ondatra zibethicus*, n = 65) survival probabilities (and 95% confidence intervals) derived from my top-ranked known-fate model. Muskrats were radiomarked and translocated into lacustrine wetlands in Voyageurs National Park near International Falls, MN, during summers of 2018 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.

Literature Cited

Ahlers, A. A. et al. 2010a. Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. – Wildl. Biol. 16: 400-408.

Ahlers, A. A. et al. 2010b. Effects of flooding and riparian buffers on survival of muskrats (*Ondatra zibethicus*) across a flashiness gradient. – Can. J. Zool. 88: 1011-1020.

Ahlers, A. A. et al. 2011. Hematologic and blood chemistry reference values for free-ranging riparian muskrats (*Ondatra zibethicus*). – J. Wildl. Dis. 47: 685-689.

Ahlers, A. A. et al. 2015. Summer precipitation predicts spatial distributions of semiaquatic mammals. – PLoS ONE 10: e0135036.

Ahlers, A. A. et al. 2016. Influences on trapper participation and per capita harvest of muskrat. – J. Wildl. Manage. 40: 548-553.

Ahlers, A. A. and Heske, E. J. 2017. Empirical evidence for declines in muskrat populations across the United States. – J. Wildl. Manage. 81: 1408-1416.

Ahlers, A. A. et al. *In Press*. Survey of *Toxoplasma gondii* exposure in muskrats in a relatively pristine ecosystem. – J. Parasitol.

Aleksiuk, M. 1970. The function of the tail as a fat storage depot in the beaver (*Castor canadensis*). – J. Mammal. 51: 145-148.

Anderson, C. B. et al. 2006. Exotic vertebrate fauna in the remote and pristine sub-Antarctic Cape Horn archipelago, Chile. – Biodivers. Conserv. 15: 3295-3313.

Bansal, S. et al. 2019. *Typha* (cattail) invasion in North American wetlands: biology, regional problems, impacts, ecosystem services, and management. – Wetlands 39: 645-684.

Berger-Tal, O. et al. 2019. Conservation translocations: a review of common difficulties and promising directions. – Anim. Conserv. doi:10.1111/acv.12534

Bhattacharjee, J. et al. 2007. Vegetation response to disturbance in a coastal marsh in Texas. – Community Ecol. 8: 15-24.

Bomske, C. M. and Ahlers, A. A. *In Revision*. How do muskrats influence ecosystems? A review of evidence. – Mammal Rev.

Brietzke, C. 2015. Muskrat ecology in the Mackenzie Delta: insights from local knowledge and ecological field surveys. – Arctic 68: 527-531.

Brulliard, N. 2018. Muskrats to the Rescue. – National Parks Magazine, Fall 2018. https://www.npca.org/articles/1919-muskrats-to-the-rescue (accessed 05 February 2020).

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. – Springer.

Calenge, C. 2006. The package adehabitatHR for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516-519.

Calvete, C. and Estrada, R. 2004. Short-term survival and dispersal of translocated European wild rabbits. Improving the release protocol. – Biol. Conserv. 120: 507-516.

Christensen, V. G. and Maki, R. P. 2014. Trophic state in Voyageurs National Park lakes before and after implementation of a revised water-level management plan. – J. Am. Water Resour. As. 51: 99-111.

Clark, W. R. 1987. Effects of harvest on annual survival of muskrats. – J. Wildl. Manage. 51: 265-272.

Clark, W. R. and Kroeker, D. W. 1993. Population dynamics of muskrats in experimental marshes at Delta, Manitoba. – Can. J. Zool. 71: 1620-1628.

Cooch, E. G. and White, G. 2008. Program MARK: a gentle introduction. 6th ed.

Cooney, S. A. et al. 2015. Comparing permeability of matrix cover types for the marsh rice rat (*Oryzomys palustris*). – Landsc. Ecol. 30: 1307-1320.

Davis, J. R. et al. 1984. Implantable telemetry in beaver. – Wildl. Soc. Bull. 12: 322-324.

Day, C. C. et al. 2013. Factors influencing mortality associated with the translocation of northern river otters (*Lontra canadensis*) in Utah. – West. N. Am. Nat. 73: 357-364.

Erb, J. E. and Perry Jr, H. R. 2003. Muskrats (*Ondatra zibethicus* and *Neofiber alleni*). Wild mammals of North America, biology, management, and conservation, Second Edition. – Johns Hopkins University Press.

Errington, P. L. 1939: Reaction of muskrat populations to drought. – Ecology 20: 168-186.

Errington, P. L. 1940. Natural restocking of muskrat-vacant habitats. – J. Wildl. Manage. 4: 173-185.

Errington, P. L. 1963. Muskrat Populations. – Iowa State University Press.

ESRI. 2016. ArcGIS desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Ganoe, L. S. et al. 2019. Using a multi-faceted approach to assess ecological components affecting muskrat (*Ondatra zibethicus*) populations. Master's Thesis

Germano, J. M. et al. 2015. Mitigation-driven translocations: are we moving in the right direction? – Front. Ecol. Environ. 13: 100-105.

Greggory, G. J. et al. 2019. Declines in muskrat (*Ondatra zibethicus*) population density on Prince Edward Island, CA. – Can. Wildl. Biol. Manage. 8: 46-60.

Hazard, E. B. 1982. The mammals of Minnesota. – University of Minnesota Press.

Hickman, G. C. 1979. The mammalian tail: a review of functions. – Mammal Rev. 9: 143-157.

Idaho Fish and Game 2015. Fur for the future. – YouTube. https://www.youtube.com/watch?v=APLz2bTprMA

Jachowski, D. S. and Lockhart, J. M. 2009. Reintroducing the black-footed ferret *Mustela nigripes* to the Great Plains of North America. – Small Mammal Conserv. 41: 58-64.

Johnston, C. A. and Windels, S. K. 2015. Using beaver works to estimate colony activity in boreal landscapes. J. Wildl. Manage. 79: 1072-1080.

Kanda, L. L. and Fuller, T. K. 2004. Demographic responses of Virginia opossums to limitations at their northern boundary. – Can. J. Zool. 82: 1126-1134.

Kiviat, E. 1978. Vertebrate use of muskrat lodges and burrows. – Estuaries 1: 196-200.

Landler, L. et al. 2018: Circular data in biology: advice for effectively implementing statistical procedures. – Behav. Ecol. Sociobiol. 72, 128. https://doi.org/10.1007/s00265-018-2538-y

Larreur, M. R. et al. 2020. Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. – Landsc. Ecol. 35: 59-68.

Laurence, S. et al. 2013. Effects of structural connectivity on fine scale population genetic structure of muskrat, *Ondatra zibethicus*. – Ecol. Evol. 3: 3524-3535.

Law, A. et al. 2016. Habitat engineering by beaver benefits aquatic biodiversity and ecosystem processes in agricultural streams. – Freshw. Biol. 61: 486-499.

Law, A. et al. 2017. Using ecosystem engineers in habitat restoration and rewilding: beaver and wetlands. – Sci. Total Environ. 605-606: 1021-1030.

Leighton, A. H. 1933. Notes on the relations of beavers to one another and to the muskrat. – J. Mammal. 14: 27-35.

Lehrer, E. W. et al. 2016. Happily ever after? Fates of translocated nuisance woodchucks in the Chicago metropolitan area. – Urban Ecosyst. 19: 1389-1403.

MacArthur, R. A. 1978. Winter movements and home ranges of the muskrat. – Can. Field-Nat. 92: 345-349.

MacArthur, R. A. 1980. Daily and seasonal activity patterns of the muskrat *Ondatra zibethicus* as revealed by radiotelemetry. – Ecography 3: 1-9.

Marinelli, L. and Messier, F. 1993. Space use and social system of muskrats. – Can. J. Zool. 71: 869-875.

McComb, W. C. and Noble, R. E. 1981. Nest-box and natural-cavity use in three mid-south forest habitats. – J. Wildl. Manage. 45: 93-101.

McKinstry, M. C. and Anderson, S. H. 2002. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. – Can. Field-Nat. 116: 60-68.

Mott, C. L. et al. 2013. Within-lodge interactions between two ecosystem engineers, beavers (*Castor Canadensis*) and muskrats (*Ondatra zibethicus*). – Behavior 150: 1325-1344.

Nummi, P. et al. 2006. Alien grazing: Indirect effects of muskrats on invertebrates. – Biol. Invasions 8: 993–999.

Nummi, P. and Holopainen, S. 2014. Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. – Aquatic Conservation 24: 623-633.

Nyman, J. A. et al. 1993. Some effects of herbivory and 30 years of weir management on emergent vegetation in Brackish Marsh. – Wetlands 13: 165-175.

Olson, P. M. O. et al. 2007. Movement and activity patterns of translocated elk (*Cervus elephus nelsoni*) on an active coal mine in Kentucky. – Wildl. Biol. Pract. 3: 1-8.

O'Neil, T. Muskrat in the Louisiana coastal marshes. – Louisiana Department of Wildlife and Fisheries. New Orleans, LA.

Paul, T. W. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. – Alaska Department of Fish and Game. Juneau, Alaska. 150pp.

Pollock, M. M. et al. 2014. Using beaver dams to restore incised stream ecosystems. – Bioscience 64: 279-290.

Reynolds, J. et al. 2004. Development of population control strategies for mink *Mustela vison*, using floating rafts as monitors and trap sites. – Biol. Conserv. 120: 533–543.

Roberts, N. M. and Crimmins, S. M. 2010. Do trends in muskrat harvest indicate widespread population declines? – Northeast. Nat. 17: 229-238.

Rosell, F. et al. 2005. Ecological impacts of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. – Mammal Rev. 35: 248-276.

Sather, J. H. 1958: Biology of the Great Plains muskrat in Nebraska. – Wildl. Monogr. 2: 1-35.

Schooley, R. L. and Branch, L. C. 2006. Space use by round-tailed muskrats in isolated wetlands. – J. Mammal. 87: 495-500.

Schooley, R. L. et al. 2012. Monitoring site occupancy for American mink in its native range. – J. Wildl. Manage. 76: 824–831.

Sikes, S. S. and the Animal Care and Use Committee of the American Society of Mammologists. 2016. 2016 Guidelines of the American Society of Mammologists for the use of wild mammals in research and education. – J. Mammal. 97: 663-688.

Smith, D. W. and Jenkins, S. H. 1997. Change in body mass and size of tail of northern beavers. – J. Mammal. 78: 869-876.

Smith, J. B. et al. 2016. Do transmitters affect survival and body condition of American Beavers (*Castor canadensis*)? – Wildl. Biol. 22: 117-123.

Straka, J. R. et al. 2018. "We used to say rats fell from the sky after a flood": temporary recovery of muskrat following ice jams in the Peace-Athabasca Delta. – Arctic 71: 218-228.

Storer, T. I. 1937. The muskrat as a native and alien. – J. Mammal. 18: 443-460.

de Szalay, F. A. and Cassidy, W. 2001. Effects of muskrat (*Ondatra zibethicus*) lodge construction on invertebrate communities in a Great Lakes coastal wetland. – Am. Midl. Nat. 146: 300-310.

Tezlaff, S. J. et al. 2019. Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. – Biol. Conserv. 236: 324-331.

Tiner, R. W. 2003. Geographically isolated wetlands of the United States. – Wetlands 23: 494-516.

Truett, J. C. et al. 2001. Translocating prairie dogs: a review. – Wildl. Soc. Bull. 29: 863-872.

Turner, C. K., et al. 2018. Springtime in the Delta: the socio-cultural importance of muskrats to Gwich'in and Inuvialuit trappers through periods of ecological and socioeconomic change. – Human Ecology 46: 601-611.

Tyndall, R. W. 2011. Long-term monitoring of two subpopulations of the federally threatened Aeschynomene virginica (sensitive joint-vetch) in Maryland. – Castanea 76: 20-27.

Van Vuren, D. et al. 1997. Translocations as a nonlethal alternative for managing California ground squirrels. – J. Wildl. Manage. 61: 351-359.

Vilasenor, N. R. et al. 2012. There is no place like home: high homing rate and increased mortality after translocation of a small mammal. – Eur. J. Wildl. Res. 59: 749-760.

Waser, P. M. 1985. Does competition drive dispersal? – Ecology. 66: 1170-1175.

Willner, G. R. et al. 1980. Ondatra zibethicus. – Mammal. Species. 141: 1-8.

Werdel, T. J. and Jenks, J. A. 2018. Survival of translocated bighorn sheep in the Deadwood region of the Black Hills, South Dakota. Northwest. Nat. 99: 222-231.

Werdel T. J. et al. 2019. Restoration of a bighorn sheep population impeded by *Mycoplasm ovipneumoniae* exposure. – Restor. Ecol. 28: 387-395.

Woodford, J. E. et al. 2013. Movement, survival, and home range size of translocated martens (*Martes americana*) in Wisconsin. – Wildl. Soc. Bull. 37: 616-622.

Yoder, J. M. et al. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. –Behav. Ecol. 3: 469-476.

Zar, J. H. 2010. Biostatistical analysis; fifth edition. – Prentice Hall.

Zollner, P. A. and Lima, S. L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. – Oikos 80: 51-60.

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.

Literature Cited

Ahlers, A. A. et al. 2010. Home ranges and space use of muskrats *Ondatra zibethicus* in restricted linear habitats. – Wildl. Biol. 16: 400-408.

Ahlers, A. A. and Heske, E. J. 2017. Empirical evidence for declines in muskrat populations across the United States. – J. Wildl. Manage. 81: 1408-1416.

Bansal, S. et al. 2019. *Typha* (cattail) invasion in North American wetlands: biology, regional problems, impacts, ecosystem services, and management. – Wetlands 39: 645-684.

Bomske, C. M. and Ahlers, A. A. *In Revision*. How do muskrats influence ecosystems? A review of evidence. – Mammal Rev.

Brulliard, N. 2018. Muskrats to the Rescue. – National Parks Magazine, Fall 2018. https://www.npca.org/articles/1919-muskrats-to-the-rescue (accessed 05 February 2020).

Gregory, G. J. et al. 2019. Declines in muskrat (*Ondatra zibethicus*) population density on Prince Edward Island, CA. – Can. Wildl. Biol. Manage. 8: 46-60.

Idaho Fish and Game 2015. Fur for the future. – YouTube. https://www.youtube.com/watch?v=APLz2bTprMA

Kiviat, E. 1978. Vertebrate use of muskrat lodges and burrows. – Estuaries 1: 196-200.

Leighton, A. H. 1933. Notes on the relations of beavers to one another and to the muskrat. – J. Mammal. 14: 27-35.

Marinelli, L. and Messier, F. 1993. Space use and social system of muskrats. – Can. J. Zool. 71: 869-875.

Mott, C. L. et al. 2013. Within-lodge interactions between two ecosystem engineers, beavers (*Castor Canadensis*) and muskrats (*Ondatra zibethicus*). – Behavior 150: 1325-1344.

Nummi, P. et al. 2006. Alien grazing: Indirect effects of muskrats on invertebrates. – Biol. Invasions 8: 993–999.

Nyman, J. A. et al. 1993. Some effects of herbivory and 30 years of weir management on emergent vegetation in Brackish Marsh. – Wetlands 13: 165-175.

O'Neil, T. Muskrat in the Louisiana coastal marshes. – Louisiana Department of Wildlife and Fisheries. New Orleans, LA.

Roberts, N. M. and Crimmins, S. M. 2010. Do trends in muskrat harvest indicate widespread population declines? – Northeast. Nat. 17: 229-238.

Rosell, F. et al. 2005. Ecological impacts of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. – Mammal Rev. 35: 248-276.

Storer, T. I. 1937. The muskrat as a native and alien. – J. Mammal. 18: 443-460.

de Szalay, F. A. and Cassidy, W. 2001. Effects of muskrat (*Ondatra zibethicus*) lodge construction on invertebrate communities in a Great Lakes coastal wetland. – Am. Midl. Nat. 146: 300-310.

Tyndall, R. W. 2011. Long-term monitoring of two subpopulations of the federally threatened Aeschynomene virginica (sensitive joint-vetch) in Maryland. – Castanea 76: 20-27.

Van Vuren, D. et al. 1997. Translocations as a nonlethal alternative for managing California ground squirrels. – J. Wildl. Manage. 61: 351-359.

White, H. B. et al. 2015. Trapping and furbearer management in North America wildlife conservation. – Int. 5: 756-769.