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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, Gregory 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). McKinsty 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* × *glaucia*; 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* × *glaucia*, 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

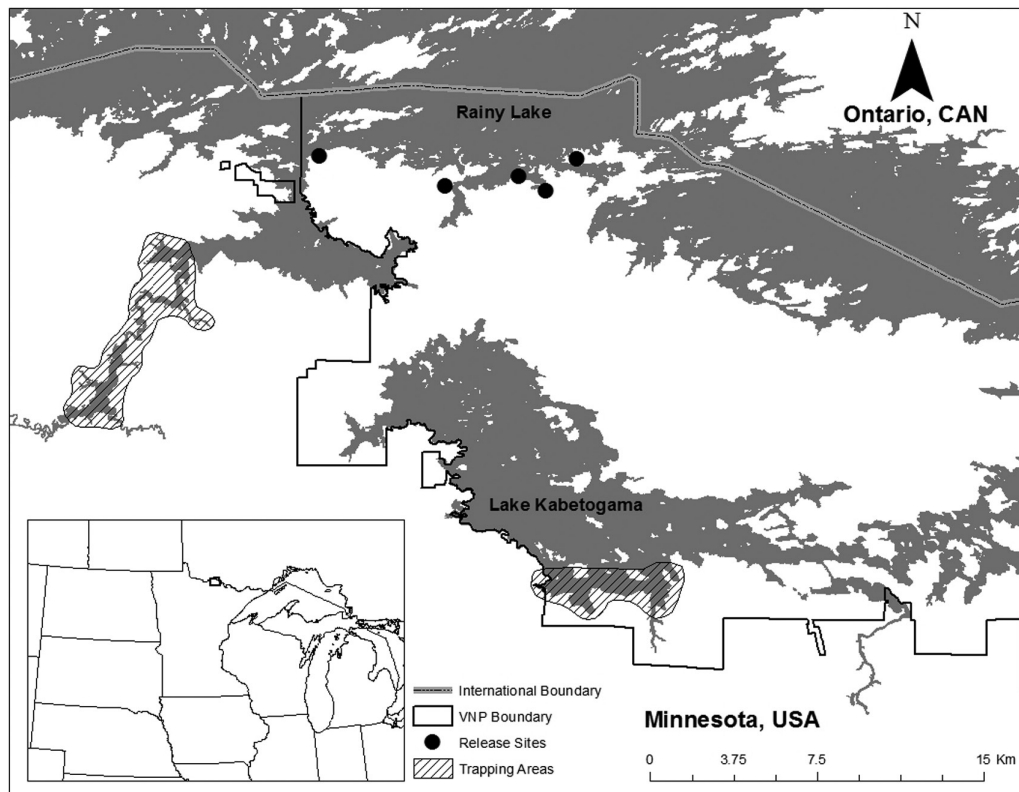


Figure 1. Spatial distribution of muskrat *Ondatra zibethicus* live-trapping areas and translocation wetlands (black circles; $n = 5$) for muskrats in Voyageurs National Park near International Falls, MN, USA during summers of 2018 and 2019.

every morning and captured muskrats (adults ≥ 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 [$0.020\text{--}0.025$ 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,

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

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 ≥ 2 h to recover post-surgery prior to translocating them to their assigned wetland.

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. x glauca*. Prospective wetlands were representative of traditional muskrat habitat (shallow to deep marsh) and vegetation communities were dominated by *T. x glauca*. Wetlands averaged 1.42 ha in size (range = 1.09–1.78 ha) and were separated by ≥ 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_i , 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 1 cm from the tip); and L = the length (mm) of the tail (base to tip). We then derived a tail index, Z_i , 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 $\bar{X}$.

We developed a time-varying covariate representing an individual's use of a beaver lodge at least once during a given week (Lodge; $1 \geq 1$ 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 $\times$ 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 ΔAIC_c of ≤ 2.00 as competitive (Burnham and Anderson 2002). Covariates that failed to improve model fit (Δ Deviance) 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)

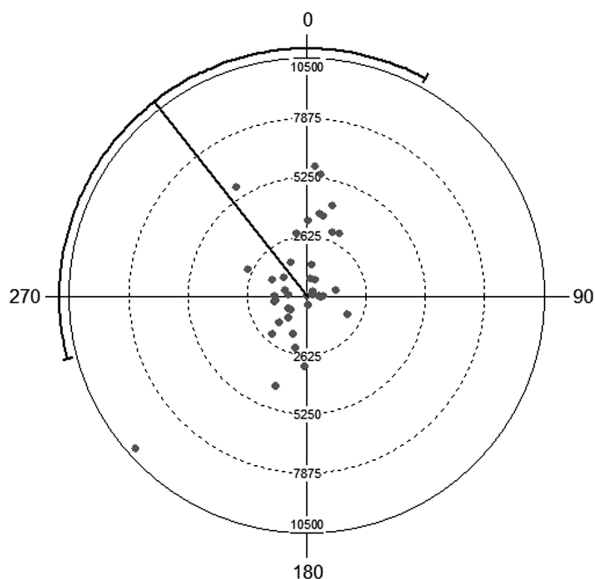


Figure 3. Post-translocation movement distances (m) and trajectories (0–360°) for radiomarked muskrats *Ondatra zibethicus* ($n=42$) scaled to their individual capture locations (0°). Muskrats were live-trapped and translocated into wetlands in Voyageurs National Park near International Falls, MN, USA 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.

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).

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; $\beta=2.04$, 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; $\beta=1.43$, 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 (Δ Deviance 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

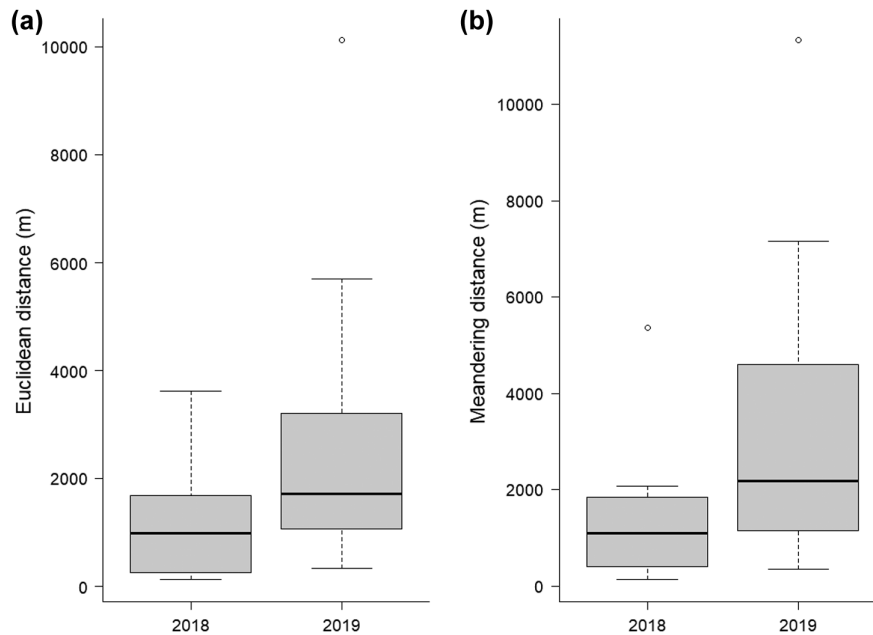


Figure 4. Annual differences in median post-translocation Euclidean (a) and meandering (b) distances moved by radiomarked muskrats *Ondatra zibethicus* ($n = 42$). Muskrats were live-trapped and translocated into wetlands in Voyageurs National Park near International Falls, MN, USA during summers of 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 land-

scapes. 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.

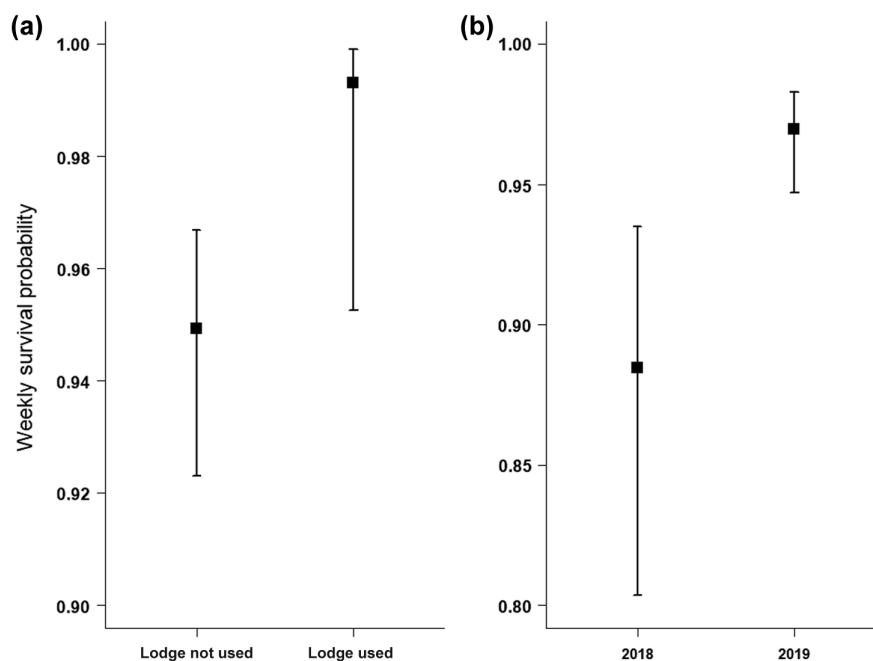


Figure 5. Post-translocation known-fate weekly survival probabilities (and 95% CIs) for adult muskrats *Ondatra zibethicus* ($n = 65$) derived from the top-ranked model including beaver *Castor canadensis* lodge use (a) and year (b). Muskrats were live-trapped and translocated to wetlands in Voyageurs 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= $-2\log$ ($[\log_e$ 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 $\times$ 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
TaillID	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, Ganoë 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, Ganoë 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 (Tetzlaff 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 indi-

vidual 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, Ganoë 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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