January 2022

Landscape Ecology Influence On Population Dynamics And Gene Flow: A Muskrat’s Tale

Ayla A. Morehouse

Recommended Citation

Morehouse, Ayla A., "Landscape Ecology Influence On Population Dynamics And Gene Flow: A Muskrat’s Tale" (2022). *Theses and Dissertations*. 4280.
https://commons.und.edu/theses/4280

LANDSCAPE ECOLOGY INFLUENCE ON POPULATION DYNAMICS AND GENE FLOW: A MUSKRAT'S TALE

By

Ayla Audrey Morehouse

Bachelor of Science, University of North Dakota, 2019

Master of Science, University of North Dakota, 2022

A thesis

Submitted to the graduate faculty

Of the University of North Dakota

In partial fulfillment of the requirements

For the degree of

Master of Science

Grand Forks, North Dakota

May

2022

Name: Ayla A Morehouse

Degree: Master of Science

This document, submitted in partial fulfillment of the requirements for the degree from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

Brian Darby

Susan Ellis-Felege

Rebecca Simmons

Stephanie Tucker

Stephanie Tucker

This document is being submitted by the appointed advisory committee as having met all the requirements of the School of Graduate Studies at the University of North Dakota and is hereby approved.

Chris Nelson

Chris Nelson
Dean of the School of Graduate Studies

5/5/2022

Date

PERMISSION

Title	LANDSCAPE ECOLOGY INFLUENCE ON POPULATION DYNAMICS AND GENE FLOW: A MUSKRAT’S TALE
Department	Biology
Degree	Master of Science

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the library of this University shall make it freely available for inspection. I further agree that permission for extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in his absence, by the Chairperson of the department or the dean of the School of Graduate Studies. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Ayla Morehouse

April 29th, 2022

Table of Contents

LIST OF FIGURES

LIST OF TABLES

Table Page

ACKNOWLEDGMENTS

I wish to express my sincere appreciation to the members of my advisory committee for their guidance and support during my time in the master's program at the University of North Dakota. Thank you, Dr. Brian Darby, for excepting me into your lab despite tight position and for putting up with me and all my quick pop-ins to your office. Thank you, Dr. Rebecca "Becky" Simmons, for supporting me and encouraging me from the beginning of my freshman year at UND all the way through the end of my masters and pushing me to chase my dreams and not setting for less. The study carried out was financially supported by several bodies: North Dakota Game and Fish using funds from the Wildlife and Sport Fish Restoration Program (CFDA# 15.611), AmericaView under USGS grant G18AP00077, and APSAC. We thank the North Dakota, North Dakota Fur Hunters and Trappers Association (NDFHTA) and North Dakota Fur Takers Association (NDFTA) trappers for their support.

I am also sincerely thankful to all my mother: Emily Morehouse, my siblings: Darah Morehouse and James Baker for their continued support through my entire life. Thank you to all my friends that have stuck with me from the beginning: Courtney Allen, Johannah Hayes, Sayo Littler, and Stephanie Honcharenko; and to those I've made along the way: Lynda LaFond, Mason Ryckman, Sally Yannuzzi, Kelsey Morin, Lydia Kantonen, and Taylor Linder. You have all seen me at my worst and best and supported in any way you could.

ABSTRACT

Understanding movement patterns across a landscape is an essential tool for wildlife managers to understand and predict population dynamics, interactions, and susceptibility to disease and environmental changes. Part of this is due to population spatial synchrony being driven by three primary factors: dispersal, the “Moran Effect”, and trophic interactions. We seek to understand if dispersal may play a larger role in population synchrony and, if so, what landscape features may hinder the movement of muskrats (*Ondatra zibethicus*), a small semiaquatic mammal that relies on ditches and shallow wetlands for habitat and local movement. In this study we genotyped eleven microsatellite loci in over 400 muskrats across the state to determine relatedness of individuals and if population genetic structure indicates candidate barriers to movement in the landscape, such as watershed boundaries or major riverways. Five population subgroups emerged, largely representing the watersheds from which the samples were collected (Devil’s Lake watershed, Red River Valley watershed, James River watershed, and Missouri River watershed), and this is consistent with the working theory that watershed boundaries may form a landscape feature that limits muskrat movement.

Keywords: Muskrat, *Ondatra zibethicus*, Wildlife Management, North Dakota, Population

INTRODUCTION

Landscape ecology is a rising field in wildlife management as technology has allowed us to account for larger landscape features that may otherwise be difficult to discern. Landscape ecology asks what large scale features could be impacting wildlife that may have been previously over looked. For example, watersheds and water basins may have a larger impact on population connectivity than previous studies (Ahlers et al. 2010b, Laurence et al. 2013a).

Muskrat populations are declining in North America, but North Dakota, USA appears to be one of the few states with a stable population (Roberts and Crimmins 2010, Ahlers and Heske 2017, Sadowski and Bowman 2021). This has lead managers to ask what might be causing North Dakota population to stand out. Could it be related to landscape characteristics?

Muskrats (*Ondatra zibethicus)* are semiaquatic mammals that have economic value (i.e., furbearer harvest)(Obbard et al. 1988, Roberts and Crimmins 2010, Ahlers et al. 2016, Triezenberg and Knuth 2018) and provide vital ecological services (e.g., increase wetland vegetation diversity and habitat heterogeneity)(Skyrienė and Paulauskas 2013, Bomske and Ahlers 2021), but there is little data on what landscape features may hinder their movement. This gap in understanding makes it difficult for managers to predict how long it would take for local populations to rejuvenate after a stochastic event (i.e., drought, flooding, or disease)(Ahlers et al. 2010b, 2010a, Miller 2018) aside from expected population cycles.

Understanding the populations' current trends and how local populations differ at the county level could provide insight into population interactions and if any cycling or synchronizing might be attributed to normal population fluctuations. Fur trapping of muskrats in North Dakota is a long-standing tradition and remains of economic importance (Roberts and Crimmins 2010, Leier 2012, Ahlers et al. 2016, Bomske and Ahlers 2021). Market trends are a primary source for population monitoring, with smaller, inexpensive programs such as Rural Mail Carrier Surveys (RMCS) supporting managers with quarterly counts for multiple populations'occurrence rates. RMCS programs have been utilized by several states in the past and continue to do so (e.g. Kansas, Nebraska, Kentucky, Wisconsin, and North Dakota) for different species based on state priorities (Greeley et al. 1962).

Landscape Genetics

Landscape features can act as barriers potentially isolating populations and putting them at risk of extinction or aid in gene flow by promoting gene dispersal and leading to large-scale genetic synchrony. For example, muskrats prefer slow-moving or non-moving water; thus, fast-flowing streams or rivers are a potential genetic barrier and are relevant environmental factors for this species (Giroux-Bougard 2014). Additionally, habitat loss due to wetland draining for agricultural production could be reducing population carrying capacity.

Examining the relationship between genetics and landscape can have varying conclusions depending on the scale. If the scale is too fine, we may not be able to detect the significance of landscape features during events such as dispersal (Le Boulengé et al. 1996, Laurence et al. 2013a). Environmental factors and relevant life history considerations determine the resolution necessary to complete objectives, like watersheds, when using a state or national scale for semiaquatic species.

Genetics is restricted by more than geography. Social behaviors can inhibit dispersal and gene flow due to territoriality among muskrat families (Le Boulengé et al. 1996). Lower morphological diversity correlates to lower immigration and emigration, with recognizable gradients of morphological traits found along dispersal corridors (Le Boulengé et al. 1996). Phenotypic evidence of gene dispersal could be a helpful indicator of gene flow between populations as decreased gene flow leads to higher rates of predictable population structure (Laurence et al. 2013a). There are 16 recognized subspecies in North America, but only 1 subspecies that dominates in North Dakota (Willner et al. 1980, Skyrienė and Paulauskas 2013). Predictable population structure with reduced emigration and immigration removes gene flow to explain genotypic changes and instead attributes changes to environmental factors that affect fitness through physiology or behavior (Frean et al. 2013).

Population Cycles

Aside from landscape influences, populations naturally experience cycles of high and low abundance. Population cycles are influenced by various factors that can cause changes in amplitude and periodicity (Myers 2018). Erb et al. (2000) lists three potential factors in muskrat cycle variation: anthropogenic influence (e.g., wetland draining, road construction), behavior/ life history changes (e.g., broadening resource use, change in movement/ behavior), and stochastic events (e.g., draught, flood); and three regulatory variables: predation, resource overuse, and disease. Additionally, there is increasing evidence correlating population cycles to ecozones (Erb et al. 2000, Ahlers et al. 2010b, 2015, Larreur et al. 2020) and other small mammal populations (Erb et al. 2000, Korpimäki et al. 2004, 2005, Huitu et al. 2004).

The first muskrat population cycle data is collected by analyzing fur trapping records (Elton and Nicholson 1942). Based on fur trapping trends, muskrat population cycles last approximately ten years (Elton and Nicholson 1942), and newer studies still support this as the average time (Erb et al. 2000). However, there is evidence of regional populations having shorter 3-4 year cycles, and that period length is a gradient correlated with ecozone (Danell 1978, Erb et al. 2000).

Cause and Consequences of Synchrony

Interspecific synchrony is when populations of different species synchronize abundance trends across time and space (Danell 1978, Korpimäki et al. 2004, 2005, Huitu et al. 2004). The relationship of abundance between multiple species can be analyzed across time to model trends and quantify how the growth or decline of one species impacts another (Ranta et al. 1998a). Interspecific synchrony influences population cycles, density dependence, and predator-prey relationships (Ranta et al. 1998a, Korpimäki et al. 2004, Ahlers et al. 2021). Intraspecific synchrony focuses on genetics and the abundance of one population synchronizing with other populations of the same species (Ranta et al. 1998a, 1999).

Most small mammal populations cycle along with other species in the same community, in the context of predator prey dynamics. For example, mink (*Neovision vision*) and red fox (*Vulpes vulpes*) are the primary predators of muskrats, but muskrats are an alternative prey species unless a stochastic event occurs to disrupt predator-prey relationships (Danell 1978, Crego et al. 2016, Ahlers et al. 2021). As a result, muskrat population cycles typically lag behind other small mammals, such as lemmings (*Dicrostonyx groenlandicus*), shrews (*Sorex araneus),* and voles (*Microtus agrestis, M.*

rossiaemeridionalis, Clethrionomys glareolus) (Danell 1978, Korpimäki et al. 2004, Huitu et al. 2004). For example, lemming abundance might peak in one year and slowly decrease then increase over the next four years before peaking again. The year lemmings decrease, vole and mole abundance would peak as resources are more available with the reduced lemming population and then follow the same decrease-increase pattern. In the third year, as voles and moles start decreasing, muskrat abundance peaks, replacing voles and moles as they did lemmings.

Intraspecific synchrony is observed through geneflow by analyzing genetics within one population, looking for genotypic adaptations, and determining genetic similarities between populations. Distance and individual dispersal are the driving factors of gene flow and, by extension, synchronization. Predator abundance and dispersal also play a significant role in prey population synchrony and can induce cyclic dynamics or phase-locking—predator-prey population density oscillations synchronize across patches (Blasius et al. 1999, Jansen 1999, Bjørnstad et al. 1999). Genetic similarity and the driving factors change with scale and species (Estay et al. 2011). The Moran effect—stochastic environmental events rather than dispersal influencing genetic similarity—and climate are likely to be primary drivers of genetic similarity on a continental scale (Ranta et al. 1998a, 1999), where distance and resources are more substantial factors on a regional scale (Estay et al. 2011).

Currently, we know how muskrat population abundance cycles in North America, but local populations may deviate from the average trend. These slight deviations are likely due to influences on movement capabilities (immigration and emigration) and could give insight into the effective local population sizes within North Dakota (Skyrienė and Paulauskas 2013, Laurence et al. 2013b). In general, muskrat populations have a 10-year cycle with minor 3 to 4-year cycles occurring within the ten-year cycle (Skyrienė and Paulauskas 2013). While we know this applies to the North American metapopulation, it is unclear how this applies at the regional or community level (Laurence et al. 2013b). In this study, we address muskrat population trends and assess which counties have similar occurrence patterns based upon available data. We hypothesize:

1. Muskrat populations are synchronized because of dispersal rather than predator cycles or environmental fluctuations at the county level.
2. There is more than one muskrat genetic cluster that appears to be constrained by landscape barriers.

METHODS

Population Dynamics

Data Collection: Rural Mail Carrier Survey

North Dakota Game and Fish conducted the RMCS quarterly (January, April, July, and September) from 1970 through 2019, with muskrats added to the survey in 1990. Postal workers voluntarily record the species seen on their rural postal delivery routes during three days of good weather. The survey also asks for a tally of muskrat predators, such as coyote (*Canis latrans*), red fox (*Vulpes vulpes*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), skunk (*Mephitis mephitis*), weasel (*Mustela* spp.), and mink (*Neovision vision*); and the total mileage traveled during the survey period. Surveys were compiled at the county level then we standardized occurrence rate by dividing the total number observed by total route mileage in kilometers and culled to years when muskrats were included on the survey (1990-2019).

Spatio-temporal Population Clustering

The objective of the Space-Time Cube analysis is to identify clusters of counties that have similar population dynamics and to see the boundaries to these county clusters coincide with candidate landscape boundaries. The survey data was uploaded as a table and related to a North Dakota county shapefile from TIGER/ line shapefiles (U.S. Census Bureau 2019) in ArcGIS Pro 2.6.1 (ESRI 2020). The geodatabase geographic coordinate system was NAD 1983 (2011) and projected to NAD 1983 (2011) Contiguous USA Albers.

The Space-Time Cube survey periods were defined as North Dakota counties with the survey data related as a table, defining 118 space-time bins or survey periods. Absent (missing) data was replaced with zeros. An emerging hot spot analysis (combination of Gertis-Ord GI* and Mann-Kendall trend statistics) was conducted using the standardized muskrat occurrence data in the space-time cube with a fixed distance of 74938.28 m. Fixed distance adds a weight element to the spatial analysis where counties with in the specified distance have a weight 1 and counties outside the distance have no weight and do not influence calculations, accounting for proximity. Fixed distance was measured with Hot Spot Analysis (Gertis-Ord GI*) using euclidean distance method where the spatial process is most “active” or pronounced. The Mann-Kendall statistics account for trends only occurring within the county over time while Gertis-Ord GI* also accounts for patterns (not trends) within the county and the potential influence of neighboring counties.

A time series clustering analysis was conducted based on the data value instead of a correlation or Fourier transformation with time series pop-ups enabled. The clustering analysis was conducted twice, first with an undefined number of clusters to determine the optimal number (which was determined to be 5), and then again with the number of clusters defined based on the initial cluster analysis.

Linear trends through time

The second analysis conducted was the emerging hotspot analysis to detect population patterns (i.e., oscilations) and trends within a county using the RMCS. At each time interval, each county was assigned to one of 17 categories that represent different occcurance pattern and trend scenarios on a gradient from historical cold spot, at one end, to historic hot spot at the other end, then averaged to determine occurrence patterns and trends. The emerging hotspot analysis did not find any patterns for muskrats within the 30 year time period.

Trophic Interactions by Granger Causality

Causation between a species and muskrat occurrence rate per county (muskrat abundance is predicted based on predator abundance) was determined using GRANGERTEST in R (R Core Team 2014). Granger causality tests correlated timeseries to determine if one timeseries actually predicts for the other beyond correlation. Total survey mileage was converted to meters, and total counts were divided by milage for a standardized occurrence rate. Additionally, bobcat counts in seven counties (Billings, Burleigh, Mercer, Oliver, Renville, Sioux, and Stutsman) were removed due to insufficient data. Finally, the occurrence rate was run through a granger causality equation where muskrat occurrence is influenced by another species (badger, coyote, fox, skunk, mink, or weasel) per county for 1 to 20 time lags. The resulting p-values were adjusted using Bonferroni correction.

Population Genetics

Donated Tissue Collection

Muskrat samples were collected during spring and fall of 2014 from a project related to trapping efficiency and incidental take (Gross et al. 2017). Fur trappers were contacted for additional samples during the 2019-2020 and 2020-2021 North Dakota trapping seasons (October through May) to expand sampling to mid and western North Dakota. Fur harvesters were contacted through the two major trapping organizations in North Dakota, North Dakota Fur Hunters and Trappers Association (NDFHTA) and North Dakota Fur Takers Association (NDFTA), via organization email announcement, winter meeting presentation, and newsletter. The announcement included project objectives, general sample collection instructions after the harvest event, and contact information. Trappers were instructed to remove a soft tissue sample of their choice (i.e., heart, liver, or muscle) from 10-20 individuals per location (within a 1 mile radius), placing individual samples in small freezer double zipper plastic bags compiled into a large zip-lock by location. Donors stored samples frozen in a commercial freezer until a coordinated pick-up. Donors provided the trapper's name, date harvested, and coordinates of the sampling site with samples. Samples were kept on ice during transportation, then transferred into 1.5ml tubes, labeled with a unique identification number, and stored at -80°C.

Molecular Methods

DNA extractions required approximately 5 mg of tissue in a 1.5 ml tube with four to six 0.2 mm fracture-resistant ceramic beads. 1000 µL of Lysis buffer was added to the 1.5 mL tube and incubated at room temperature for 15 minutes before frozen at -80°C overnight. The tissue was defrosted to room temperature then shaken in the Tissuelyser at a frequency of 30 n/s, for 15 minutes. Samples were rotated 180° on the X-axis and switched, then shaken for an additional 15 minutes. Lysed samples were centrifuged at 1000 rpm for 2 minutes. The supernatant was aspirated off without disturbing the debris into a silicon filter 96-well plate. DNA was extracted and purified using the *quick*-DNA Micro Prep Kit (Zymo Research Corporation; Irving, CA) per the manufacturer's instructions for "soft tissue extraction" with a final elution of 50 µL in elution buffer.

DNA was genotyped using 11 non-coding microsatellite regions (OZ06b, OZ08b, OZ16b, OZ17b, OZ22b, OZ27b, OZ32b, OZ34b, OZ41b, OZ43b, and OZ44b). Each microsatellite was amplified with DreamTaq Hot Start PCR master mix (Thermo Fisher Scientific Waltham, MA). Amplified poducts were pooled by individual, cleaned of excess primers and nucleotides, and underwent a second amplification round, to add barcoding primers (Laurence et al. 2009, 2011, Darby et al. 2016). The final barcoded libraries were pooled, cleaned of excess primers and nucleotides, and sequenced using the Illumina MiSeq platform at the University of North Dakota School of Medical and Health Sciences Genomics Core. The sequencing reads were merged and dereplicated with USEARCH (Edgar 2010, 2013). The resulting sequences were sorted with a custom python script to determine the genotype of individual loci.

Genetic Clustering

GENELAND in R (Guillot et al. 2005a, 2005b, 2012) was used to determine the genetic population structure in North Dakota. GENELAND uses a Markov Chain Monte Carlo (MCMC) approach to simulate a probabalistic model of allele identity, allowing for better inference when working with complex Bayesian models and accounting for spatial correlations. The MCMC (without admixture) computed the number of populations (clusters), individual population membership, F_{st} (between populations), and F_{is} (between individuals, within a population). Diploid data was processed assuming that allele frequencies are uncorrelated (when an allele is rare in one population, it is not necessarily rare in all populations) with 100,000 MCMC iterations and only saving every 100th. The permutations were then post-processed where x and y pixels are a 1:8 ratio of North Dakota length and width (482:321km to 60:40 px) and burnin 200 of the 1000 saved iterations.

Population membership and probability of population membership utilize Poisson-Voronoi tessellations as the underlying spatial model. Poisson-Voronoi tessellations assume an unknown number of pixels centering around the spatial point that approximate true population spread. Additionally, each tessellation for the probability of population is calculated independently from other probability of population aside from other population spatial points.

For visualization, samples coordinates were loaded into ArcPro as points. Coordinates were originally collected in WGS 1984 and projected to NAD 1983 (2011) Contiguous USA Albers. Additional landscape shapefiles for US Level III Ecoregions ecological regions (EPA 2022), HUC6 basins, HUC8 subbasin, HUC10 watersheds and lakes (NDGIS 2021) were retrieved and projected to NAD 1983 (2011) Contiguous USA Albers.

RESULTS

Population Dynamics

Population Cycles Synchronizing through Time

Synchronized population cycles at the county level would indicate that the populations must be influenced by some variable in the same or similar way. Four counties required all 118 survey periods to be filled with zeros and 25-117 filled for several other counties (Figure 1). We initially clustered the time series without a defined number of clusters (maximum 10) to determine the optimal amount (Figure 1) . The optimal number of clusters was five (Figure 2) based on the pseudo-F-statistic in the first time series analysis (F =17.919, Table 1) meaning counties exhibited primarily five population cycles in North Dakota. We found that one cluster had a downward trend, though not significant ($z = -1.7897$, $p = 0.073$, Table 2). Additionally, county abundance over time is graphed per cluster to visualize county similarities (Figure 3).

Linear trends through time

We analyzed linear population trends using the Mann-Kendall, determining significance for each location when $z > 1.96$. First, we determined population trends at the county level, where we found that 15 counties have had a downward population trend over the last 30 years (Table 4). Slope , Adams, Richland, Grant, Golden Valley counties had the most significant downward population trends with a 99% confidence interval ($-4.404 \geq z \leq -2.761$, $0.000011 \geq p \leq 0.00576$). McKenzie, Towner, Eddy, McLean, Mountrail, and Dickey counties also had a significant downward trend within the 95%

confidence interval ($-2.575 \geq z \leq -1.992$, $0.01 \geq p \leq 0.046$). Barnas, Cavalier, and McIntosh counties had slight, but not significant, downwards trends ($-1.9 \geq z \leq -1.853$, $0.0574 \geq p \leq 0.0625$). Only two of the 53 counties (Stark and Cass) had slight upward trends within the 90% confidence interval ($z = 1.777$, $p= 0.75$; $z=1.958$, 0.05 respectively). All other counties had no significant trend.

Trophic Interactions by Granger Causality

In general, there were few counties in which one of the monitored species appear to have a Granger-type casuality relationship with muskrats, with Emmons county having the greatest number of causal relationships at different time lags (Figure 5), and those that did typically had an inconsistent optimal lag value (Table 4). Overall, skunk occurrence had the least effect on muskrat occurrence with only two counties causing a significant influence (p =1.1E-6, 0.072), followed by badger, which influenced three counties (p = 6.05E-10, 3.22E-6, 0.033). Fox, mink, and weasel have significant influence in four counties each while coyote occurrence influenced muskrat occurrence in 5 counties, the most compared to the other predator species (p = 3.44E-11, 3.55E-8, 1.93E-5, 0.0048, 0.0084).

Population Genetics

As the only study relating to muskrat populations in North Dakota was related to subspecies dispersal, we expected at least one population and found five genetic clusters (Figure 6). Cluster one samples occurred in the eastern-central portion of the state, cluster two in Sheridan County, cluster three the majority of the west, cluster four the South-Eastern corner, and cluster five the North-Eastern Corner (Figure 7). Pairwise F_{st} ranged from 0.147 to 0.025 (Table 5) and is significant ($p < 0.05$) between three populations, population 1 and 4 (p = 0.048), 1 and 5 (p = 0.025), and 4 and 5 (p = 0.049). Cluster one and four were the only clusters to have a significant F_{is} (p = 0.04, 0.011 respectively; Table 6). Clusters were visualized with ecological regions, HUC6 basins, HUC8 subbasin, HUC10 watersheds and lakes (Figure 8).

DISCUSSION

Muskrats use land and waterways for population connectivety, but little is known about what landscape features act as barriers or corridors, particularly in North Dakota where there is little topographic variation and ample wetlands across the state. The county-wise population dynamic clustering resulted in five different clusters whose locations were consistent with a watershed (such as Devils Lake in Ramsey County) and counties including McLean and Burleigh along the Missouri River. This finding offers provisional support for watersheds and large rivers as potential boundaries for muskrat movement if it is interpreted that the population dynamics within the counties are synchronized largely by dispersal.

There are three primary mechanisms for population synchrony: dispersal, environment (“the Moran’s effect”) and trophic/predation dynamics. As county-wise linear trends were not consistent with the five population clusters, it is not likely that environmental forcing (or Moran’s effect) is driving the synchrony for the five defined clusters.

Similarly, predators were expected to influence muskrat populations, specifically mink and fox (Ranta et al. 1998b, Savill and Hogeweg 1999, Haydon et al. 2001, Crego et al. 2016, Ahlers et al. 2021). While predators did have significant influence on muskrat populations in some counties, no one species or combination of species consistently influenced populations enough to explain population clustering.

The idea of dispersal as the driving force of synchrony was further tested by population genetics and the assumption that more freely individuals are dispersing between points that cluster together and lack a landscape barrier to movement. The analysis supported five genetic clusters in North Dakota. While visualizing the genetic clusters, we determined HUC6 basin designation and lake approximation were the best explainations, with other watershed designations appearing too localized (Figure 7). This aligns with muskrat survival needs as they depend on water systems for habitat and avoid predation (Errington 1941, Ahlers et al. 2010a, Le Galliard et al. 2012). The state's western genetic cluster is geographically larger, likely due to limited suitable habitat along the Missouri River. This could mean the western population highly relies on the river to survive as the western part of North Dakota has more rugged terrain and overall much drier habitat. Additionally, the decrease in western muskrat populations could mean the river carrying capacity is met with minimal fluctuations due to environmental and/ or anthropic strain.

Limitations

This study looked at two different complementary datsets to interpret landscape barriers to movement: RMCS data and population genetics. A strength of the RMCS data, for this purpose, is that it is relatively long term (30+ years), relatively high temporal resolution (3 months), and broad and uniform representation (data points by count). However, the postal survey is limited for this purpose by the lack of uniform observations and geographic precision. Observers may vary in skill or attention, while postal routes vary in length and location (between survey periods). Furthermore, the survey is conducted from the road side, roads might at as barriers and deter movement near them, and is county-wide with borders that may not necessarily align with boundaries that are relevant to wildlife.

Genetic sampling in our study was limited by the inconsistency in sites being repeatedly sampled across multiple years. While samples were collected from 2014 to 2021, there was a four-year gap between sampling events. However, we expect that this problem is minimal as one 2014 sample location is clustered with the 2019-2021 samples. A more significant limitation is that ideally samples would have been more systematically collected with more broad and uniform geographic representation and better understanding of landscape feature scale. The present study relied on volunteer-contributed samples, but a more ideal sampling effort would have collected a grid or lattice pattern with nearly equal distances between samples locations.

Conclusion and Management Implications

This study aimed to analyze how landscape features influence muskrat population trends and gene flow. Our efforts resulted in recognizing five populations where abundance is influenced by ecological region and geneflow is predicted by HUC6 watersheds and lake proximity. This is the first work to suggest there are multiple populations within North Dakota instead of one population extending across all of North Dakota (Willner et al. 1980, Skyrienė and Paulauskas 2013). Thus, management plans may need reevaluation to account for multiple populations at disproportionate risk based on habitat availability and population connectivity requiring different monitoring levels.

Such revisions could mean the development of muskrat zones for monitoring purposes if different populations were to need further management intervention in the future.

References

Ahlers, A. A., L. A. Cotner, P. J. Wolff, M. A. Mitchell, E. J. Heske, and R. L. Schooley. 2015. Summer precipitation predicts spatial distributions of semiaquatic mammals. PLOS ONE 10:e0135036.

Ahlers, A. A., and E. J. Heske. 2017. Empirical evidence for declines in muskrat populations across the United States: muskrat population declines. The Journal of Wildlife Management 81:1408–1416.

Ahlers, A. A., E. J. Heske, and C. A. Miller. 2016. Economic influences on trapper participation and per capita harvest of muskrat: economics and trapping. Wildlife Society Bulletin 40:548–553.

Ahlers, A. A., E. J. Heske, R. L. Schooley, and M. A. Mitchell. 2010a. Home ranges and space use of muskrats Ondatra zibethicus in restricted linear habitats. Wildlife Biology 16:400–408.

Ahlers, A. A., T. P. Lyons, and E. J. Heske. 2021. Population dynamics of muskrats (Ondatra zibethicus) and american mink (Neovison vison): investigating contemporary patterns in a classic predator–prey system. Canadian Journal of Zoology 99:681–688.

Ahlers, A. A., R. L. Schooley, E. J. Heske, and M. A. Mitchell. 2010b. Effects of flooding and riparian buffers on survival of muskrats (Ondatra zibethicus) across a flashiness gradient. Canadian Journal of Zoology 88:1011–1020.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology & Evolution 14:427–432.

Blasius, B., A. Huppert, and L. Stone. 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. Nature 399:354–359.

Bomske, C. M., and A. A. Ahlers. 2021. How do muskrats (Ondatra zibethicus) affect ecosystems? A review of evidence. Mammal Review 51:40–50.

Crego, R. D., J. E. Jiménez, and R. Rozzi. 2016. A synergistic trio of invasive mammals? Facilitative interactions among beavers, muskrats, and mink at the southern end of the Americas. Biological Invasions 18:1923–1938.

Danell, K. 1978. Population Dynamics of the Muskrat in a Shallow Swedish Lake. The Journal of Animal Ecology 47:697.

Darby, B. J., S. F. Erickson, S. D. Hervey, and S. N. Ellis-Felege. 2016. Digital fragment analysis of short tandem repeats by high-throughput amplicon sequencing. Ecology and Evolution 6:4502–4512.

Edgar, R. C. 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26:2460–2461.

Edgar, R. C. 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nature Methods 10:996–998.

Elton, C., and M. Nicholson. 1942. Fluctuations in Numbers of the Muskrat (Ondatra zibethica) in Canada. The Journal of Animal Ecology 11:96.

EPA. 2022. US Level III ecoregions without state boundies. United States Environmental Protection Agency.

Erb, J., N. C. Stenseth, and M. S. Boyce. 2000. Geographic variation in population cycles of Canadian muskrats (Ondatra zibethicus) 78:8.

Errington, P. L. 1941. Versatility in feeding and population maintenance of the muskrat. The Journal of Wildlife Management 5:68.

ESRI. 2020. ArcGIS Pro 2.6.1. Environmenal Systems Research Institute, Redlands, CA.

Estay, S. A., A. A. Albornoz, M. Lima, M. S. Boyce, and N. C. Stenseth. 2011. A Simultaneous Test of Synchrony Causal Factors in Muskrat and Mink Fur Returns at Different Scales across Canada. PLoS ONE 6:e27766.

Frean, M., P. B. Rainey, and A. Traulsen. 2013. The effect of population structure on the rate of evolution. Proceedings of the Royal Society B: Biological Sciences 280:20130211.

Giroux-Bougard, X. 2014. Gene flow in an Arctic wetland: modelling landscape effects on fine- scale genetic variation in an isolated muskrat (Ondatra zibethicus) population:81.

Greeley, F., R. F. Labisky, and S. H. Mann. 1962. Distribution and abundane of pheasants in Illinois.

Gross, R., S. Tucker, B. Darby, and S. N. Ellis-Felege. 2017. Difference in exposure of water birds to covered and uncovered float muskrat sets. Wildlife Biology 2017:1–8.

Guillot, G., A. Estoup, F. Mortier, and J. F. Cosson. 2005a. A spatial statistical model for landscape genetics. Genetics 170:1261–1280.

Guillot, G., F. Mortier, and A. Estoup. 2005b. Geneland: a computer package for landscape genetics. Molecular Ecology Notes 5:712–715.

Guillot, G., S. Renaud, R. Ledevin, J. Michaux, and J. Claude. 2012. A unifying model for the analysis of phenotypic, genetic, and geographic data. Systematic Biology 61:897–911.

Haydon, D. T., N. C. Stenseth, M. S. Boyce, and P. E. Greenwood. 2001. Phase coupling and synchrony in the spatiotemporal dynamics of muskrat and mink populations across Canada. Proceedings of the National Academy of Sciences 98:13149–13154.

Huitu, O., K. Norrdahl, and E. Korpimäki. 2004. Competition, predation and interspecific synchrony in cyclic small mammal communities. Ecography 27:197–206.

Jansen, V. A. A. 1999. Phase locking: another casue of synchronicity in predator-prey systems. Trends in Ecology & Evolution 14:279.

Korpimäki, E., P. R. Brown, J. Jacob, and R. P. Pech. 2004. The Puzzles of Population Cycles and Outbreaks of Small Mammals Solved? BioScience 54:1071.

Korpimäki, E., K. Norrdahl, O. Huitu, and T. Klemola. 2005. Predator–induced synchrony in population oscillations of coexisting small mammal species. Proceedings of the Royal Society B: Biological Sciences 272:193–202.

Larreur, M. R., S. K. Windels, B. T. Olson, and A. A. Ahlers. 2020. Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. Landscape Ecology 35:59–68.

Laurence, S., A. J. Bewick, D. W. Coltman, C. S. Davis, S. C. Elsasser, A. G. Kidd, D. Lesbarrères, and A. I. Schulte-Hostedde. 2009. Isolation and characterization of polymorphic microsatellite loci in muskrat, Ondatra zibethicus: permanent genetic resources note. Molecular Ecology Resources 9:654–657.

Laurence, S., D. W. Coltman, J. C. Gorrell, and A. I. Schulte-Hostedde. 2011. Genetic structure of muskrat (Ondatra zibethicus) and its concordance with taxonomy in North America. Journal of Heredity 102:688–696.

Laurence, S., M. J. Smith, and A. I. Schulte-Hostedde. 2013a. Effects of structural connectivity on fine scale population genetic structure of muskrat, Ondatra zibethicus. Ecology and Evolution 3:3524–3535.

Laurence, S., M. J. Smith, and A. I. Schulte-Hostedde. 2013b. Effects of structural connectivity on fine scale population genetic structure of muskrat, Ondatra zibethicus. Ecology and Evolution:3524–3535.

Le Boulengé, É., P. Legendre, C. de le Court, P. L. Boulengé-Nguyen, and M. Languy. 1996. Microgeographic Morphological Differentiation in Muskrats. Journal of Mammalogy 77:684.

Le Galliard, J.-F., A. Rémy, R. A. Ims, and X. Lambin. 2012. Patterns and processes of dispersal behaviour in arvicoline rodents: dispersal mechanisms in microtine rodents. Molecular Ecology 21:505–523.

Leier, D. 2012, September. Trapping traditions slowly fading in North Dakota. Dakota Country Magazine:112.

Miller, J. E. 2018. Muskrats. Wildlife Damage Management Technical Series 14.

Myers, J. H. 2018. Population cycles: generalities, exceptions and remaining mysteries. Proceedings of the Royal Society B: Biological Sciences 285:20172841.

NDGIS. 2021. North Dakota GIS Hub data portal. North Dakota Geographic Information Systems, Bismarck, ND.

Obbard, M. E., J. G. Jones, R. Newman, A. Booth, A. J. Satterthwaite, G. Linscombe, Q. Park, and G. Linscombe. 1988. Furbearer harvests in North America. Ministry of Natural Resources.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical. CRAN, Vienna, Austria.

Ranta, E., V. Kaitala, and P. Lundberg. 1998a. Population Variability in Space and Time: The Dynamics of Synchronous Population Fluctuations. Oikos 83:376–382.

Ranta, E., V. Kaitala, and P. Lundberg. 1998b. Population variability in space and time: the dynamics of synchronous population fluctuations. Oikos 83:376.

Ranta, E., V. Kaitala, and P. Lundberg. 1999. Synchronicity in population systems: cause and consequence mixed. Trends in Ecology & Evolution 14:400–401.

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

Sadowski, C., and J. Bowman. 2021. Historical surveys reveal a long-term decline in muskrat populations. Ecology and Evolution 11:7557–7568.

Savill, N. J., and P. Hogeweg. 1999. Competition and dispersal in predator–prey waves. Theoretical Population Biology 56:243–263.

Skyrienė, G., and A. Paulauskas. 2013. Distribution of invasive muskrats (Ondatra zibethicus) and impact on ecosystem. Ekologija 58.

Swanson, B. J., and D. R. Johnson. 1999. Distinguishing causes of intraspecific synchrony in population dynamics. Oikos 86:265.

Thermo Fisher Scientific. 2022. DreamTaq Hot Start Green PCR Master Mix (2X). Waltham, MA.

Triezenberg, H. A., and B. A. Knuth. 2018. Limiting conflicts when managing public lands for furbearer trapping and dog-related recreation. Wildlife Society Bulletin:wsb.931.

U.S. Census Bureau. 2019. TIGER/Line Shapefiles. U.S. Census Bureau, Washington DC.

Ward, E. M., K. A. Solari, A. Varudkar, S. M. Gorelick, and E. A. Hadly. 2021. Muskrats as a bellwether of a drying delta. Communications Biology 4:750.

Willner, G. R., G. A. Felhamer, E. E. Zucker, and J. A. Chapman. 1980. Ondatra zibethicus. The American Society of Mammologists 141:1–8.

Figures

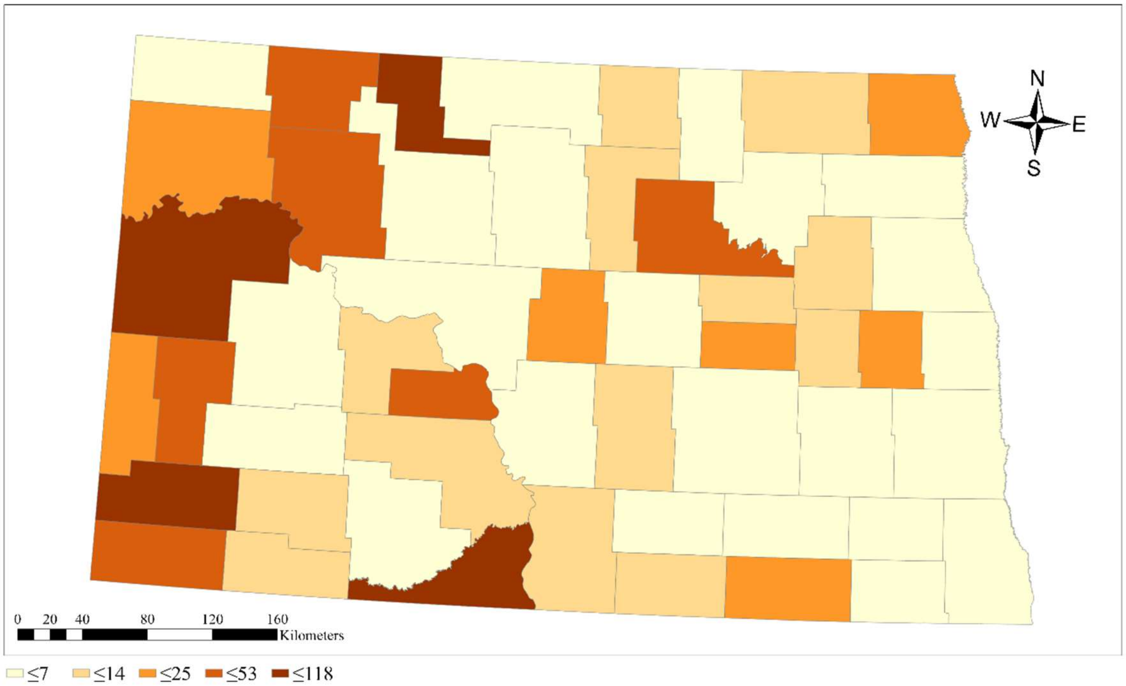

Figure 1. Space Time Cube Filled Survey Periods. Number of survey periods in which missing values are filled as zero per county in the muskrat (*Ondatra zibethicus*) dataset. Survey period equals the number of timesteps analyzed (four timesteps per year from 1990 through 2019) for a max of 120. County boundaries shapefile is provided by U.S. Census Bureau *(U.S. Census Bureau 2019)*.

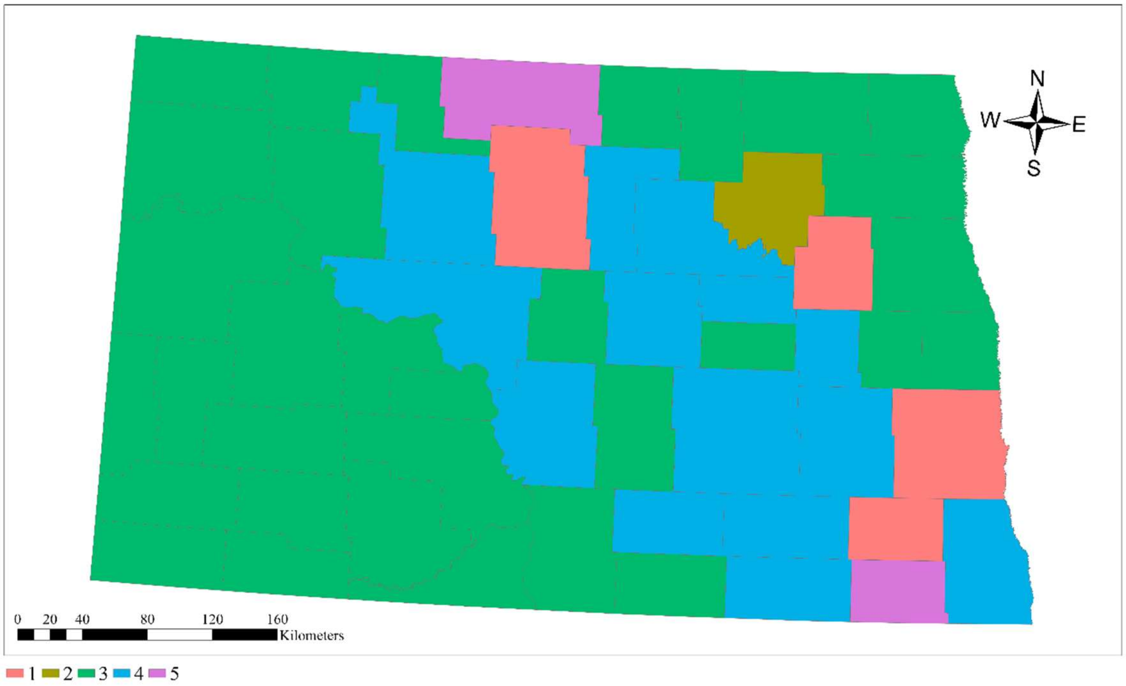

Figure 2. Muskrat Population Clusters. North Dakota muskrat (*Ondatra zibethicus*) optimized population clusters at the county level. Population trajectory is based on Fst. Muskrat data was collected four times a year from 1990 through 2019. County boundaries shapefile is provided by U.S. Census Bureau *(U.S. Census Bureau 2019)*.

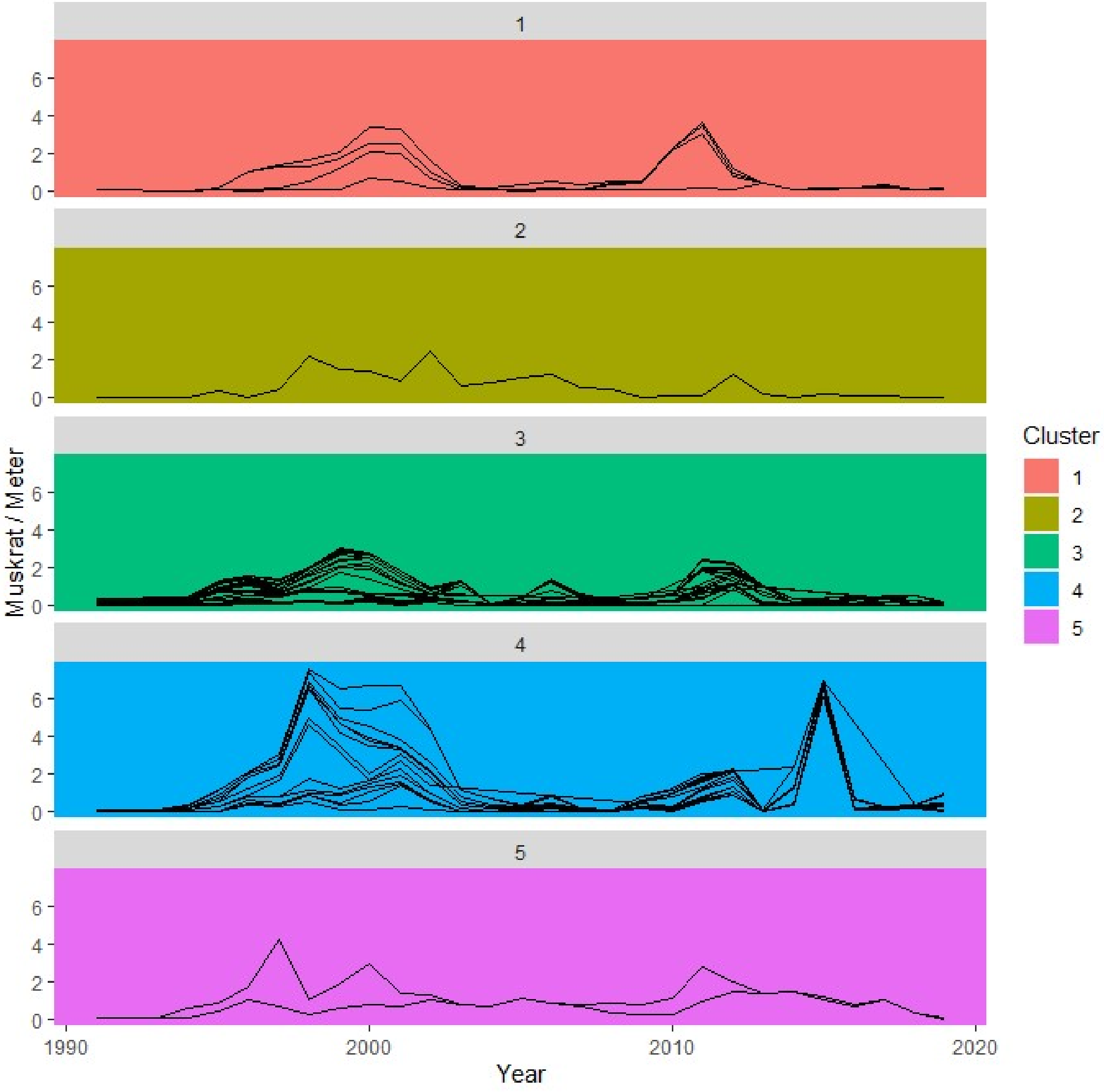

Figure 3. County Clusters Abundance Through Time. North Dakota county abundance of muskrat (*Ondatra zibethicus*) from 1990 through 2019 grouped into optimized clusters at the county level.

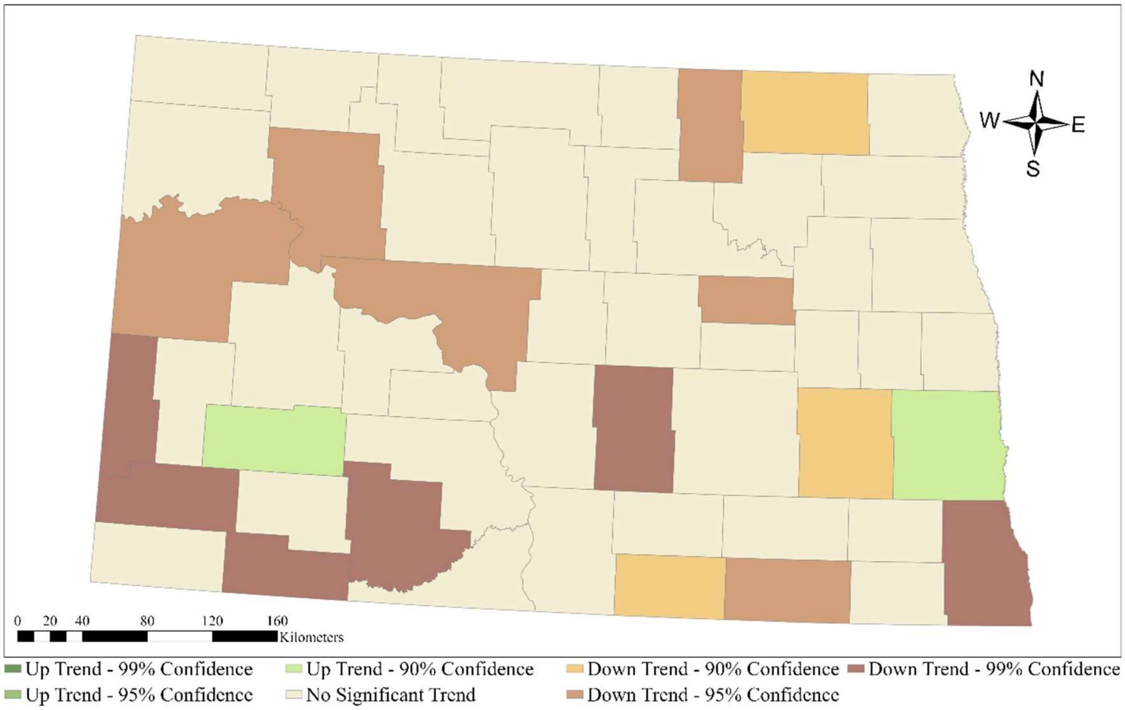

Figure 4. Muskrat Population Trends. North Dakota muskrat (*Ondatra zibethicus*) population trends at the county level. Population trajectory is based on counts collected four times a year from 1990 through 2019. County boundaries shapefile is provided by U.S. Census Bureau *(U.S. Census Bureau 2019)*.

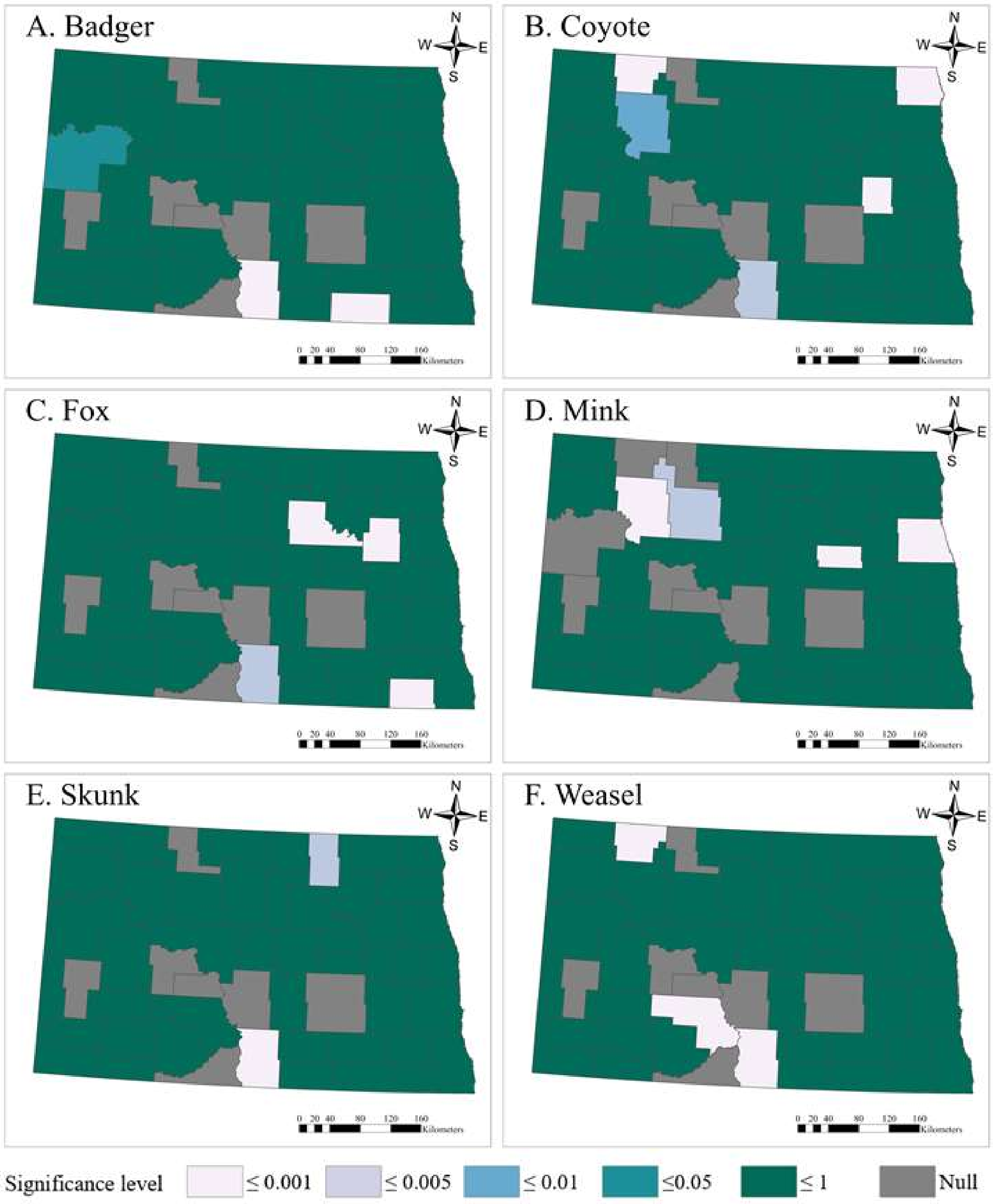

Figure 5. Species Influence on Muskrat Populations. Granger causality Bonferroni corrected p-values per county for A. badger *(Taxidea taxus),* B. coyote *(Canis latrans),* C. red fox *(Vulpes vulpes),* D. mink *(Neovision vision),* E. skunk *(Mephitis mephitis),* and F. weasel *(Mustela* spp.*)* predicting for muskrat based on rural postal survey counts from 1990 through 2019. P-value overlays county with greyed out counties without values were excluded from analysis due to lack of data. County boundaries shapefile is provided by U.S. Census Bureau *(U.S. Census Bureau 2019)*.

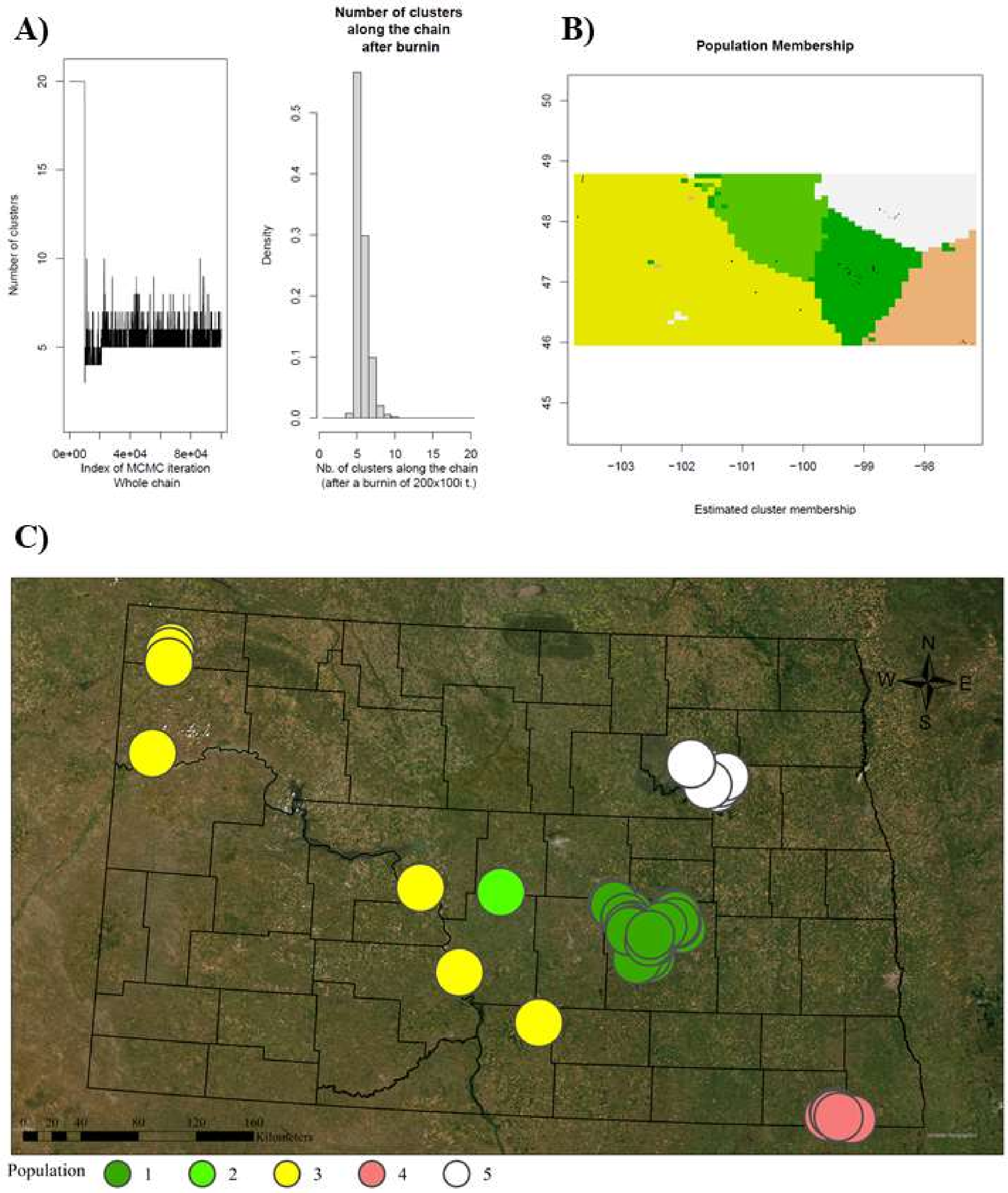

Figure 6. Genetic Population Clustering. Optimal clustering of muskrats (*Ondatra zibethicus*) sampled in North Dakota (A.), population cluster site membership (B.), satellite image of sampled locations with colors corresponding to population cluster site membership (C.).

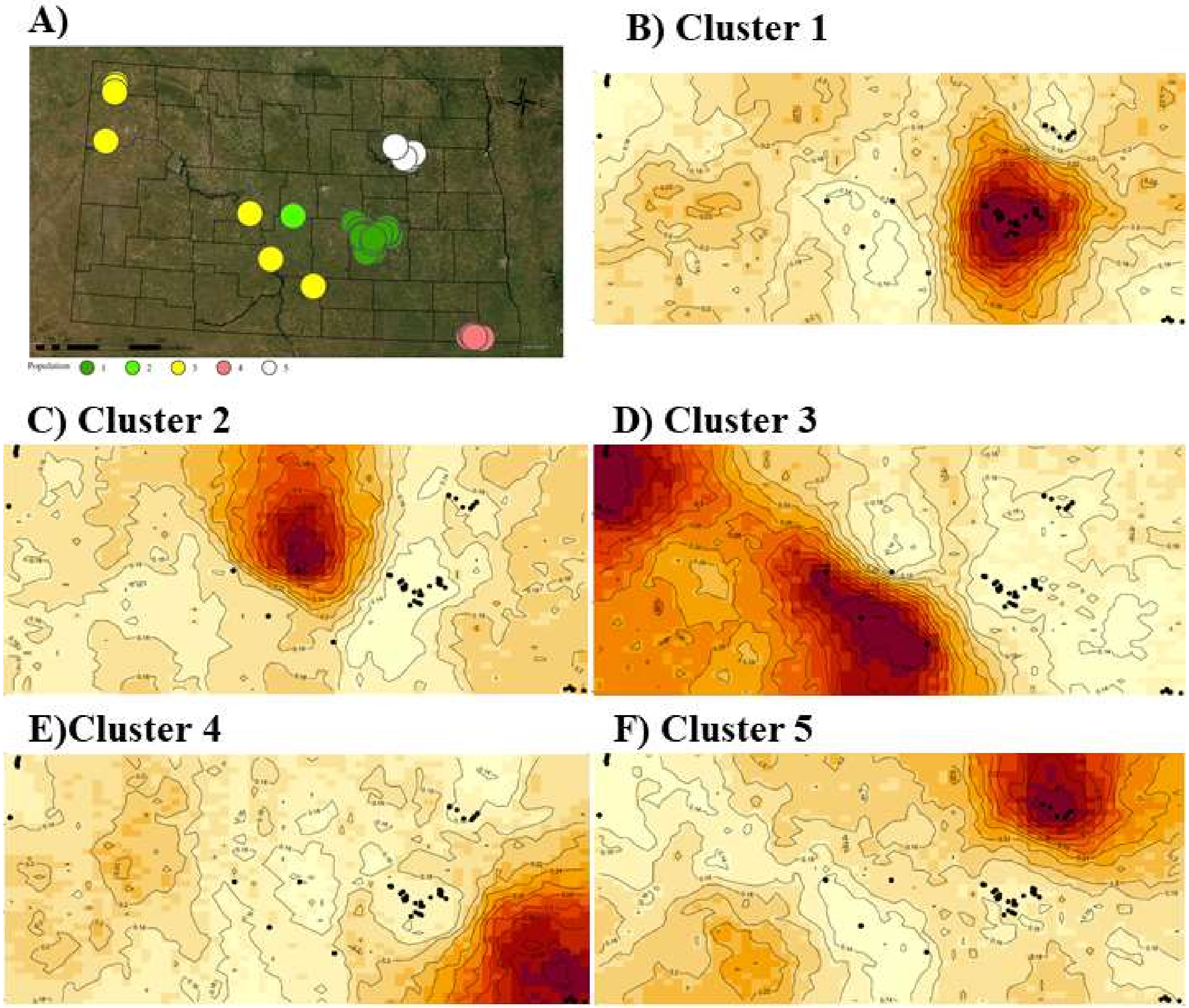

Figure 7. Probability of Population membership. Optimal clustering of muskrats (*Ondatra zibethicus*) on satellite image of sampled locations with colors corresponding to population cluster membership (A.), and B. through F. show probability of a muskrat genetically belonging to the population.

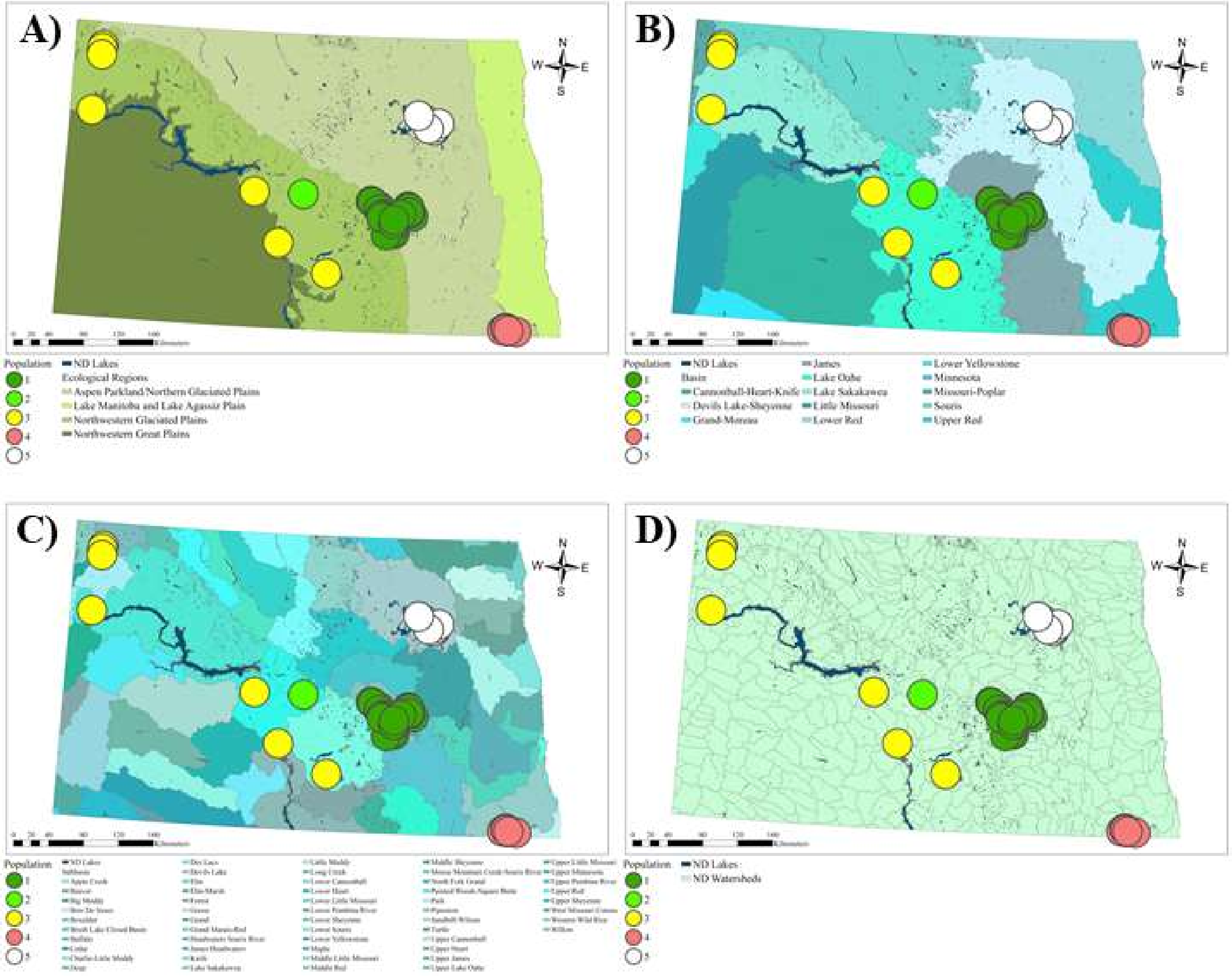

Figure 8. Landscape Relationship with Population Clusters. Landscape features potentially influencing muskrat (*Ondatra zibethicus*) population genetics in North Dakota: A. ecological regions *(EPA 2022)*, B. HUC6 basins, C. HUC8 subbasins, and D. HUC10 watersheds. *(NDGIS 2021)*.

Tables

Table 1. Cluster pseudo-F. Muskrat (*Ondatra zibethicus*) time-series cluster analysis is optimized at five clusters at the North Dakota County level as determined by highest pseudo-F.

Number of clusters	Highest Psuedo F
2	7.89
3	5.65
4	10.32
5	17.92
6	13.41
7	14.62
8	13.73
9	14.09
10	12.20

Table 2. Cluster Trends. Muskrat (*Ondatra zibethicus*) time-series cluster population trends North Dakota County level as determined by z-score biased on abundance from 1990 to 2019.

Cluster ID	Direction	Statistic	p-value
1	Not Significant	0.6387	0.523
2	Not Significant	-1.521	0.1282
3	Decreasing	-1.7897	0.0735
4	Not Significant	-0.2835	0.7768
5	Not Significant	0.3286	0.7425

Table 3. Counties per Cluster. Number of North Dakota counties associated with each cluster in the optimal muskrat (*Ondatra zibethicus*) time-series clustering analysis.

Cluster ID	Number of Locations
1	4
2	1
3	32
4	14
5	2

Table 4. County Bonferroni Values. Significant granger causality Bonferroni corrected p-values per county where badger (*Taxidea taxus*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*), mink (*Neovision vision*), skunk (*Mephitis mephitis*), and weasel (*Mustela spp.*) are predicting for muskrat (*Ondatra zibethicus*) based on rural postal survey counts from 1990 to 2019. Only significant p-values are reported with the lag required as the subscript.

County	Badger	Coyote	Fox	Mink	Skunk	Weasel
Benson			2.93E-04^{17}			
Burke		1.93E-05^{2}				1.40E-05^{5}
Dickey	6.05E-10^{19}					
Eddy				5.38E-04^{16}		
Emmons	3.22E-06^{7}	4.79E-03^{14}	1.23E-03^{7}		1.10E-06^{15}	7.26E-13^{13}
Grand Forks				2.21E-05^{4}		
Griggs		3.55E-08^{19}				
McKenzie	3.32E-02^{7}					
Morton						1.91E-08^{2}
Mountrail		8.41E-03^{17}		2.23E-10^{4}		
Nelson			1.17E-05^{15}			
Pembina		3.44E-11^{9}				
Sargent			3.88E-05^{19}			
Towner					2.69E-03^{2}	
Ward				3.01E-03^{10}		

Table 5. Population Fst Comparison. North Dakota muskrat (*Ondatra zibethicus*) genetic clustering Fst values comparing populations against each other.

Population	1	2	3	4	5
1	0				
2	0.115926	0			
3	0.059457	0.112707	0		
4	0.048759	0.147218	0.079498	0	
5	0.025077	0.1292	0.060026	0.049639	0

Table 6. Population FIS. Genetic relatedness within muskrat (*Ondatra ziberthicus*) populations (FIS) in North Dakota.

Population	FIS
1	0.039555
2	0.099868
3	0.445009
4	0.011203
5	0.083798