

Ecological and biogeographic patterns of muskrat and American mink

by

Caleb Michael Bomske

B.S., Pensacola Christian College, 2015

M.S., University of Nebraska at Kearney, 2017

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the
requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Horticulture and Natural Resources
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2026

Abstract

Semiaquatic mammals are ecologically important to wetlands, but little is known about the extent of their ecological effects, their distribution patterns in human-influenced landscapes, and how morphological patterns vary on a continental scale. Muskrats (*Ondatra zibethicus*) and American mink (*Neogale vison*), a well-known predator of muskrats, co-occur in wetlands embedded in rapidly changing prairie ecosystems. First, muskrats have wide-ranging effects on wetland habitats and are sometimes considered ‘keystone species’ or ‘ecosystem engineers.’ To evaluate these claims, we conducted a thorough review of the scientific literature. Of 363 publications, only 6% explicitly considered muskrats to be ecosystem engineers ($n = 9$) or keystone species ($n = 4$). While muskrats have broad effects on wetland flora and fauna, studies investigating these effects generally occurred over small spatiotemporal scales and used dissimilar methods and reporting, which limited inference. On a broader spatial scale, we assessed how local- and landscape-scale variables affect spatial distributions of muskrat and mink. We used detection/non-detection data from 104 isolated wetlands in Kansas, USA, from 2019-2020. Wetland occupancy by muskrats was best predicted by local variables including higher emergent vegetation diversity, larger wetlands, and larger watersheds. Mink wetland occupancy was related to landscape-scale effects including greater prairie landcover, farther distances to the nearest adjacent wetland, and less woody vegetation. At the broadest spatial scales, semiaquatic mammals tend to be larger than terrestrial counterparts – a pattern that may reflect conformity to Bergmann’s rule. To test Bergmann’s rule for muskrat and American mink, we investigated latitudinal gradients in size across their native North American distribution. Using museum collections and data from state wildlife departments ($n = 708$ muskrat and $n = 94$ mink), we used AIC model selection to see if latitude best predicted changes in size for both species. We found support for Bergmann’s rule in muskrat, but not for mink. While no relationships

between size and latitude were found for male mink, we did find support for the reverse pattern of Bergmann's rule in female mink. Collectively, our findings contribute to a better understanding of semiaquatic mammal ecology across multiple scales.

Ecological and biogeographic patterns of muskrat and American mink

by

Caleb Michael Bomske

B.S., Pensacola Christian College, 2015

M.S., University of Nebraska at Kearney, 2017

A DISSERTATION

submitted in partial fulfillment of the
requirements for the degree

DOCTOR OF PHILOSOPHY

Department of Horticulture and Natural Resources
College of Agriculture

KANSAS STATE UNIVERSITY
Manhattan, Kansas

2026

Approved by:

Major Professor
Adam Ahlers

Copyright

© Caleb Michael Bomske 2026.

Abstract

Semiaquatic mammals are ecologically important to wetlands, but little is known about the extent of their ecological effects, their distribution patterns in human-influenced landscapes, and how morphological patterns vary on a continental scale. Muskrats (*Ondatra zibethicus*) and American mink (*Neogale vison*), a well-known predator of muskrats, co-occur in wetlands embedded in rapidly changing prairie ecosystems. First, muskrats have wide-ranging effects on wetland habitats and are sometimes considered ‘keystone species’ or ‘ecosystem engineers.’ To evaluate these claims, we conducted a thorough review of the scientific literature. Of 363 publications, only 6% explicitly considered muskrats to be ecosystem engineers ($n = 9$) or keystone species ($n = 4$). While muskrats have broad effects on wetland flora and fauna, studies investigating these effects generally occurred over small spatiotemporal scales and used dissimilar methods and reporting, which limited inference. On a broader spatial scale, we assessed how local- and landscape-scale variables affect spatial distributions of muskrat and mink. We used detection/non-detection data from 104 isolated wetlands in Kansas, USA, from 2019-2020. Wetland occupancy by muskrats was best predicted by local variables including higher emergent vegetation diversity, larger wetlands, and larger watersheds. Mink wetland occupancy was related to landscape-scale effects including greater prairie landcover, farther distances to the nearest adjacent wetland, and less woody vegetation. At the broadest spatial scales, semiaquatic mammals tend to be larger than terrestrial counterparts – a pattern that may reflect conformity to Bergmann’s rule. To test Bergmann’s rule for muskrat and American mink, we investigated latitudinal gradients in size across their native North American distribution. Using museum collections and data from state wildlife departments ($n = 708$ muskrat and $n = 94$ mink), we used AIC model selection to see if latitude best predicted changes in size for both species. We found support for Bergmann’s rule in muskrat, but not for mink. While no relationships

between size and latitude were found for male mink, we did find support for the reverse pattern of Bergmann's rule in female mink. Collectively, our findings contribute to a better understanding of semiaquatic mammal ecology across multiple scales.

Table of Contents

List of Figures	x
List of Tables	xi
Acknowledgements	xiv
Dedication	xv
1 How do muskrats <i>Ondatra zibethicus</i> affect ecosystems? A review of evidence . . .	1
1.1 Introduction	2
1.2 Methods	4
1.3 Results and Discussion	6
1.3.1 Identification of Muskrats as Keystone Species or Ecosystem Engineers	6
1.3.2 Effects on Plant Communities	7
1.3.3 Effects on Animal Communities	9
1.3.4 The Muskrat as an Invasive Species	11
1.3.5 Density-Mediated Effects	12
1.3.6 Future Research Directions	13
1.4 Conclusions	13
1.5 Acknowledgements	14
2 Wetland occupancy by muskrat and American mink in an agro-prairie ecosystem .	17
2.1 Introduction	18
2.2 Materials and Methods	20
2.2.1 Study Area	20

2.2.2	Site Selection	21
2.2.3	Survey Design	21
2.2.4	Habitat Covariates	22
2.2.5	Occupancy Analysis	24
2.3	Results	25
2.3.1	Muskrat Occupancy	25
2.3.2	Mink Occupancy	25
2.4	Discussion	26
2.5	Acknowledgements	29
3	Bergmann's rule is not consistent between sexes or across species: an example from a classic predator-prey system	37
3.1	Introduction	38
3.2	Methods and Analysis	40
3.3	Results	42
3.4	Discussion and Conclusions	42
3.5	Acknowledgements	45
	Bibliography	50
A	Supplementary Material for Chapter 1	81
B	Supplementary Material for Chapter 2	96

List of Figures

1.1	Muskrat ecosystem engineer or keystone species publications	15
1.2	Ecological muskrat publications	16
2.1	Study area landcover heterogeneity	31
2.2	Predicted muskrat wetland occupancy	35
2.3	Predicted American mink wetland occupancy	36
3.1	Location points for muskrat and American mink	47
3.2	Muskrat body size and latitude	48
3.3	Mink body size and latitude	49

List of Tables

2.1 Local- and landscape-scale covariates used to predict wetland occupancy probabilities for muskrat (*Ondatra zibethicus*) and American mink (*Neogale vison*) in Kansas, USA. We present the description of each covariate along with the associated mean, range (minimum and maximum values), and standard deviation. Local-scale variables were measured at sampled wetlands each year (2019-2020). Landscape-scale variables were derived from remotely sensed landcover data. 32

2.2 Single-season models for detection and wetland occupancy probabilities of muskrats (*Ondatra zibethicus*) in Kansas, USA, from 2019-2020. ΔAICc (Akaike's information criterion corrected for small sample sizes) = difference between the model of interest and the model with the lowest AICc value, w = model weight, $-2l = -2(\text{Log likelihood})$, and K = number of parameters in each model. Detection covariates included 'Observer' (three covariates, one for each observer compared to a baseline observer), 'Date' (day of year, out of 365), 'Year' (2019 or 2020), and 'Precipitation' (total amount of rain in cm, seven days prior to survey). Occupancy covariates include 'SHDI' (Shannon diversity index of wetland plants), 'Size' (PC1 for wetland surface area and depth), 'Watershed' (area of wetland-specific catchment in hectares), 'Distance' (distance in meters to nearest permanent water), 'Agriculture' (proportion of row-crop agriculture landcover within a 5 km buffer), 'Prairie' (proportion of tallgrass prairie landcover within a 5 km buffer), and 'Forest' (proportion of forest landcover within a 5 km buffer). The top detection model (denoted by *) was used as the null occupancy model. We only present competitive models ($\Delta\text{AICc} \geq 2.00$) along with the null model. . . . 33

2.3	Single-season models for detection and wetland occupancy probabilities of American mink (<i>Neogale vison</i>) in Kansas, USA, from 2019-2020. ΔAICc (Akaike's information criterion corrected for small sample sizes) = the difference between the model of interest and the model with lowest AICc value, w_i = model weight, $-2l_i = -2(\text{Log likelihood})$, and K = number of parameters in each model. Detection covariates included 'Observer' (three covariates, one for each observer compared to a baseline observer), 'Date' (day of year, out of 365); 'Year' (2019 and 2020), and 'Precipitation' (total amount of rain [cm] seven days prior to survey). Occupancy covariates included 'SHDI' (Shannon diversity index of wetland plants), 'Size' (PCA for wetland surface area and depth), 'Wood' (percent cover of woody vegetation), 'Watershed' (area of wetland-specific watershed [ha]), 'Distance' (distance to nearest permanent waterbody [m]), 'Agriculture' (proportion of row-crop agriculture landcover within a 5 km circular buffer), 'Prairie' (proportion of tallgrass prairie within a 5 km circular buffer), and 'Forest' (proportion of forest landcover within a 5 km circular buffer). The top detection model (denoted by *) was used as the null occupancy model. We present competitive models for each parameter ($\Delta\text{AICc} \geq 2.00$) along with the null model.	34
A.1	Table of all publications used in the review.	81
B.1	Complete model set for muskrat and mink occupancy and detection	96

Acknowledgments

First, I would like to thank my God for giving me grace through the course of this endeavor. Secondly, I am grateful for the love and support of my beautiful wife, Stephanie. I would also like to thank my siblings and parents for their encouragement and support. I am particularly grateful to my mother, Norma Bomske, and her mother, Maxine Guilderson, who taught me to be kind, loving, and to bring peace into nature. Among my fellow Canadians who fostered my love for nature and encouraged me to follow a scientific path are Dr. John Krell, who told me that science needed someone like me, and Mr. John Acorn who answered my fan mail, educated me on biological subjects, and encouraged me to be a nature nut. My gratitude to my chief advisor, Dr. Adam Ahlers, cannot be overstated. Out of the many times I have felt discouraged and disillusioned by the realities of scientific process, Dr. Ahlers lifted me out of the ruts and got my feet moving again. There is no chance I could ever have completed this degree without someone as committed to my success as Dr. Ahlers. His views of conservation and stewardship of the natural world have changed me profoundly and given me a great appreciation for America's heritage of trapping and hunting. His duty to excellence in science has made me a disciple of the scientific method and an ambassador of "strong inference." I will pass on his unwavering adherence to good science as I teach others. I would also like to thank my committee members Dr. Drew Ricketts, Dr. Dan Sullins, and Dr. Andrew Hope. I am grateful for their flexibility through COVID-19, their compassion through a failed preliminary exam, and their commitment to my success. Without Dr. Hope's input and thoughtful discussion, chapter 3 of this dissertation may not exist. I deeply appreciate the approachability of Dr. Sullins, who suggested needed improvements without making me feel inferior. Finally, Dr. Ricketts challenged me to pursue uncompromising excellence in science. I am grateful to my committee for their unwavering commitment to the proper handling of data. I have been stretched to not only be a better scientist, but a better outdoorsman.

Dedication

This dissertation is dedicated to my father, David Bomske. I will never take the good father you are for granted. You stayed out with me to catch frogs after dark. You took me on canoe trips between the Canadian lakes. You backpacked with me in the Canadian Rockies. You have made me who I am today more than anyone else I know through your godly example, honesty, and moral character.

Chapter 1

How do muskrats *Ondatra zibethicus* affect ecosystems? A review of evidence

Muskrats *Ondatra zibethicus* are reported to have wide-ranging effects on wetland habitats, sometimes earning them the labels ‘keystone species’ or ‘ecosystem engineers’. We conducted an extensive review of the scientific literature and evaluated evidence for muskrats as potential keystone species or ecosystem engineers, and more generally, their known impacts on wetland ecosystems. We identified 363 publications (peer-reviewed articles, books, theses, and reports) regarding muskrats, 202 of which were in an ecological context. Only 6% (n = 13) of these explicitly considered muskrats as ecosystem engineers (n = 9) or keystone species (n = 4). Our review found that muskrat populations may have broad effects on both wetland flora and fauna. However, studies generally occurred over small spatiotemporal scales and used dissimilar methods and reporting, which limited our inference regarding muskrats’ influence on wetland ecosystems. Research explicitly identifying muskrats as ecosystem engineers or keystone species is limited, but published evidence suggests that muskrats may influence plant species diversity and habitat heterogeneity, which in turn may influence other animal species. However, long-term and experimental research is needed to uncover impacts

that muskrats have on ecosystems.

1.1 Introduction

Muskrats (*Ondatra zibethicus*) are ecologically and economically important semi-aquatic mammals whose populations appear to be declining throughout their native range in North America (Roberts and Crimmins 2010, Ahlers and Heske 2017, Greenhorn et al. 2017, Gregory et al. 2019). They are also an invasive species in Europe, South America and Asia (Anderson et al. 2006, Xu et al. 2006). Various authors have suggested that muskrats are keystone species (Danell 1996, Nummi et al. 2006, Law 2014, Brunke et al. 2017) or ecosystem engineers (Toner et al. 2010, Mott et al. 2013, Bridgewater and Aricò 2016, Greenhorn et al. 2017, etc.). Terminology can have significant conservation implications (Fischer et al. 2015), so it is important to avoid imprecise or misleading jargon. To our knowledge, there has not been a comprehensive review assessing ecosystem-level impacts that muskrats have on wetland ecosystems in their native and non-native geographic ranges.

The keystone species concept refers to impacts a species can have on an ecosystem (Paine 1966, 1969). While the concept originally described effects of a predator on prey populations (Paine 1966, 1969), ecologists expanded the ideas to include other important trophic roles, including top-down influences of herbivory (Williams 1980) and bottom-up influences of producers (Young 1980) and primary consumers (Buren et al. 2014). Inanimate objects (e.g. driftwood) that have disproportionately large impacts on an ecosystem (Young 1980) and communities of organisms that collectively change major aspects of their ecosystem (Hermosillo-Núñez et al. 2018) could also have a keystone effect. Some studies suggest a more fluid approach to categorizing species' impacts on their environment in favor of the keystone concept (Mills et al. 1993), prompting efforts to refine the concept to emphasize the proportional strength of species' impacts on other species (Power et al. 1996). Under revised definition, a keystone species must have a disproportionally large impact on its ecosystem relative to its abundance (Power et al. 1996, Davic 2003, Davidson et al. 2012). We define keystone species after Davic (2003), as a species that has a “top-down effect on

species diversity and competition [that] is large relative to its biomass dominance within a functional group.”

Ecosystem engineers are organisms that change or modify their ecosystem directly (Jones et al. 1994, Gutiérrez et al. 2014), eliciting a physical change to structure and function of an ecosystem (Gutiérrez et al. 2014). Jones et al. (1994) identified two types of ecological engineer: (1) autogenic engineers that modify ecosystems through their own living or dead tissues (e.g. accumulating bog moss, trees via leaf litter deposition, coral reef via growth), and (2) allogenic engineers that change ecosystems by actively moving materials (animate or inanimate). Examples of the latter include sea otter *Enhydra lutris* predation that increases community diversity (Singh et al. 2013), black-tailed prairie dog *Cynomys ludovicianus* disturbance in plant communities (Connell et al. 2018), and beaver *Castor canadensis* and *Castor fiber* dams that alter water catchments (Rozhkova-Timina et al. 2018). In terms of cause and effect, ecosystem engineers create a structural change to the environment, which in turn influences abiotic and biotic changes in systems (Jones et al. 2010). The impact of ecosystem engineers must be lasting, rather than brief and/or easily reversible (Jones 2012, Raynaud et al. 2013). Predation and herbivory can be examples of ecosystem engineering, if their effects have a broad, lasting impact on ecosystem function (Davic 2003, Sanders et al. 2014, Parsons et al. 2016), but they are not usually good examples of ecosystem engineering (Dickman 1999).

Early definitions of keystone species applied only to native species (Paine 1969). Keystone or ‘foundation’ species have a positive influence on their ecosystems (Paine 1969, Dodson 1970, Dayton 1972, Soran et al. 1997, etc.). Therefore, ecologists should not consider invasive, non-native species as keystone, because of their detrimental impacts on ecosystems (Nuñez and Simberloff 2005). In contrast to keystone species, ecosystem engineers can have positive or negative impacts on their ecosystem, even as invasive species (Cuddington and Hastings 2004, Gutiérrez et al. 2014, Guy-Haim et al. 2018). At the conception of the ‘ecosystem engineer’ model, Jones et al. (1994) was the first to categorize a semi-aquatic mammal (the North American beaver *Castor canadensis*) as both an ecosystem engineer and a keystone species. Beavers are now widely accepted examples of ecosystem engineers

(Naiman et al. 1988, Rosell et al. 2005, Rozhkova-Timina et al. 2018). Other rodents, including rats *Ratus* spp. and nutria *Myocastor coypus* have occasionally been mentioned as ecosystem engineers (Simberloff 2009).

Few studies were focused on muskrat ecology prior to 1940 (but see Bailey 1937, Errington 1939), and early seminal work regarding muskrat ecology (e.g., Errington 1939, 1943, 1951, Errington et al. 1963) occurred before formalization of keystone species and ecosystem engineering concepts. Perry (1998) anecdotally concluded that muskrats were recognized as “indisputably the most obvious and probably most ecologically significant [mammal] in the emergent wetland.”

In this review, we assess the published scientific evidence for muskrats’ impacts on wetland ecosystems and their potential as keystone species and ecosystem engineers. Our objectives were to conduct a comprehensive review of the scientific literature to assess reported effects that muskrats have on wetland ecosystems. Additionally, we investigated support in the literature for muskrats as ecosystem engineers or keystone species in their native and non-native ranges.

1.2 Methods

We conducted two systematic searches of scientific literature regarding muskrats, by using Web of Science and Google Scholar online databases. For historical context and summary information about impacts of muskrats on ecosystems, we also referenced books in our extensive personal collections of muskrat literature and at Kansas State University libraries. We also included articles and books cited in other publications and not directly revealed by our formal searches.

Paine (1969) coined the term ‘keystone species’ and introduced the concept in 1969, so our search did not precede that year. We used keywords relevant to muskrat ecology, particularly those pertaining to their role as ecosystem engineers and keystone species. We included 10 search criteria: “*Ondatra zibethicus* keystone species,” “*Ondatra zibethicus* ecosystem engineer,” “*Ondatra zibethicus* ecology,” “Muskrat keystone species,” “Muskrat

ecosystem engineer,” “Muskrat ecology,” “Semi-aquatic mammal keystone species,” “Semi-aquatic mammal ecosystem engineer,” “Semi-aquatic mammal ecology,” and “muskrat.”

We used the term “ecology” to broaden our search into articles that could assert muskrats as either keystone species or ecosystem engineers but did not mention it explicitly. We used the phrase “semi-aquatic mammal” to search for other potential examples of keystone engineers that may be ecologically similar to muskrats (e.g., beavers, nutria). We categorized relevant articles as mentioning muskrat ecology with or without using the terms “ecosystem engineer” or “keystone species.” Because we wanted to be as inclusive as possible in our last search, we only included the keyword “muskrat” in our online query. We assessed all articles that explicitly mentioned muskrats in some capacity, regardless of the focus of the article. We omitted articles that were irrelevant to this review (e.g., studies discussing rodent genes that bear the name “muskrat” without discussing muskrats on an organismal level). We omitted results only focusing on muskrats in allegorical, cultural, or poetic contexts. Broader, density-independent implications of the ‘cultural keystone species concept’ (Garibaldi and Turner 2004, Nuñez and Simberloff 2004), to which muskrats are easily applied (Turner et al. 2018), were not assessed in this review.

Non-English-speaking countries have populations of non-native muskrats, so it is likely that some publications relevant to this review are in other languages. We attempted to include these publications in our review but, because our literature searches were in English, we probably underrepresented other languages. Our use of the scientific name of the muskrat may help to mitigate some of this potential bias. Our initial objectives were to use robust statistical analyses to describe patterns in the published literature; however, the surprisingly limited information regarding muskrats’ impacts on ecosystems (see Results) necessitated only qualitative comparisons.

1.3 Results and Discussion

1.3.1 Identification of Muskrats as Keystone Species or Ecosystem Engineers

We identified 363 peer-reviewed journal articles (92%, $n = 334$), books (4%, $n = 13$), theses (3%, $n = 10$), and reports (2%, $n = 6$) for this review (Appendix A). Fifty-six percent ($n = 202$) were in the context of ecology, 20% ($n = 74$) were focused on physiology and cell biology (e.g., DNA, hormones, metabolism, etc.), 13% ($n = 49$) were focused on disease (e.g. muskrat parasites), 9% ($n = 31$) were focused on wildlife management, and 2% ($n = 7$) were focused on paleontology and evolution. Forty percent ($n = 147$) were focused on muskrats as their primary subject. Only 4% ($n = 13$) of publications (7 articles, 3 theses, 2 books, and 1 report) explicitly considered muskrats as ecosystem engineers ($n = 9$) or keystone species ($n = 4$; Fig. 1).

Of 202 publications mentioning muskrats in an ecological context, 87% ($n = 176$) were articles, 6% ($n = 13$) were book chapters, 5% ($n = 10$) were theses, and 1% ($n = 3$) were reports. The percentage of publications mentioning muskrats as keystone species or ecosystem engineers was slightly higher for a strictly ecological context (6%, $n = 13$) than for all contexts together (4%, $n = 13$). However, 44% ($n = 4$) of publications mentioning muskrats as keystone species or ecosystem engineers in an ecological context did not overtly focus on muskrats, and 33% ($n = 3$) were in the context of muskrats as non-native species. Altogether, 76% ($n = 153$) of publications in an ecological context considered muskrats as native species, while 24% ($n = 49$) considered muskrats as non-native species (Fig. 2).

Almost all studies investigating muskrats' impact on ecosystems were correlative, occurred over small spatiotemporal scales, and were difficult to compare due to their use of various research methods. Because of these issues, making robust inferences about the effects of muskrat populations on wetland ecosystems is challenging. The number of ecology publications that mention muskrats as keystone species or ecosystem engineers since these terms were formalized is moderate (4%; $n = 9$). Additionally, muskrats were described as

ecosystem engineers or keystone species in a smaller percentage of journal articles than of books and theses (Fig. 1). The rigorous review process for journal articles may explain why authors are less likely to claim keystone species or ecosystem engineer status for muskrats in those publications. Most studies did not suggest muskrats were ecosystem engineers or keystone species.

Three of four publications describing muskrats as keystone species were in the context of invasive species (Danell 1996, Nummi et al. 2006, Law 2014). However, the keystone species concept does not apply well to non-native species (Paine 1969), precluding these examples from our specific definition. A physical alteration to ecosystems by non-native species could be a result of ecosystem engineering (Cuddington and Hastings 2004, Gutiérrez et al. 2014, Guy-Haim et al. 2018), but not by a keystone species. However, authors were more likely to apply both keystone species and ecosystem engineer concepts where muskrats are native (Fig. 2).

1.3.2 Effects on Plant Communities

Because wetland plants are their primary source of food, muskrats are associated with high densities of vegetation (Lacki et al. 1990, Wlosinski and Wlosinski 1998, Larreur et al. 2019). The most-established effect that muskrats have on their habitat is removal of emergent vegetation via herbivory and hut construction (Connors et al. 2000, Higgins and Mitsch 2001, Farrell et al. 2010). Muskrat presence resulted in a significant reduction in vegetation biomass in a freshwater tidal marsh associated with New York’s Hudson River (Connors et al. 2000). Higgins and Mitsch (2001) observed similar reductions in biomass for artificial, experimental wetlands. Under high muskrat population densities, these effects may negatively affect native plants, causing barren patches called ‘eat-outs’ (Lynch et al. 1947, Dozier et al. 1948, Visser et al. 2006, Kadlec et al. 2007, Sarneel et al. 2014). This effect is likely to be stronger in wetlands that no longer have a natural flooding and drying regime (Wesson 1977, van der Valk and Davis 1978, Proulx and Gilbert 1983). Muskrats introduced to areas outside of their native ranges can have a negative impact on native plant species (Sarneel et

al. 2011, Vermaat et al. 2016) by reducing native plant diversity (Smirnov and Tretyakov 1998).

When muskrat population levels are stable, herbivory from muskrats decreases competition from dominant plant species and increases overall plant species richness (Penfound and Hathaway 1938, Kangas and Hannan 1985, Hewitt and Miyanishi 1997). Hewitt and Miyanishi (1997) found that wetland disturbances caused by mammals, primarily muskrats, caused an increase in plant species richness of over 70%. Mean species richness increased from 1.7 to 2.9 in pathways (Hewitt and Miyanishi 1997). Muskrats can allow establishment of rare plant species that would otherwise be outcompeted by more abundant species (Tyndall 2011). Patterns of plant colonization and ecological succession in eat-outs also increase species richness in wetlands (van der Valk and Davis 1978, Batzer et al. 2006). This kind of top-down selective consumption is a classic keystone species effect (Paine 1969). Regarding changes in plant species richness, several studies have considered muskrats as keystone species (Danell 1996, Nummi et al. 2006, Law 2014) and ecosystem engineers (Toner et al. 2010, Bridgewater and Aricò 2016).

All published studies that referred to muskrats as keystone species because of their effects on plant communities were in the context of muskrats as invasive species (Danell 1996, Nummi et al. 2006, Law 2014). The original keystone species definition does not include invasive species (Paine 1969). In a native context, muskrat-mediated changes in vegetation structure from herbivory are consistent with definitions of keystone species (McMillan et al. 2011) and ecosystem engineers (Prugh and Brashares 2012).

Microbial diversity and soil nutrient cycling also influences wetland plant composition. Composting piles of vegetation created by muskrats can facilitate nutrient turnover in wetlands by increasing microbial diversity (Wainscott et al. 1990, Connors et al. 2000). Connors et al. (2000) found a significant increase in nitrification and potential nitrogen mineralization rates in areas with muskrat activity in a New York tidal marsh. Additionally, muskrat burrows aerate wetland soil (Connors et al. 2000, Bollen 2013) and alter nutrient cycling in the substrate (Fink and Mitsch 2004, Beutel et al. 2014). Effects of composting vegetation can be examples of ecosystem engineering, provided the effect is comparatively permanent (Jones

2012, Raynaud et al. 2013). Modifications to soil systems and nutrient cycles typically have long-lasting impacts on wetlands (Pringle et al. 2010, Hagenah and Bennett 2013, Bryce et al. 2013, Fleming et al. 2014, Gutiérrez et al. 2014), which is consistent with ecosystem engineering. However, for muskrats, these effects seem to be dependent on muskrat presence and may diminish over time (Connors et al. 2000). Therefore, when considering nutrient turnover rates, muskrats are poor examples of ecosystem engineers.

1.3.3 Effects on Animal Communities

By constructing huts and increasing wetland plant disconformity, muskrats increase aquatic invertebrate species richness (Messier and Virgl 1992, de Szalay and Cassidy 2001). Additionally, some *Hemiquedius* beetles (Brunke et al. 2017) and certain aquatic insects, such as chironomid midges and gammarid scuds (de Szalay and Cassidy 2001, Nummi et al. 2006), use muskrat huts as a preferred habitat. Nummi et al. (2006) determined that size and community structure of invertebrates differs significantly throughout successional stages of vegetation growth following muskrat occupancy. This can have wide-ranging effects on invertebrate predators, including increased fish abundances in adjacent areas (Nummi et al. 2006). Although trophic interactions are not usually good examples of ecosystem engineering (Dickman 1999), trophic cascades that increase species diversity are an effect of keystone species (Paine 1969, Dodson 1970, Dayton 1972, Mann and Breen 1972, etc.).

Although muskrats are herbivores, they occasionally consume animals, such as freshwater bivalves, and this may have a negative impact on rare bivalve species (Owen et al. 2011, Williamson and Clark 2011, Hersey et al. 2013, Edelman et al. 2015). In some cases, bivalve predation can have a proportionally large impact on wetland community structure, but the effects are not long-lasting (Diggins and Stewart 2000, Owen et al. 2011). Selective consumption of freshwater mussels by muskrats (Tyrrell and Hornbach 1998) could be considered a keystone-species effect if proportionally significant (Davic 2003, Sanders et al. 2014). However, these effects are density-dependent (Edelman et al. 2015). Additional research is needed to determine if muskrat predation on freshwater mussels is disproportionate

enough to be an example of a keystone species effect.

Many vertebrate species use muskrat huts and burrows (Kiviat 1978). Alaska blackfish (*Dallia pectoralis*) and catfish (*Ictalurus* spp.) are associated with winter activities of muskrats, because muskrat movements maintain open, well-oxygenated water during winter (Errington 1957, 1961, 1963, Fraley et al. 2018). Smaller fish species, such as eastern mudminnow (*Umbra pygmaea*), use muskrat burrows as refugia (Bean 1903). Muskrat lodges and burrows can be important for reptile and amphibian habitats in wetlands. Anurans (*Anaxyrus* and *Lithobates* spp.) use muskrat lodges as hibernacula (Errington 1957, Schwartz and Schwartz 1959, Errington 1961, Browne and Paszkowski 2010). Many turtle species (*Chelydra serpentina*, *Chrysemys picta*, *Clemmys guttata*, *Emydoidea blandingii*, *Glyptemys* spp., *Graptemys pseudogeographica*, *Kinosternon* spp., and *Trachemys scripta*) also use muskrat lodges and dens for shelter and as winter hibernacula (Kiviat 1978, Ernst et al. 1989, Meeks and Ultsch 1990, Ernst et al. 1994, Litzgus et al. 1999, Starking-Szymanski et al. 2018). Turtles (*Chelydra serpentina*, *Chrysemys picta*, *Kinosternon subrubrum*, *Malaclemys terrapin*, and *Sternotherus odoratus*) and skinks (*Scincella lateralis* and *Plestiodon septentrionalis*) use muskrat lodges and burrows as nesting sites (Black 1976, Kiviat 1978, Elsey et al. 2016). Lodges can also serve as basking sites for turtles (*Chelydra serpentina*, *Chrysemys picta*, and *Emydoidea blandingii*; Conant 1938, Schwartz and Schwartz 1959, Kiviat 1978, Ernst et al. 1994). It also has been suggested that a Blanding’s turtle (*Emydoidea blandingii*) utilizes muskrat eat-outs as an important habitat (Ernst et al. 1994). Northern water snakes (*Nerodia sipedon*), fox snakes (*Pantherophis vulpinus*), and garter snakes (*Thamnophis* spp.) use muskrat lodges and burrows for shelter, basking, and hibernacula (Johnson 1925, Conant 1938, Errington 1943). Extensive use of muskrat lodges and burrows by reptiles and amphibians may have a proportionally high impact on species abundances. However, to evaluate these effects quantitatively, further research is necessary.

Birds are probably the most conspicuous beneficiaries of the muskrat’s influence on wetlands. Waterfowl (Anatidae), terns (*Chlidonias niger* and *Sterna* spp.), pied-billed grebes (*Podilymbus podiceps*), and other wetland birds benefit from muskrat huts as nesting sites (Kiviat 1978, Hickey and Malecki 1997, Ness and Klaver 2016). Muskrat eat-outs and asso-

ciated changes in vegetation composition provide habitat for herons (Ardeidae), rails (Rallidae), waterfowl (Anatidae), and passerines (Icteridae and Corvidae; Risley 1933, Weller and Spatcher 1965, Wesson 1977, Kangas and Hannan 1985, Perry 1998, Ness and Klaver 2016).

Shrews (*Sorex* spp. and *Cryptotis* sp.), moles (*Condylura cristata*), rabbits (*Sylvilagus floridanus*), American mink (*Neogale vison*), polecats (*Mustela putorius*), striped skunks (*Mephitis mephitis*), and a variety of rodents (Rodentia) use muskrat burrows and lodges for housing (Hamilton 1931, Errington 1943, 1957, Jackson 1961, Kiviat 1978). Muskrats are an important food source for many mammalian and avian predators, including American mink (Ahlers et al. 2010, Ahlers et al. 2016, Holland et al. 2018), coyotes (*Canis latrans*; Ahlers et al. 2010), wolves (*Canis lupus*; Chavez and Gese 2005), fisher (*Pekania pennanti*; Johnson-Bice et al. 2019), and raptors such as great horned owls (*Bubo virginianus*; Coefield et al. 2010) and western marsh harriers (*Circus aeruginosus*; Tornberg and Haapala 2013).

1.3.4 The Muskrat as an Invasive Species

As an invasive species, the muskrat's role as a prey species may have far-reaching ecological effects (Saveljev et al. 2015, Castillo et al. 2017) and economic impacts (Nentwig et al. 2010). Native predators can benefit from new sources of food (Tornberg and Haapala 2013); however, the facilitative affect that introduced muskrats have on invasive predators, such as American mink in South America, can disrupt local food chains (Crego et al. 2016). Muskrats and North American beavers are sympatric in their native ranges, and muskrats often use beaver lodges in favour of their own huts (Mott et al. 2013, Crego et al. 2016). Synergistic impacts of beavers and muskrats can be devastating where they are both invasive (Valenzuela et al. 2013). Additionally, muskrats compete for resources with native species, including waterfowl (Pöysä et al. 2017). Invasive muskrats may also have a negative impact on nesting success of some birds (Schofield and Reyes-Arriagada 2013).

The relationship between muskrats and vegetation is similar for both native and invasive contexts. As in their native range, introduced muskrats can increase plant species diversity (Heine and van der Velde 1978, Danell 1977). High densities of muskrats can reduce plant

species richness and abundances (Danell 1979, Sarneel et al. 2011, Vermaat et al. 2016). However, most studies dealing with the negative impacts of invasive muskrats have been conducted in restricted ecosystems, such as small wetland patches or islands (Sarneel et al. 2011, Valenzuela et al. 2013, Vermaat et al. 2016). The effects of muskrats may be different in environments that are more expansive. Although these impacts are ecologically significant regardless of muskrat abundances (Vermaat et al. 2016), invasive species should not be considered to be keystone species (Paine 1969). However, physical alterations to the environment (e.g. changes in plant species composition) are ecosystem engineering, even in an invasive context, provided the effects are long-lasting. We recommend further research to determine the impact of invasive muskrats both spatially and temporally. Future research should investigate the quantitative impacts of muskrats on ecosystems throughout their non-native range, to inform potential management strategies.

1.3.5 Density-Mediated Effects

The keystone species concept is density-dependent, but significant ecological effects may occur from comparatively low population densities (Power et al. 1996, Davic 2003, Davidson et al. 2012). Eat-outs and other muskrat-mediated changes to the landscape are most obvious when population numbers are particularly high (Lynch et al. 1947, Dozier et al. 1948, Visser et al. 2006, Kadlec et al. 2007, Sarneel et al. 2014). Additionally, muskrat populations are cyclic, responding to predation, food availability, and habitat quality (Errington 1963, Erb et al. 2001, Viljugrein et al. 2001, Zhang et al. 2003, Brzeziński et al. 2010, Luati and Proietti 2010). When abundance is relatively low, eat-outs are replaced by ecologically successive plant species (Penfound and Hathaway 1938, Kangas and Hannan 1985, Hewitt and Miyanishi 1997). Thus, the relative effects that muskrats can have on wetland structure and composition, as well as on wetland flora and fauna, may be density dependent.

1.3.6 Future Research Directions

The muskrat is one of the most economically significant invaders throughout Europe (Nentwig et al. 2010) and its effects can be both positive and negative (Heine and van der Velde 1978, Danell 1996, Bakker and Bos 2019). Muskrats' effects on ecosystems in their native range are also complicated. Based on our review, muskrats are unlikely to comply with strict definitions of ecosystem engineering, and their influence as a keystone species is tentative. However, many small-scale studies link muskrats correlatively to measurable or anecdotal changes in wetland ecosystems. The lack of consistent evidence to associate the effects of muskrats to ecosystem changes underscores the need for long-term experimental investigations. To understand muskrats' roles in ecosystem changes more fully, we recommend multi-year replicated experimental studies that are stratified by varying muskrat population abundances in both their native and non-native ranges. In this way, scale- and abundance-effects can be measured without bias.

1.4 Conclusions

Studies that provide direct support for muskrats as ecosystem engineers are rare. Only 4% of scientific publications regarding some aspect of muskrat ecology explicitly suggest that they are ecosystem engineers or keystone species. There is correlative and anecdotal evidence that muskrat-induced changes to plant species richness and habitat heterogeneity may conform to working definitions of keystone species, but, because of the potential time-mediation of their effects, muskrats probably do not conform to strict definitions of ecosystem engineers. The influence of muskrats on other animal species' abundances through lodge, burrow, and eat-out construction is noted in the scientific literature. However, we recommend further research on the proportional significance of these effects, as they may apply to keystone species or ecosystem engineering concepts. We conclude that there is some evidence for top-down impacts of muskrats on plant diversity, vegetation composition, habitat heterogeneity, and creation of important habitat for some species. These effects, however, were not consis-

tent, were correlatively assessed at small spatiotemporal scales, and were unreplicated. To elucidate density-dependent and scale-dependent effects of muskrat populations on wetland ecosystems, we recommend experimental investigations in both their native and non-native ranges.

1.5 Acknowledgements

We are thankful for support from Kansas State University's graduate Scientific Writing class of Spring 2019. The Federal Aid in Wildlife Restoration Fund (through the Kansas Department of Wildlife, Parks and Tourism) and the Department of Horticulture and Natural Resources (Kansas State University) provided funding for this study.

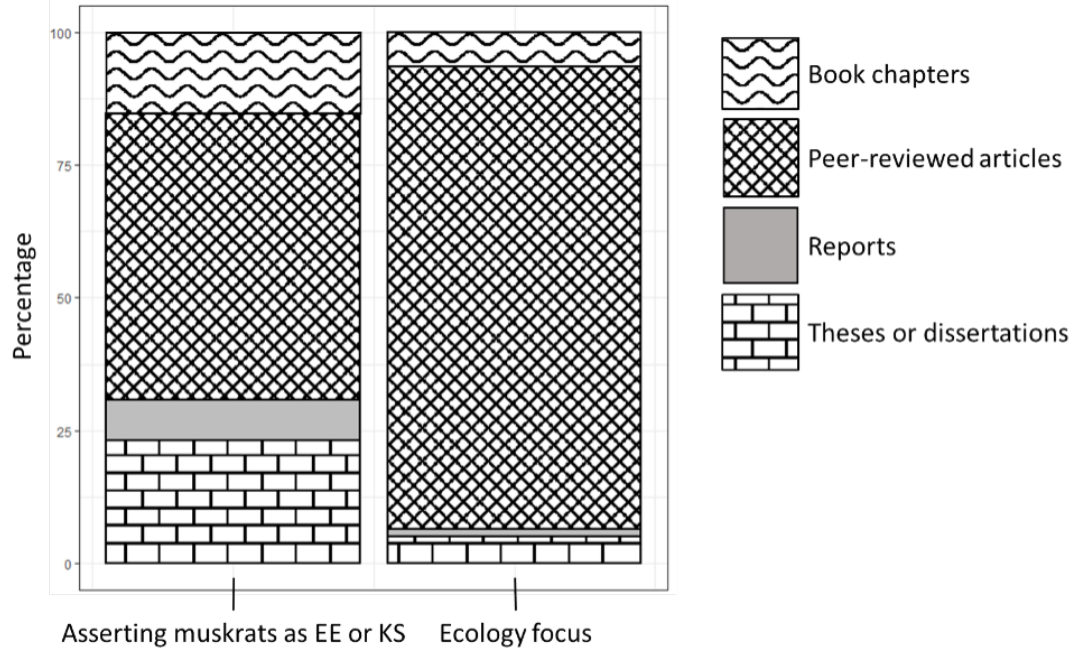


Figure 1.1: Percent of scientific publication types (articles [$n = 176$], theses [$n = 10$], books [$n = 13$], and reports [$n = 3$]) explicitly stating that muskrats are keystone species (KS; $n = 4$) or ecosystem engineers (EE; $n = 9$) and those mentioning muskrats in an ecological context.

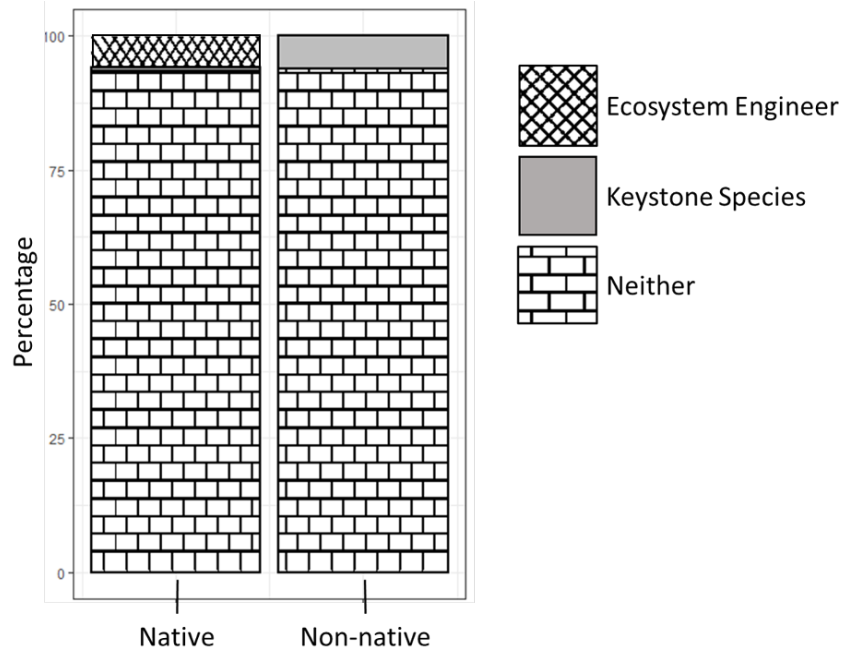


Figure 1.2: Percent of scientific publications focusing on native ($n = 153$) and non-native ($n = 49$) muskrat populations in an ecological context.

Chapter 2

Wetland occupancy by muskrat and American mink in an agro-prairie ecosystem

Land-use changes in tallgrass prairie ecosystems are prevalent (e.g., agriculture, woody encroachment) resulting in novel landscape mosaics that semiaquatic mammals must navigate when searching for suitable wetlands. It is unclear, however, how local (e.g., wetland quality) or landscape-scale effects structure wetland-occupancy patterns by semiaquatic mammals in these changing ecosystems. Muskrat (*Ondatra zibethicus*) and American mink (*Neogale vison*; hereafter ‘mink’), a well-known model in predator-prey ecology, are semiaquatic mammals that co-occur in wetlands embedded in rapidly changing prairie ecosystems. We used detection/non-detection data from 104 isolated wetlands in Kansas, USA from 2019-2020 to assess how local- and landscape-scale effects affected spatial distributions of muskrat and mink. Wetland occupancy by muskrats was most related to local wetland-quality indices including positive associations with emergent vegetation diversity, wetland size, and watershed size. Conversely, wetland occupancy patterns by mink were related to landscape-scale effects including positive associations with the amount of prairie landcover surrounding wetlands (within 5km) and distance to nearest wetland. Mink were also less likely to occupy wetlands

surrounded by woody vegetation (within 5km).

2.1 Introduction

Tallgrass prairies are reduced to 4% of their historic range in North America, largely due to agricultural expansion post European colonialism (Samson and Knopf 1994, DeLuca and Zabinski 2011, Berger et al. 2020). The Flint Hills ecoregion of Kansas and Oklahoma, USA, represents the largest remaining tract of tallgrass prairie in North America (Knapp and Seastedt 1986, Middendorf et al. 2009). Dynamic land-use practices continue to affect ecosystems in the Flint Hills, including row-crop production (Hamilton et al. 2000), overgrazing by cattle (*Bos taurus*; Hamilton 2007), woody encroachment (Ratajczak et al. 2016), urbanization (Wait et al. 2018), and widespread construction of man-made wetlands (Keane 2018). Constructed wetlands are usually developed to provide water for cattle ranching operations (Keane 2018), but also serve as critical habitat for wetland biodiversity in the region (Knutson et al. 2004, Canals et al. 2011, Johnson 2019, Smith et al. 2021, Swartz and Miller 2021). Muskrats (*Ondatra zibethicus*) and American mink (*Neogale vison*; hereafter ‘mink’) are semiaquatic mammals that occur in isolated prairie wetlands (Marchbanks 1992, Payne et al. 2001, McDonald 2006, Geluso et al. 2020). It is unclear, however, how wetland occupancy by both species is affected by land-use changes in these agro-prairie ecosystems.

Muskrats and mink are semiaquatic mammals native to North American and invasive throughout much of Europe, Asia, and South America (Bonesi and Palazon 2007, Skyriene and Paulauskas 2012, Crego et al. 2016). Muskrats are generally herbivores and may serve as keystone species (Bomske and Ahlers 2021), though long-term population declines are likely occurring across their native range (Roberts and Crimmins 2010, Ahlers and Heske 2017, Sadowski and Bowman 2021). Muskrats generally will not use upland areas and most movements are restricted to within-water habitats (Ahlers et al. 2010a) though overland movements are common during dispersal in spring (Errington 1963). Mink are small carnivores and key predators of muskrats (Errington 1943, Ahlers et al. 2010b, Ahlers et al. 2016b). Mink generally forage close to water for prey (e.g., crayfish, muskrats, fish), but

will readily use upland habitats for foraging and dispersal (Gerell 1970, Zschille et al. 2012, Ahlers et al. 2015). Previous work documented habitat-use patterns by both species in connected riparian systems in agricultural regions (e.g., Cotner and Schooley 2011, Ahlers et al. 2010a, Ahlers et al. 2016b, Holland et al. 2019a,b). In isolated wetland systems, however, it is less clear how both local-scale wetland quality and landscape composition influences wetland occupancy patterns by both species.

It is plausible that wetland occupancy patterns by semiaquatic mammals may reflect island biogeography theory (MacArthur and Wilson 1967) where smaller and/or more isolated wetlands are less likely to be occupied. In regions where wetlands are isolated among a patchy matrix of landcover types, wetland occupancy by both species may also reflect local wetland quality, spatial distribution of available wetlands, or surrounding landscape context. For instance, metapopulations of round-tailed muskrats (*Neofiber alleni*) depend on habitat connectivity for colonization and occupancy (Schooley and Branch 2011). Both muskrats and mink are vulnerable to predation risks in wetlands with low water levels (Errington 1963) and larger, deeper wetlands may provide areas to persist during drought or provide better habitat quality (e.g., more or consistent prey, less likely to completely freeze, more shoreline vegetation). Muskrats are more likely to use areas within wetlands with greater amounts of cattail coverage (*Typha* spp; Clark 1994, Larreur et al. 2020) and deeper and more open water (Larreur et al. 2020) – likely choosing these areas based on increased habitat quality. Mink also rely on supplemental resources and are more likely to occupy wetlands more isolated from permanent water resources (Ahlers et al. 2016b, Holland et al. 2019b) or based on occurrence of prey species such as muskrats (Ahlers et al. 2016b).

Matrix composition between isolated wetlands may also structure wetland occupancy patterns by muskrats and mink (Bunn et al. 2000, Giroux-Bougard 2014). Forested landcover can act as barriers to muskrat movements (Schooley and Branch 2009, Laurence et al. 2013, Matykiewicz et al. 2021) and widespread woody encroachment in the Flint Hills may preclude muskrats from finding wetlands to occupy. It is unclear how row-crop agriculture affects wetland occupancy by both muskrats and mink, though both species experience greater mortality risks when using these areas (Ahlers et al. 2015). Although muskrats

and mink have coexisted within prairie-dominated landscapes prior to widespread landscape changes (Hibbard and Taylor 1960, Paulson 1961, Hibbard 1963), it is unclear how prairie landcover within the matrix affects wetland occupancy by muskrats and mink.

We used two years of detection/non-detection surveys and stacked, single-season occupancy models to assess local- and landscape-scale factors associated with wetland occupancy by both muskrats and mink. Consistent with island biogeography theory, we predicted that smaller, more isolated wetlands would be less likely to be occupied by muskrat and mink. Because woody encroachment on prairie landscapes reduces available food resources (shade decreases herbaceous plant diversity; Walton et al. 2021, Swartz and Miller 2021), we predicted that wetland occupancy by muskrat and mink would be negatively affected by the amount of forest landcover surrounding wetlands and positively affected by the amount of prairie landcover surrounding wetlands. Row-crop agriculture may pose greater mortality risks for muskrat and mink, so we predicted lower occupancy probabilities at wetlands surrounded by agriculture. We predicted emergent vegetation diversity would positively influence wetland occupancy by muskrats and mink by directly providing forage for muskrats and increased foraging opportunities for mink.

2.2 Materials and Methods

2.2.1 Study Area

Our study was conducted in the northern Flint Hills of Kansas, USA (Fig. 1). The Flint Hills are characterized by shallow, rocky soils over Cambrian and Permian limestone and flint. Elevation in our study area ranged from 300 – 500 m. During the duration of our study, monthly precipitation and temperature ranged from 20 – 184 cm (mean 105 cm) and -14° – 37° C (mean 23° C), respectively. Our study wetlands were created by landowners as retention ponds for watering cattle and are equipped with a drainage pipe through the embankment that functions as a spillway to keep water from flowing over and washing out the embankment following precipitation events. Water is contained with an embankment of soil

and rocks, usually drawn from pond bed. These man-made wetlands serve as critical habitat for aquatic and semiaquatic species (Knutson et al. 2004, Canals et al. 2011, Johnson 2019, Smith et al. 2021, Swartz and Miller 2021) and common aquatic and emergent plants include spikerush (*Eleocharis* sp.), milfoil (*Myriophyllum* sp.), pondweed (*Potamogeton* sp.), sedges (*Cyperus* sp.), arrowhead (*Sagittaria* sp.), knotweed (*Polygonum* sp.), cattail (*Typha* sp.), bullrushes (*Schoenoplectus* sp.), duckweed (*Lemna* sp.), and mud plantain (*Heteranthera* sp.). Upland landcover included grasses (primarily *Sorghastrum* sp., *Schizachyrium* sp., and *Andropogon* sp.) and forbs (including *Solidago* sp., *Verbena* sp., *Asclepias* sp., and *Euphorbia* sp.). Woody vegetation was composed primarily of eastern redcedar (*Juniperus virginiana*), smooth sumac (*Rhus glabra*), and roughleaf dogwood (*Cornus drummondii*).

2.2.2 Site Selection

We randomly selected 104 wetlands from within an 80-km buffer surrounding Manhattan, Kansas (Fig. 1). Wetlands were isolated amid a landcover matrix composed of developed, agricultural, forested, hayed, and native prairie landscapes (Fig. 1). Wetland surface area ranged from 146 – 25,424 m² (mean: 2,839 m²) and they were positioned an average of 0.3 km (range = 0.01 – 1.2 km) from the nearest permanent water source (e.g., riparian areas or other wetlands). Our sampled wetlands were separated by an average of 4.4 km (range = 1 – 15 km).

Wetlands were located on private land, except for two sites on federal military property (Fort Riley). Landowners were contacted via phone calls and verbal permissions were requested. In cases where a landowner could not be reached over the phone, we visited the address associated with the number and sought in-person verbal permissions.

2.2.3 Survey Design

Two observers conducted detection/non-detection surveys for muskrat and mink at 104 wetlands from September through November in 2019 and 2020. Each year, both observers walked the perimeter of each wetland, moving in opposite directions and searching for sign

of muskrat (e.g., tracks, scat, clippings, burrows, huts) and mink (e.g., tracks, scat), up to 6 m away from water’s edge. Observers also searched below dam and down spillway up to 12 m. Average survey time per observer was about 30 minutes. Observers used an independent survey effort during each visit (MacKenzie and Royle 2005) resulting in 2 independent surveys during the first visit to a wetland and 2 independent surveys during the second visit. We used a removal design approach (MacKenzie et al. 2018) based on presence of muskrats at wetlands – if muskrats were detected during the first set of surveys during a given year we did not return to that wetland for additional surveys that year (Ahlers et al. 2016b). This removal design assumes occupancy status remains constant throughout the sampling season (closure) and sites occupied during the first survey remain occupied during subsequent survey occasions within the same season (MacKenzie et al. 2018). Therefore, wetlands were visited once (if muskrats were detected during first visit) or twice each year. We conducted both wetland visits within two weeks to ensure population closure each year (MacKenzie et al. 2018). Our species-specific annual detection histories for each site ranged from 2-4 detection events each year (1 = species detected, 0 = species not detected). Our survey methods were approved by the Kansas State University Institutional Animal Care and Use Committee (Approval no. 4074) and consistent with guidelines provided by the American Society of Mammalogists (Sikes et al. 2016).

2.2.4 Habitat Covariates

We measured local-scale habitat characteristics at each wetland immediately following first wetland visits each year (Table 1). At each wetland, we established 10-m transects at 6-m intervals along the wetland shoreline. Each transect ran perpendicular to the shoreline, beginning 2 meters from shore in the wetland and ending 8 meters away from the wetland. Number of transects varied depending on the length of wetland shoreline and averaged 3 transects (range = 1 – 8) per wetland. We measured habitat characteristics with a 1x1 m Daubenmire frame, at five evenly spaced intervals along each transect. At each sampling interval along transects, we estimated proportion cover of woody vegetation (Wood), num-

ber of wetland plant species (range = 0 – 7), and proportion of vegetation cover (wetland and terrestrial species). From the proportion of wetland plant species at each wetland, we calculated the diversity of vegetation community using a Shannon Diversity Index (SHDI). We estimated water depths (average depth = 3.3 m, range = 0.5 – 10 m), averaged from five casts of an iBobber® (ReelSonar: Seattle, Washington) from a fishing rod. Three casts were from the dam face (usually deepest part of wetland) and two casts were from shorelines perpendicular to dam. For each wetland, we averaged measurements across all transects to obtain a single site-level covariate for each habitat variable. Wetland surface area was obtained from the National Hydrography Dataset (NHD 2021), which includes manmade wetlands. Independent measures of wetland surface area and wetland depth are both surrogates of available habitat for semiaquatic mammals. We used a Principal Components Analysis (PCA) with an orthogonal (varimax) rotation to combine wetland surface area and depth into a composite variable representing wetland size (Size) using the first eigenvector which explained 72% of variance.

We used QGIS 3.16 (QGIS 2021) to extract landscape-scale covariates (Table 1) from National Land Cover Dataset (30 m raster; NLCD 2019). We measured proportional landcover classes (Prairie, Agriculture, and Forest) within a 5-km circular buffer surrounding each wetland (Fig. 1). We also considered alternative buffer scales (0.5 km, 1 km, 2 km) and extracted landcover metrics from these. All landscape metrics, however, were correlated across all scales so we moved forward with a 5 km buffer to best reflect potential broad-scale landcover effects on muskrat and mink wetland occupancy patterns. In addition to proportion of landcover classes for each wetland, we also measured watershed size (Watershed; amount of land area [ha] drained specific to individual wetlands) and Euclidean distance (Distance) to nearest wetland. Although developed land (e.g., urban areas, roads) was initially considered potentially important, it represented only a small proportion (0.04) of total landcover surrounding our study wetlands. Landcover variables ‘Agriculture’ and ‘Prairie’ were negatively correlated ($r = -0.93$) so we did not include these two variables in the same model.

2.2.5 Occupancy Analysis

We used single-species, single season occupancy models (Program PRESENCE Version 2.13.10) to estimate wetland occupancy probabilities by both muskrat and mink. We used a single-season stacked occupancy modeling approach (e.g., Fuller et al. 2016, Asad et al. 2020), rather than a multiseason approach, because we observed too few local colonization and extinction events between years to model colonization and persistence rates (see Results). We considered four factors which may have affected our ability to detect both muskrat and mink at wetlands. To account for differences in survey effort or ability between observers (Observer), we selected a baseline observer (CB) to compare detection probabilities across three remaining observers. We also controlled for survey date (Date) and amount of total rain (cm) 7-days prior to each survey (Precipitation). We obtained rainfall data from US Climate Data (2021) website, from Manhattan, Kansas, weather station. We also modeled ‘Year’ as a dummy variable for each survey year, where 0 = 2019 and 1 = 2020, to account for unmodeled variation in detection between years (Fuller et al. 2016). Using both single and additive effects, we considered 16 models of detection along with an intercept-only model (null; Supplementary Data SD1) for muskrat and mink. For each species, we considered both local- and landscape-scale effects that had potential to affect wetland occupancy. We constructed a candidate set of occupancy models using both single and additive effects of our measured covariates along with an intercept-only model (null; Supplementary Data SD1). We did not include ‘Agriculture’ and ‘Prairie’ in the same models because of multicollinearity issues ($r = -0.93$).

We used a sequential-by-sub model strategy where we chose the most-supported detection model to include in all models within our candidate set of occupancy models (Morin et al. 2020). Models for each parameter were ranked using Akaike’s Information Criterion corrected for small sample sizes (AICc). Models with a $\Delta AICc < 2$ were considered competitive. When selecting for a best fit-model for both detection and occupancy, we used an information-theoretic approach (Burnham and Anderson 2002, Arnold 2010).

2.3 Results

We surveyed 101 sites in 2019 and 92 sites in 2020. We detected muskrats at 27% ($n = 27$) of surveyed wetlands in 2019 and 21% ($n = 19$) in 2020. We detected mink at 33% ($n = 33$) of surveyed wetlands in 2019 and 37% ($n = 34$) in 2020. Naïve occupancy was 0.24 for muskrat and 0.35 for mink. Modeled detection probability was 0.60 ($SE = 0.22$) and corrected occupancy probability was 0.24 ($SE = 0.20$) for muskrat. Modeled detection probability was 0.39 ($SE = 0.30$) and corrected occupancy probability was 0.43 ($SE = 0.14$) for mink.

2.3.1 Muskrat Occupancy

Our top muskrat detection models included Observer (Obs1: $\beta = -1.66$, $SE = 0.53$, Obs2: $\beta = -0.92$, $SE = 0.62$, Obs3: $\beta = -0.77$, $SE = 0.67$) and Date ($\beta = 0.01$, $SE = 0.001$). Competitive detection models (Table 2.2) included Year and Precipitation, but model fit was not improved. This is consistent with previous studies that demonstrate the importance of observer (Crockett et al. 2024) and date (Cotner and Schooley 2011, Holland et al. 2019) in modeling muskrat detection probabilities. Our top occupancy model for muskrats included the positive effects of SHDI ($\beta = 0.87$, $SE = 0.21$; Fig. 2A), Size ($\beta = 0.47$, $SE = 0.19$; Fig. 2B), and Watershed ($\beta = 0.37$, $SE = 0.17$, Fig. 2C). The sum model weight was $w = 0.99$ for SHDI, $w = 0.88$ for Size, and $w = 0.73$ for Watershed. There were four competitive muskrat occupancy models (Table 2.2) including Distance, Agriculture, Prairie, and Forest. Addition of each of these covariates did not improve model fit and model estimates for Agriculture, Prairie, and Forest had confidence intervals overlapping 0. See Appendix B for the full model set.

2.3.2 Mink Occupancy

Our most-supported detection models for mink included Precipitation ($\beta = -0.04$, $SE = 0.01$) and Date ($\beta = 0.03$, $SE = 0.001$). There was an additional competitive model (Precipitation

+ Date + Year) which did not improve model fit (Table 2.3), and Year had a confidence interval overlapping 0. Our top occupancy model for mink included Distance (distance to the nearest wetland; $\beta = 0.38$, $SE = 0.19$), Forest ($\beta = -0.45$, $SE = 0.21$), and Prairie ($\beta = 0.37$, $SE = 0.19$). The sum model weight was $w = 0.63$ for Distance, $w = 0.69$ for Forest, and $w = 0.53$ for Prairie. Mink were less likely to occupy wetlands closer to other permanent water sources (Fig. 3A) or surrounded by greater coverages of forested landcover (Fig. 3B), and more likely to occupy wetlands surrounded by greater coverages of prairie landcover (Fig. 3C). Three other competitive models included Wood, SHDI, and Size, which all had confidence intervals overlapping 0. However, model fit remained similar across all competitive models, suggesting that these covariates were not informative. See Appendix B for the full model set.

2.4 Discussion

Muskrats were more likely to occupy larger, deeper wetlands and wetlands occurring in larger watersheds (though these two variables were uncorrelated). This pattern is consistent with traditional island biogeography theory, where larger “islands” (in this case, wetlands) are more likely to be occupied than smaller ones (MacArthur and Wilson 1967). Larger wetlands may be easier to find and colonize during dispersal events (Errington 1963). Additionally, they may be more resistant to drought and/or freezing providing sufficient water for prey avoidance during those times. Wetlands occurring in larger watersheds collect water runoff over larger areas increasing the likelihood that wetlands have sufficient water levels to sustain muskrat populations. Muskrat populations are sensitive to water level fluctuations, including flooding or drought (Toner et al. 2010, Straka et al. 2018, Ward and Gorelick 2018) and choosing hydrologically stable wetlands may buffer them from effects of prolonged or intense drought. Muskrats were also more likely to occupy wetlands with greater forage diversity. Importance of wetland plant diversity to muskrats may represent increased feeding opportunities but may be more likely to also reflect ecological and hydrological stability of wetlands (Bellrose and Brown 1941).

Our results demonstrate that wetland occupancy by muskrats was more related to local-scale wetland quality than landscape-scale factors. Positive associations of watershed and wetland size, and plant species diversity, emphasize the importance of wetland quality over composition of the intervening matrix (Schooley and Branch 2007, 2011). Indeed, muskrats rarely use upland habitats for reasons other than dispersal (Laurence et al. 2013, Miller 2018, Matykiewicz et al. 2021) and local-scale wetland quality may be relatively more important at sustaining local populations than landscape composition surrounding wetlands. Widespread landscape changes have functionally altered connectivity in the Flint Hills tallgrass prairie (Hamilton et al. 2000, Hamilton 2007, Ratajczak et al. 2016, Wait et al. 2018) and it is plausible that muskrats are also affected. Paradoxically, it is important to note that our sampled wetlands were manmade and that occurrence of muskrat and other wetland-obligate species, outside of natural wetlands and riparian areas, is dependent on this important landscape change. The number of man-made wetlands has been increasing in the Midwest (including prairie states; Smith et al. 2002) Patterns observed from our study likely apply to muskrat populations occurring in natural wetlands and riparian areas as well.

Wetland colonization by muskrats was rare during our study suggesting that movement rates between wetlands were low. This could be a result of impermeable matrix landcover surrounding wetlands or that we conducted our study while muskrat abundances were too low to provide individuals to colonize wetlands. Our study region experienced a severe drought during summer and fall 2018 (Ozment et al. 2021, Wedel et al. 2021) resulting in significant wetland drying and water loss throughout the Flint Hills. Previous surveys for muskrats during this time revealed many wetlands were dry and muskrats were absent (Bomske, personal observation). The drought conditions likely had a negative effect on regional muskrat populations and their populations may not have fully recovered by 2019 and 2020. Larger wetlands may have provided refugia for individuals during the drought and provided source populations for future wetland colonization in the Flint Hills. Studies linking population genetics to landscape permeability and wetland colonization rates would likely reveal important information regarding metapopulation dynamics of muskrats in the Flint Hills.

Wetland occupancy by mink was more influenced by landscape-scale effects than local-scale wetland quality - likely underscoring the ability of mink to move in upland areas to forage between wetlands (Gerell 1970, Zschille et al. 2012, Ahlers et al. 2015). Our results suggest that mink were more likely to occupy wetlands surrounded by prairie landcover and were less likely to occupy wetlands surrounded by forest landcover. While the Flint Hills remains a stronghold for tallgrass prairie conservation (Knapp and Seastedt 1986, Middendorf et al. 2009), widespread neglect of historic fire regimes (Briggs et al. 2002b) has resulted in woody encroachment by eastern redcedar (*Juniperus virginiana*) and deciduous forests (Owensby et al. 1973, Knight et al. 1994, Briggs et al. 2002a, Ratajczak et al. 2016). Native small mammal species including mink prey are reduced in areas invaded by woody encroachment in prairie ecosystems (Kaufman et al. 2000, Horncastle et al. 2005, Matlack et al. 2008). This potentially effects aquatic prey as well, like frogs (Swartz and Miller 2018) and crustaceans (Adams et al. 2021), which are both negatively impacted by woody encroachment. Native tallgrass prairie has greater diversity of herbaceous plants and small mammals than areas affected by woody encroachment (Alford et al. 2012, Ratajczak et al. 2012). Additionally, avian predators of mink benefit from the use of tree perches when hunting in grasslands (Atuo and O’Connell 2017). We observed both hawks (*Buteo* sp.) and owls (*Bubo virginianus*) in trees near wetlands in our study area, both of which are known to prey on mink (Larivière 1999). Ours is not the first study to report a negative influence of forest cover on mink distributions (e.g., Holland et al. 2019b). Negative associations between forest landcover and wetland occupancy by mink suggests that woody encroachment in the great plains may be limiting functional connectivity of wetlands for mink or reducing habitat quality of wetlands surrounded by woody encroachment (via increased predation risks).

Although not intuitive, the positive relationship between wetland occupancy probabilities by mink and distance to nearest wetland is consistent with previous studies (Ahlers et al. 2016b, Holland et al. 2019b). Mink may be allocating more time at isolated wetlands when functional connectivity to other wetlands is reduced (Ahlers et al. 2016b, Holland et al. 2019b). This is also consistent with marginal value theorem (Charnov 1976), which predicts giving up time at patches (e.g., amount of time spent at wetlands) would increase with

increasing distance to other patches (e.g., other wetlands). Moreover, costs associated with moving between wetlands may be increased for mink – especially in areas where landcover may be dominated by agricultural production (Ahlers et al. 2015). Fine-scale habitat-selection and population genetic studies in agro-prairie ecosystems would likely enhance our mechanistic understanding of how landscape composition and wetland isolation affect movement choices by mink and their relative mortality risks.

Muskrat and mink are well-studied models of predator-prey dynamics (e.g., Erb et al. 2000, Erb et al. 2001, Holmengen et al. 2009, Ahlers et al. 2021). However, muskrat and mink co-occurred at only 9 sites, and preliminary analysis of co-occurrence found significant model-selection uncertainty in our model set. Limited co-occurrence may reflect small sample sizes, or the inability of muskrats to escape mink in small, isolated wetlands. There was no relationship between co-occurrence and wetland size ($r = 0.08$, $p = 0.29$). We suggest that future studies with more robust datasets investigate potential interaction dynamics between muskrat and mink in agro-prairie ecosystems.

Our findings underscore how the relative importance of local- and landscape-scale factors may vary for similar sized semiaquatic mammals occurring in agro-prairie landscapes. Mink and muskrat metapopulation dynamics are complex and require additional information to fully understand how distributions of both species are structured in multiuse landscapes. Future research should incorporate fine-scale space use and genetic information to better understand multiscale wetland use and turnover by both species.

2.5 Acknowledgements

Our research occurred on lands historically home to Native nations including the Kaw, Osage, and Pawnee, among others. This work was funded by the Department of Horticulture and Natural Resources at Kansas State University and the Kansas Department of Wildlife and Parks via the US Federal Aid in Wildlife Restoration Fund. We are thankful for the field work of M. Larreur, G. Long, M. Zurschmiede, and S. Bomske. We also thank A. Ricketts, D. Sullins, and A. Hope for advice and suggestions on improving this research. We thank

the farmers and ranchers who gave us permission to study on their privately-owned wetlands and would also like to thank Konza Prairie Biological Station, Kansas State University, and Fort Riley for allowing us to collect data on their properties.

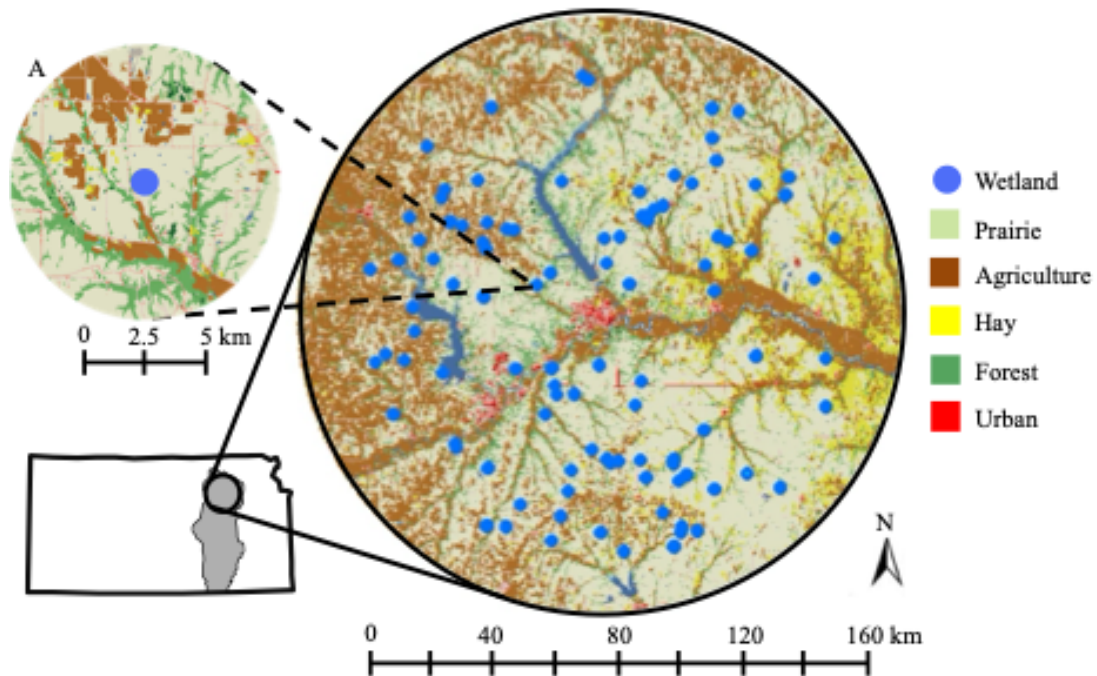


Figure 2.1: Study area demonstrating landcover heterogeneity in the Flint Hills of Kansas, USA where we surveyed 104 randomly selected wetlands (blue dots) for presence of muskrat (*Ondatra zibethicus*) and American mink (*Neogale vison*) for two years (2019-2020). Map of Kansas and spatial extent of the Flint Hills ecoregion highlighted in gray. Inset 'A' depicts the complexity of landcover types surrounding (5km circular buffer) one of our sampled wetlands. Wetlands (blue circles) are not to scale.

Table 2.1: Local- and landscape-scale covariates used to predict wetland occupancy probabilities for muskrat (*Ondatra zibethicus*) and American mink (*Neogale vison*) in Kansas, USA. We present the description of each covariate along with the associated mean, range (minimum and maximum values), and standard deviation. Local-scale variables were measured at sampled wetlands each year (2019-2020). Landscape-scale variables were derived from remotely sensed landcover data.

Covariate	Description	Mean	Min	Max	SD
Local-scale					
SHDI	Shannon diversity index for wetland plant species	0.45	0.12	0.74	0.16
Wood	Proportion cover of woody vegetation	0.01	0.00	0.09	0.02
Size	Composite variable derived from a principal component analysis representing wetland surface area (ha) and depth (m)	0.21	0.00	0.58	0.16
Landscape-scale					
Watershed (ha)	Area of wetland-specific watershed	25	1	211	31
Distance (m)	Euclidean distance to nearest permanent waterbody	378	11	1200	249
Agriculture	Proportion row-crop agriculture within 5km circular buffer surrounding wetland	0.21	0.00	0.58	0.16
Prairie	Proportion tallgrass prairie within 5km circular buffer surrounding wetland	0.45	0.12	0.74	0.16
Forest	Proportion forest land within 5km circular buffer	0.07	0.00	0.27	0.05

Table 2.2: Single-season models for detection and wetland occupancy probabilities of muskrats (*Ondatra zibethicus*) in Kansas, USA, from 2019-2020. ΔAICc (Akaike's information criterion corrected for small sample sizes) = difference between the model of interest and the model with the lowest AICc value, w = model weight, $-2l = -2(\text{Log likelihood})$, and K = number of parameters in each model. Detection covariates included 'Observer' (three covariates, one for each observer compared to a baseline observer), 'Date' (day of year, out of 365), 'Year' (2019 or 2020), and 'Precipitation' (total amount of rain in cm, seven days prior to survey). Occupancy covariates include 'SHDI' (Shannon diversity index of wetland plants), 'Size' (PC1 for wetland surface area and depth), 'Watershed' (area of wetland-specific catchment in hectares), 'Distance' (distance in meters to nearest permanent water), 'Agriculture' (proportion of row-crop agriculture landcover within a 5 km buffer), 'Prairie' (proportion of tallgrass prairie landcover within a 5 km buffer), and 'Forest' (proportion of forest landcover within a 5 km buffer). The top detection model (denoted by *) was used as the null occupancy model. We only present competitive models ($\Delta\text{AICc} \geq 2.00$) along with the null model.

Parameter	Model	ΔAICc	w	$-2l$	K
Detection	Observer + Date*	0.00	0.25	345.30	6
	Observer + Date + Year	0.89	0.16	344.19	7
	Observer + Date + Precipitation	1.00	0.15	344.30	7
	Observer	1.39	0.13	348.69	5
	Observer + Date + Year + Precipitation	1.73	0.11	343.03	8
	Null	8.68	0.00	361.98	2
Occupancy	SHDI + Size + Watershed	0.00	0.24	306.21	9
	SHDI + Size + Watershed + Distance	1.05	0.14	305.26	10
	SHDI + Size + Watershed + Agriculture	1.40	0.12	305.61	10
	SHDI + Size + Watershed + Prairie	1.74	0.10	305.95	10
	SHDI + Size + Watershed + Forest	1.85	0.09	306.06	10
	Null	33.09	0.00	345.30	6

Table 2.3: Single-season models for detection and wetland occupancy probabilities of American mink (*Neogale vison*) in Kansas, USA, from 2019-2020. ΔAICc (Akaike’s information criterion corrected for small sample sizes) = the difference between the model of interest and the model with lowest AICc value, w = model weight, $-2l = -2(\text{Log likelihood})$, and K = number of parameters in each model. Detection covariates included ‘Observer’ (three covariates, one for each observer compared to a baseline observer), ‘Date’ (day of year, out of 365); ‘Year’ (2019 and 2020), and ‘Precipitation’ (total amount of rain [cm] seven days prior to survey). Occupancy covariates included ‘SHDI’ (Shannon diversity index of wetland plants), ‘Size’ (PCA for wetland surface area and depth), ‘Wood’ (percent cover of woody vegetation), ‘Watershed; (area of wetland-specific watershed [ha]), ‘Distance’ (distance to nearest permanent waterbody [m]), ‘Agriculture’ (proportion of row-crop agriculture landcover within a 5 km circular buffer), ‘Prairie’ (proportion of tallgrass prairie within a 5 km circular buffer), and ‘Forest’ (proportion of forest landcover within a 5 km circular buffer). The top detection model (denoted by *) was used as the null occupancy model. We present competitive models for each parameter ($\Delta\text{AICc} \geq 2.00$) along with the null model.

Parameter	Model	ΔAICc	w	$-2l$	K
Detection	Precipitation + Date*	0.00	0.59	505.25	4
	Precipitation + Date + Year	1.29	0.31	504.54	5
	Null	80.36	0.00	589.61	2
Occupancy	Distance + Forest + Prairie	0.00	0.10	495.13	7
	Distance + Forest + Prairie + Wood	0.43	0.08	493.56	8
	Distance + Forest + Prairie + SHDI	1.68	0.04	494.81	8
	Distance + Forest + Prairie + Size	1.99	0.03	495.12	8
	Null	4.12	0.01	505.25	4

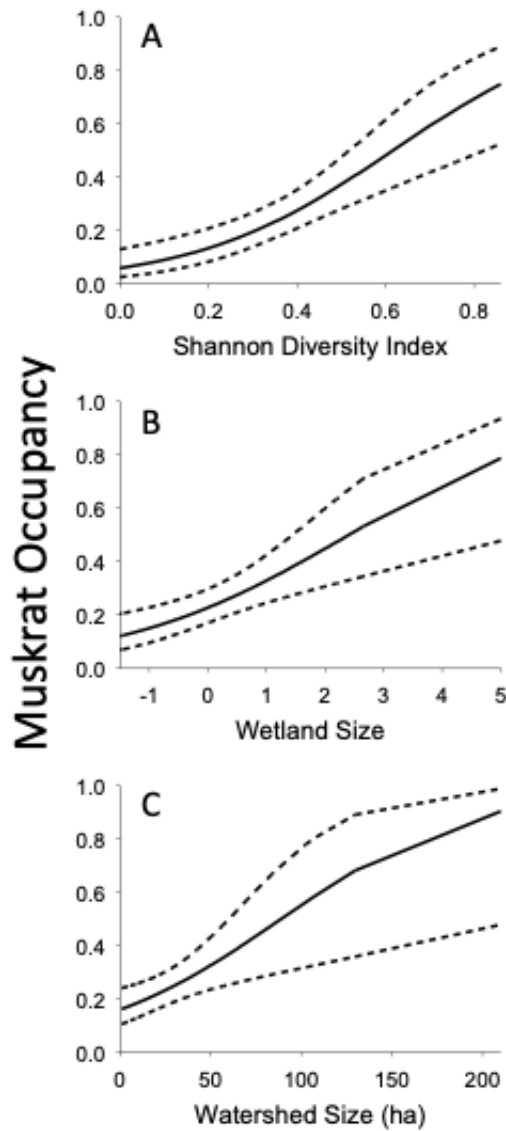


Figure 2.2: Predicted effects and 95% confidence intervals from our most-supported model of wetland occupancy by muskrats (*Ondatra zibethicus*) at 104 wetlands in the Flint Hills, Kansas, USA during 2019 and 2020. Effects include (A) the Shannon Diversity Index of aquatic and emergent wetland plant species, (B) wetland size (composite variable including surface area [ha] and depth [m]), and (C) watershed size (ha). We assessed wetland occupancy by muskrats using detection/non-detection sign surveys and single-season occupancy modeling.

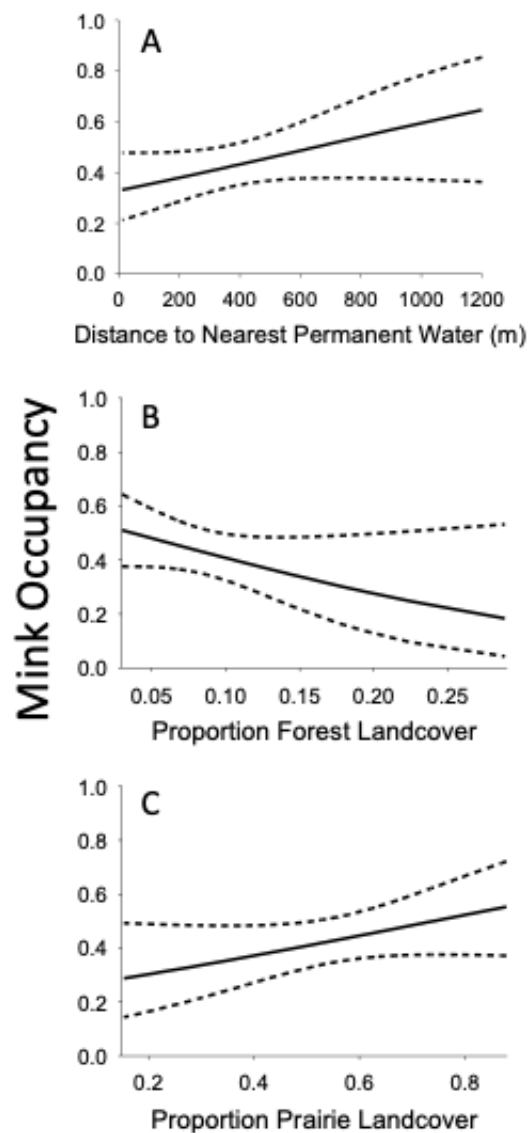


Figure 2.3: Predicted effects and 95% confidence intervals from our most-supported model of wetland occupancy by American mink (*Neogale vison*) at 104 wetlands in the Flint Hills, Kansas, USA during 2019 and 2020. Effects include (A) Euclidean distance (m) to nearest wetland, (B) proportion of forest landcover within 5km, and (C) proportion of prairie landcover within 5km. We assessed wetland occupancy by mink using detection/non-detection sign surveys and single-season occupancy modeling.

Chapter 3

Bergmann's rule is not consistent between sexes or across species: an example from a classic predator-prey system

Semiaquatic mammals tend to be larger than similar terrestrial species. The mechanisms for this pattern are poorly understood but may reflect conformity to Bergmann's rule. To test this hypothesis in two semiaquatic mammals, common muskrat and American mink, we investigated latitudinal gradients in size across their native North American distribution. Using museum collections and data from state wildlife departments, we were able to include 708 muskrat and 94 mink. We created a Principal Component for size using total length and tail length and used AIC model selection to see if latitude best predicted changes in size for both species. We found support for Bergmann's rule in muskrat, but not for mink. While no relationships between size and latitude were found for male mink, we did find support for the reverse pattern of Bergmann's rule in female mink. These results may reflect ecological or physiological relationships of mink and muskrat, but further research is needed to fully test proposed mechanisms for the observed morphological patterns.

3.1 Introduction

Bergmann (1847) observed that homeotherms tend to average larger sizes in more northerly latitudes. They proposed the underlying mechanism was metabolic (e.g., heat budgets; Meiri 2011). Because larger animals have less surface area for their size, they lose proportionally less heat than smaller animals and hypothetically maintain consistent body temperatures better in colder (more northerly) climates (Salewski and Watt 2017). Bergmann’s rule has been applied broadly across higher taxonomic groups (Blackburn et al. 1999) but it may be better applied to family- or species-level taxa (Wolff and Guthrie 1985, Alhajeri and Stepan 2016, Maestri et al. 2016, Rodrigues et al. 2023). Bergmann’s rule has been observed across a wide range of homeothermic mammals and birds (Meiri and Dayan 2003, Meiri 2011, Smith and Lyons 2011), albeit with some exceptions. Meiri and Dayan (2003) recognized that Bergmann’s rule often does not apply to smaller mammals (<0.16 kg; Freckleton et al. 2003), perhaps because of unique life history strategies (e.g., burrowing; Ashton et al. 2000). Bergmann’s rule likely does not apply to taxa in warmer climates (Rodríguez et al. 2008). The rule is consistent among diverse groups of marine mammals (Torres-Romero et al. 2016, Adamczak et al. 2020), including sirenians (Pyenson and Vermeij 2016). The tendency for semiaquatic mammals to be larger than their terrestrial counterparts may reflect Bergmann’s rule (Farina et al. 2023). Three hypotheses were proposed by Wolff and Guthrie (1985) to account for larger body sizes in semiaquatic mammals: (1) thermoregulation (conforming to Bergmann’s rule), (2) predation avoidance, and (3) resource competition. Farina et al. (2023) suggested Bergmann’s rule (thermoregulatory constraints) was the best-supported hypothesis.

Intraspecifically, small mammals do not increase in size at higher latitudes (Meiri and Dayan 2003, Balčiauskas et al. 2020, Teta et al. 2022, Quiroga-Carmona et al. 2023, Valladares-Gómez et al. 2024), which may suggest that heat conservation is not the primary selective pressure for larger sizes in rodents (Ashton et al. 2000). When broader taxonomic scales (orders, families) are investigated, there is some support for Bergmann’s rule in rodents (Ashton et al. 2000). Boyce (1978) found that rainfall and seasonal availability of food were

better predictors of muskrat (*Ondatra zibethicus*), a semiaquatic herbivore widely distributed across North America, size than latitudinal changes. However, muskrats in areas with more extreme seasonal variation (including higher latitudes) tended to be larger. This may reflect resistance to starvation, not heat loss (Boyce 1978).

Mustelids, especially larger species, generally adhere to Bergmann’s rule (Klein 1986, Meiri and Dayan 2003). However, the reverse-trend of Bergmann’s rule is observed in European pine martens (*Martes martes*; Monakhov and Hamilton 2020). Semiaquatic mustelid lineages are generally larger than terrestrial ones (Rodrigues et al. 2023), and latitude has generally been the best predictor of size (Yom-Tov et al. 2006, Meiri et al. 2007). But this does not necessarily imply unequivocal conformity to Bergmann’s rule. Spatial scale appears to be an important consideration for altitudinal size trends in mustelids. For one latitudinal range, Bergmann’s rule can apply to otters (*Lontra canadensis*, *Lutra lutra*), but at a different latitudinal range, it runs contrary (McNab 1971, Yom-Tov et al. 2010). Bergmann’s rule may not apply to smaller mustelid species (Rodrigues et al. 2023) but, to date, no one has tested the rule on small, semiaquatic mustelids like the American mink (*Neogale vison*; hereafter ‘mink’).

Muskrats are semiaquatic herbivores native to most of North America that range in size from 456-553mm in length and 700-1800g in weight (Willner et al. 1980). Size does not vary between sexes (Willner et al. 1980) but cranial measurements suggest that there is variation in muskrat size latitudinally (Boyce 1978). Mink are sexually dimorphic, with males ranging in size from 504-680mm and females from 488-580mm (Lariviere 1999). Female mink are 50% smaller than males, at 455-840g and 905-1392g, respectively (Hall 1981). Thom et al. (2004) suggested that sexual dimorphism in mink could be partly attributed to niche partitioning, but indicated that the primary reason was likely linked to energetics and prey availability.

Our study investigated latitudinal body size gradients in two semiaquatic species, muskrat and mink. Semiaquatic rodents (Martin 2019) and carnivores (Botton-Divet et al. 2017) have additional metabolic costs associated with living in water. Water is a greater conductor than air, which increases heat loss in aquatic mammals (MacArthur 1989). Smaller mammals can

be more affected by heat loss than larger mammals (Riek and Geiser 2013) and, in sexually dimorphic species, females tend to adhere to Bergmann’s rule more closely than males, which reduces dimorphism on a latitudinal gradient (Speakman and Król 2010). We hypothesize that semiaquatic mammals like muskrat and mink will follow Bergmann’s rule. Additionally, we hypothesize that female mink will adhere more strongly to Bergmann’s rule than males.

3.2 Methods and Analysis

We used online databases from the National Museum of Natural History (Smithsonian Institution) and data provided by regional organizations (Florida Fish and Wildlife Conservation Commission, Georgia Museum of Natural History, Indiana Department of Natural Resources, Kansas State University, Ohio Department of Natural Resources). We recovered information on 708 muskrat and 94 mink specimens (Fig. 1) between 1889 and 2024 for which measures of size (total length and tail length) and geographic location (to at least the county level) were recorded. Location descriptions were variable across samples and included latitude and longitude, city names, county names, road intersections, and/or other descriptors. If we could not identify the location of a specimen to at least county level, we did not include that specimen in our analysis. Mean annual temperature differences are negligible within individual home ranges (Boucher-Lalonde and Currie 2016) and, for some semiaquatic mammals (e.g., mink; Yamaguchi and Macdonald 2003, Ahlers 2015), home ranges can average 5-7 km of linear distance. If we could not determine the location of an animal to at least the county level, it was omitted from our data set (muskrat = 708, mink = 94). We obtained two measures of size for muskrat and mink: total length (mm) and tail length (mm). Total length is defined as the distance from the snout to the tip of the tail and tail length is defined as the distance from the base of the tail to the tip (DeBlase 1981). Both measures exclude hairs that may extend past the tip of the tail. These basic measures have regularly and historically been recorded for individual specimens by scientific institutions and were readily available in the databases we accessed. We only used adult muskrat (456-553mm total length, 200-254mm tail length; Willner et al. 1980) and adult mink (male: 504-680mm to-

tal length, 167-200mm tail length; female: 488-580mm total length, 152-185mm tail length; Larivière 1999) for our analyses. We did not include records below these accepted adult sizes to avoid bias related to growth patterns and fecundity instead of latitudinal trends in size. Because mink are sexually dimorphic, we separated males ($N = 54$) and females ($N = 40$) and performed separate analyses on each. We did not re-measure any specimens ourselves, we only used museum records.

Both total length and tail length were correlated for both species (muskrat mean $r = 0.69$, mink mean $r = 0.87$). Thus, we conducted a Principal Components Analysis (PCA; R Core Team 2025) on total length and tail length for muskrat and mink to create a composite variable representing ‘Body Size’ for both species. We performed a k-Nearest Neighbors (kNN) imputation ($k = 5$) on morphometric data (total length, tail length) using the “VIM” package (Kowarik and Templ 2016) and scaled the data to prepare it for the PCA. Unlike simpler methods (e.g., simple mean imputation) kNN preserves variance in the data by estimating missing values based on locally similar specimens. We used $k=5$ to balance robustness with sensitivity to variations in our data. For muskrat, we found clusters of data centered around 40° latitude. Therefore, we binned the data to 1° latitudes using the “dplyr” package (Wickham et al. 2023) and randomly subsampled bins to a maximum of 75 muskrats per bin. We explored various bin sizes, varying by factors of 5, and found 75 maintained variance and covariance within bins while equalizing the weight of sampling effort bias at 40° latitude. PC1 captured 81.8% of the total variance for muskrats. PC1 captured 93.9% of the total variance for mink. Only 226 of our muskrat specimens had data describing collection date.

We used general additive models (“mgcv” package) to assess support for our hypotheses that mink and muskrat body sizes follow Bergmann’s rule across a latitudinal gradient in North America. We produced three model sets for 1) muskrat, 2) male mink, and 3) female mink. For each model set, we included one model with latitude as a covariate and a null model with only the intercept. We used AIC model selection (Burnham et al. 2011) and compared the deltaAIC, AIC weight, and log-likelihood to determine model fit for our competing hypotheses. Parametric coefficients were inspected individually to see positive or

negative associations and confirm interpretability.

3.3 Results

We found support for Bergmann’s rule in muskrats. Our top model, which included latitude as an explanatory variable ($\beta = 0.099$, $SE = 0.022$), had a weight of 1.00 (Table 1). Muskrat body sizes were larger at more northerly latitudes (Fig 2).

Our mink models suggest male mink do not conform to Bergmann’s rule, and patterns of female mink body sizes are opposite of Bergmann’s rule (Fig. 3). For male mink, our null model was the most-supported model of body size (Table 1). Parameter estimates for our model including latitude ($\beta = 0.035$, $SE = 0.24$) were non-informative. For female mink, our top model included latitude ($\beta = -0.57$, $SE = 0.28$) and had a weight of 0.74 (Table 1).

3.4 Discussion and Conclusions

Semiaquatic mammals are ecologically diverse species that face unique challenges to energy acquisition and conservation. Our study provides additional evidence that Bergmann’s rule likely applies to muskrats across their native North American range (Fig. 2), an association that was also suggested by Boyce (1978). Heat conservation may explain Bergmann’s rule in marine (Torres-Romero et al. 2016) and terrestrial mammals (Blackburn et al. 1999), but future research is needed to investigate possible metabolic mechanisms behind Bergmann’s rule in semiaquatic species. Thermoregulatory behavior in muskrats is well-known (e.g., MacArthur and Campbell 1994, MacArthur et al. 1997) and may suggest that heat conservation is an important driver of larger sizes in semiaquatic mammals (Wolff and Guthrie 1985). Consistent with this hypothesis, Gearty et al. (2018) suggest that semiaquatic mammals are constrained to larger sizes by the costs of thermoregulation in water.

Alternatively, larger sizes in semiaquatic mammals may help them avoid predators (Wolff and Guthrie 1985). While terrestrial mammals consistently show trends in size that reflect

coevolution of predator and prey, aquatic mammals generally do not follow this trend (Tucker and Rogers 2014). However, muskrat and mink are a well-studied example of coevolution of predator and prey in ecological systems (Cortez and Weitz 2014), so the predator avoidance hypothesis should not be dismissed. Larger sizes in muskrats may also reflect competition for food (Wolff and Guthrie 1985). Specifically, vegetation in aquatic environments tend to have patchy distributions and competition for these resources may, in part, depend on being larger than competitors (Wolff and Guthrie 1985). For terrestrial rodents, food availability does appear to be the primary driver of larger sizes (Alhajeri and Steppan 2016) instead of metabolic constraints. While the thermoregulatory benefit of larger size appears to be the favored hypothesis for aquatic mammals (Farina et al. 2023), these alternative hypotheses need to be explored more thoroughly in future analyses of semiaquatic mammals.

Our data indicate no association between changes in male mink size and latitude (Fig. 3), consistent with past research (Stevens and Kennedy 2006, Zalewski and Bartoszewicz 2012). Aquatic mustelids tend to be more robust than terrestrial mustelids (Law 2021) but this is not the case for mink, which are among the smallest semiaquatic mustelids (Powell and Zielinski 1983). Mustelids have long, thin bodies, which may make increases in size counterproductive to heat conservation (Brown and Lasiewski 1972). Rather than minimizing heat loss with more mass (Brown and Lee 1969), mustelids are long and thin to maximize their ability to capture prey in difficult places (Brown and Lasiewski 1972, Noonan et al. 2016, Law 2019, Rodrigues et al. 2023). Mink morphology appears to maximize caloric intake (hunting efficiency), instead of minimizing caloric losses (heat lost through surface area).

We found a significant, opposite trend toward smaller female mink occurring at more northerly latitudes (Fig. 3). Zalewski and Bartoszewicz (2012) found the same pattern for invasive populations of mink in Poland, where female size had a negative association with latitude. In contrast, measures of size derived from mink cranial characters (Stevens and Kennedy 2006) indicate female mink increase in size with latitude. However, skull traits may reflect muscle attachment and strength consistent with sexual dimorphism, not necessarily body size (Gálvez-López et al. 2022). This is especially true for animals with adaptations to stronger bite forces such as mustelids (Hartstone-Rose et al. 2019, Mitchell et al. 2024).

The reason female mink decrease in size with increasing latitude, while males do not, has not received much attention in the literature. Size differences between male and female mammals are often the result of food availability (Isaac 2005). Because they are smaller, female mink hunt smaller prey than males (Birks and Dunstone 1985, Isaac 2005). If prey availability is even more limited in northern latitudes, smaller sizes of females may limit competition with males for food. However, food partitioning does not appear to drive sexual dimorphism in other semiaquatic mustelids (e.g., otters; Isaac 2005) and it is not known if these differences would also produce sex-specific size variations across latitudes.

Alternatively, Brown and Lasiewski (1972) suggested that sexual dimorphism in mink is a result of metabolic constraints. Moors (1980) believed that smaller sizes in female mustelids are selectively advantageous primarily because smaller bodies require less energy and increase hunting efficacy. This may reflect the higher metabolic demands of reproduction compared to males (Sandell 1989). Sandell (1989) used a model of energetics to predict mustelid sizes and supported Moors (1980) suggestion that smaller females are energetically more efficient. If this hypothesis is true, the reverse-Bergmann trends observed in female mink may reflect the metabolic advantages to a unique body shape (Brown and Lasiewski 1972) but future research will need to test alternative hypotheses. To explore why female mink decrease in size with increasing latitude while males do not, we recommend future research investigate the hypothesis that females have 1) greater metabolic needs than males (Moors 1980) and 2) hunting niche strategies distinct from males (Birks and Dunstone 1985).

Our data suggest that small, semiaquatic mammals do not universally conform to Bergmann's rule. While latitudinal changes in muskrat size appear to be consistent with Bergmann's rule, mink do not follow Bergmann's rule. Bergmann's rule may not be a ubiquitous ecological principle (Oskyrko et al. 2026). Instead, it appears that thermoregulatory requirements influencing size along latitudinal gradients are specific to adaptive strategies that may even be population-specific, rather than species-specific (He et al. 2023, Oskyrko et al. 2026). A growing body of evidence suggests that latitudinal trends in homeotherm size depend on specific ecological histories of species, not universal principles or generalizations (He et al. 2023, Oskyrko et al. 2026).

Variation in mink size in our dataset suggest that sexual dimorphism can complicate generalizations about latitudinal size trends intraspecifically. Across very broad taxonomic groups, sexually dimorphic species may display patterns consistent with or opposite of Bergmann’s rule (Blanckenhorn et al. 2006). Males tend to display latitudinal patterns in size more clearly than females (Blanckenhorn et al. 2006), but this is not the case with mink in our study. To our knowledge, this is the first study to empirically test for intraspecific latitudinal size trends between mink sexes.

Allen’s rule postulates that, within a species, higher latitudes produce individuals with shorter appendages than those closer to the equator (Allen 1877, Tilkens et al. 2007). In rodents, Allen’s rule appears to be most conspicuous in tails (Alhajeri et al. 2020). It is possible that including tail length in our measures of muskrat and mink tests Allen’s rule rather than Bergmann’s rule. However, tail length and body length correlated with one another for both species in this study (muskrat $r = 0.69$, mink $r = 0.87$), suggesting that Allen’s rule may not apply to semiaquatic mammals. Nevertheless, we urge caution in interpreting our results.

While our sampling distribution is uneven, we have done our best to account for this by binning our data during analysis. We recommend that future researchers select sites for data collection carefully to represent the distribution of these two semiaquatic mammals more evenly. By using primarily museum specimens, we are subject not only to sampling biases, but also possible measurement error. Our data hint at several intriguing possibilities for ecology and metabolism of semiaquatic mammals. We anticipate more rigorous studies in the future will address these questions.

3.5 Acknowledgements

We would like to thank Maria Schmitz, Sarah Bomske, Alyssa Knaup, Geriann Albers, Nicole Pontzer, and Lisa Smith for access to muskrat and mink data. We also thank Indiana Department of Natural Resources, Georgia Museum of Natural History, and Florida Fish and Wildlife Conservation Commission for help procuring data. We are also grateful to

the National Museum of Natural History and the Smithsonian Institute for their online databases.

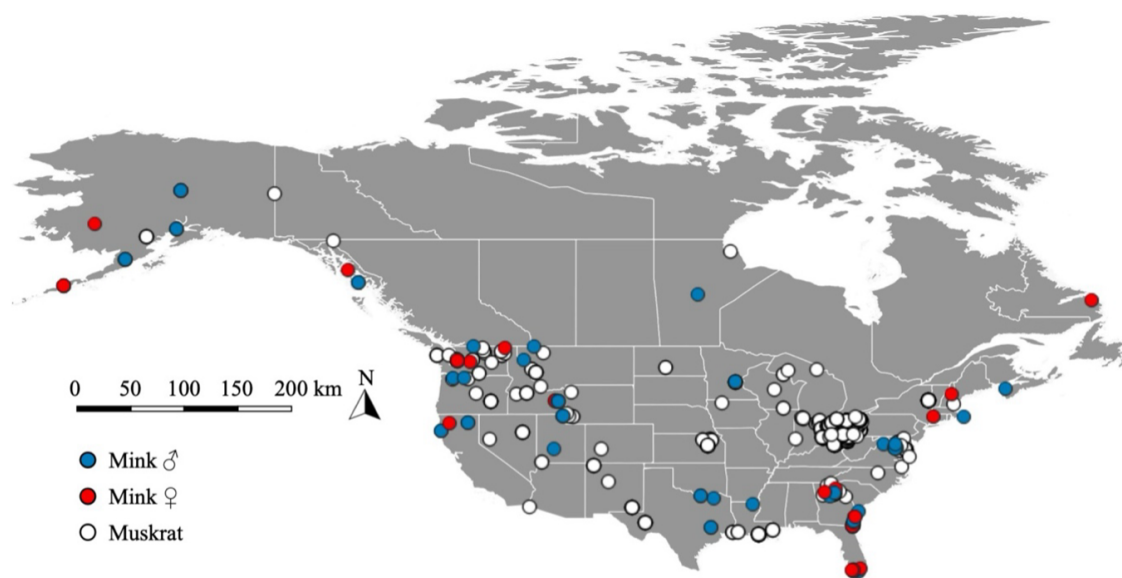


Figure 3.1: Location points for 708 muskrat and 94 American mink in museum, university, and state collections in North America. Where sampling bias existed (e.g., Ohio) we set a maximum of 75 muskrats within 1° latitude bins.

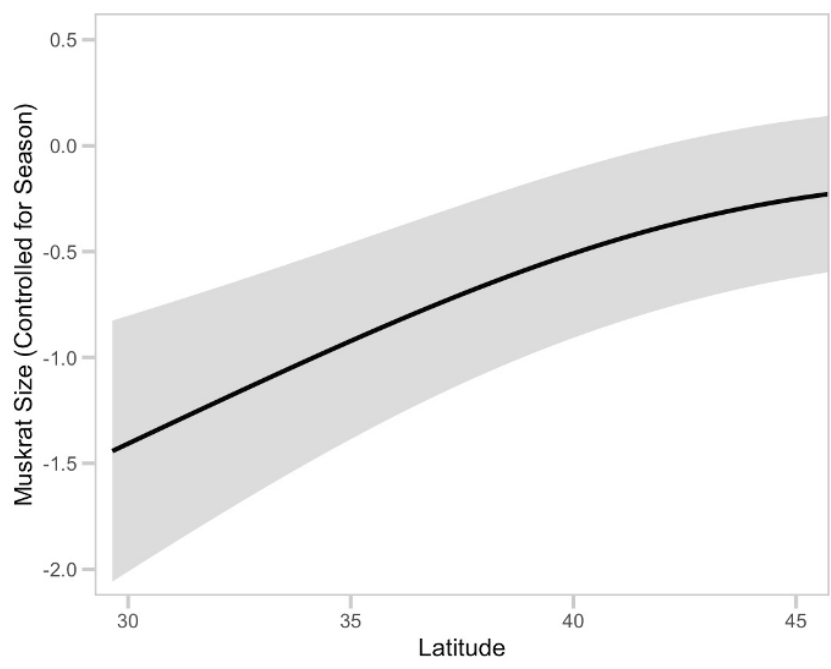


Figure 3.2: Muskrat (*Ondatra zibethicus*) body size and 95% CI in relation to the effect of latitude. We obtained total length and tail length from museums specimens distributed across the continental United States and used a principal components analysis to derive a single measure of body size. Size estimates are derived from a Principal Components Analysis of total length and tail length. We used PC1, which captured 81.8% of the variance. Muskrat size increases with increasing latitude, consistent with Bergmann's rule.

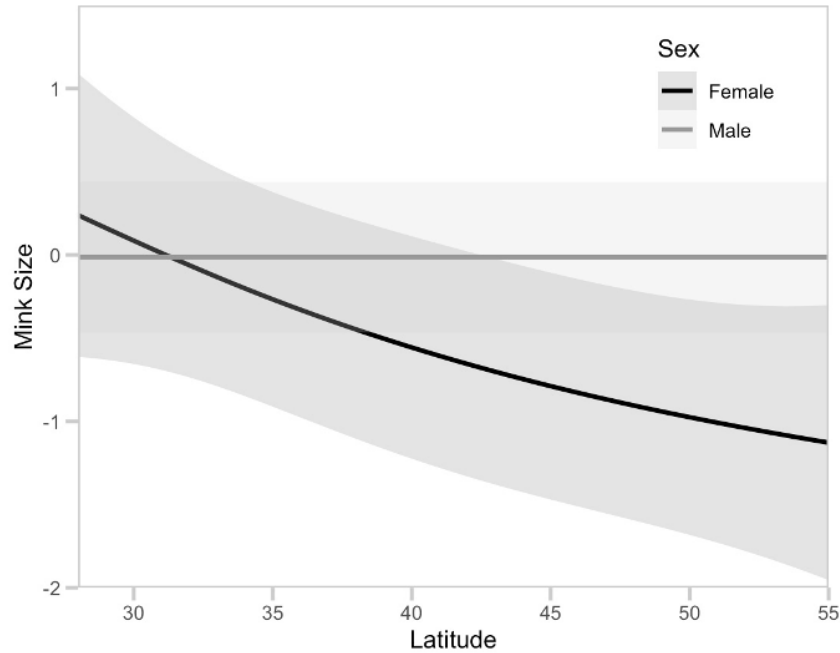


Figure 3.3: The effects of male and female American mink (*Neogale vison*) body size (and 95% confidence interval) in relation to latitude. We obtained total length and tail length from museums specimens distributed across the continental United States and used a principal components analysis to derive a ‘body size’ variable. Size estimates are derived from a Principal Components Analysis of total length and tail length. We used PC1, which captured 93.9% of the variance. Female mink decrease in size with increasing latitude, opposite of Bergmann’s rule, but there is no discernible change in male mink size across latitudes.

Bibliography

- [1] S. K. Adamczak, D. A. Pabst, W. A. McLellan, and L. H. Thorne. Do bigger bodies require bigger radiators? insights into thermal ecology from closely related marine mammal species and implications for ecogeographic rules. *Journal of Biogeography*, 47:1193–1206, 2020.
- [2] S. B. Adams, S. G. Hereford, and C. Hyseni. Burrow densities of primary burrowing crayfishes in relation to prescribed fire and mechanical vegetation treatments. *Water*, 13:1854, 2021.
- [3] A. A. Ahlers, L. A. Cotner, P. J. Wolff, M. A. Mitchell, E. J. Heske, and R. L. Schooley. Summer precipitation predicts spatial distributions of semiaquatic mammals. *PLoS ONE*, 10:e0135036, 2015.
- [4] A. A. Ahlers and E. J. Heske. Empirical evidence for declines in muskrat populations across the united states. *Journal of Wildlife Management*, 81:1408–1416, 2017.
- [5] A. A. Ahlers, E. J. Heske, and C. A. Miller. Economic influences on trapper participation and per capita harvest of muskrat: economics and trapping. *Wildlife Society Bulletin*, 40:548–553, 2016a.
- [6] A. A. Ahlers, E. J. Heske, and R. L. Schooley. Prey distribution, potential landscape supplementation, and urbanization affect occupancy of american mink in streams. *Landscape Ecology*, 31:1601–1613, 2016b.
- [7] A. A. Ahlers, E. J. Heske, R. L. Schooley, and M. A. Mitchell. Home ranges and space use of muskrats, *ondatra zibethicus*, in restricted linear habitats. *Wildlife Biology*, 16: 400–408, 2010.

- [8] A. A. Ahlers, R. L. Schooley, E. J. Heske, and M. A. Mitchell. Effects of flooding and riparian buffers on survival of muskrats (*ondatra zibethicus*) across a flashiness gradient. *Canadian Journal of Zoology*, 88:1011–1020, 2010.
- [9] A. A. Ahlers, T. P. Lyons, and E. J. Heske. Population dynamics of muskrat (*ondatra zibethicus*) and american mink (*neovison vison*): investigating contemporary patterns in a classic predator-prey system. *Canadian Journal of Mammalogy*, 99:681–688, 2021.
- [10] A. A. Ahlers. *Habitat selection, survival, and disease risk of semiaquatic mammals in a highly altered landscape*. PhD thesis, University of Illinois at Urbana-Champaign, Urbana, USA, 2015.
- [11] B. H. Alhajeri, Y. Fourcade, N. S. Upham, and H. Alhaddad. A global test of allen’s rule in rodents. *Global Ecology and Biogeography*, 29:2248–2260, 2020.
- [12] B. H. Alhajeri and S. J. Steppan. Association between climate and body size in rodents: a phylogenetic test of bergmann’s rule. *Mammalian Biology*, 81:219–225, 2016.
- [13] A. L. Alford, E. C. Hellgren, R. Limb, and D. M. Engle. Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecological Applications*, 22:947–958, 2012.
- [14] J. A. Allen. The influence of physical conditions in the genesis of species. *Radical Review*, 1:108–140, 1877.
- [15] C. B. Anderson, R. Rozzi, J. C. Torres-Mura, S. M. Mcgehee, M. F. Sherriffs, E. Schüttler, and A. D. Rosemond. Exotic vertebrate fauna in the remote and pristine sub-antarctic cape horn archipelago, chile. *Biodiversity and Conservation*, 15: 3295–3313, 2006.
- [16] T. W. Arnold. Uninformative parameters and model selection using akaike’s information criterion. *Journal of Wildlife Management*, 74:1175–1178, 2010.

- [17] S. Asad, J. F. Abrams, R. Guharajan, J. Sikui, A. Wilting, and M. O. Rödel. Stream amphibian detectability and habitat associations in a reduced impact logging concession in malaysian borneo. *Journal of Herpetology*, 54:385–392, 2020.
- [18] K. G. Ashton, M. C. Tracy, and A. Queiroz. Is bergmann’s rule valid for mammals? *American Naturalist*, 156:390–415, 2000.
- [19] F. A. Atuo and T. J. O’Connell. The landscape of fear as an emergent property of heterogeneity: Contrasting patterns of predation risk in grassland ecosystems. *Ecology and Evolution*, 7:4782–4793, 2017.
- [20] V. Bailey. The maryland muskrat marshes. *Journal of Mammalogy*, 18:350–354, 1937.
- [21] E. S. Bakker and D. Bos. Invloed van muskusratten op moerasontwikkeling en biodiversiteit. Technical report, Altenburg & Wymenga Ecologisch Onderzoek, Feanwâlden, the Netherlands, 2019. A&W-rapport 2540.
- [22] L. Balčiauskas, A. Amshokova, L. Balčiauskienė, A. M. Benedek, J. Cichocki, A. Csanady, P. G. de Mendonca, and V. Nistoreanu. Geographical clines in the size of the herb field mouse (*apodemus uralensis*). *Integrative Zoology*, 15:55–68, 2020.
- [23] D. P. Batzer, R. Cooper, and S. W. Wissinger. Wetland animal ecology. In *Ecology of Freshwater and Estuarine Wetlands*, pages 242–284. University of California Press, California, USA, 2006. D. Batzer and R. R. Sharitz, eds.
- [24] TH. Bean. Catalogue of the fishes of new york. *New York State Museum Bulletin*, 60: 784, 1903.
- [25] F. C. Bellrose and L. G. Brown. The effect of fluctuating water levels on the muskrat population of the illinois river valley. *Journal of Wildlife Management*, 5:206–212, 1941.
- [26] C. Bergmann. *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Vandenhoeck und Ruprecht, 1847.

- [27] H. Berger, C. K. Meyer, A. Mummert, L. Tirado, L. Saucedo, H. Bonello, D. V. Arsdale, and G. Williams. Land use dynamics within the tallgrass prairie ecosystem: the case for the conservation reserve program (crp). *Theoretical Ecology*, 13:289–300, 2020.
- [28] M. W. Beutel, M. R. Morgan, J. J. Erlenmeyer, and E. S. Brouillard. Phosphorus removal in a surface-flow constructed wetland treating agricultural runoff. *Journal of Environmental Quality*, 43:1071–1080, 2014.
- [29] J. D. S. Birks and N. Dunstone. Sex-related difference in the diet of the mink mustela vison. *Holarctic Ecology*, 8:245–252, 1985.
- [30] J. H. Black. Escape behavior of the southern plains skink. *Herpetological Review*, 7: 111, 1976.
- [31] T. M. Blackburn, K. J. Gaston, and N. Loder. Geographic gradients in body size: a clarification of bergmann’s rule. *Diversity and Distributions*, 5:165–174, 1999.
- [32] W. U. Blanckenhorn, R. C. Stillwell, K. A. Young, C. W. Fox, and K. G. Ashton. When rensch meets bergmann: does sexual size dimorphism change systematically with latitude? *Evolution*, 60:2004–2011, 2006.
- [33] E. E. Blankenship, M. W. Perkins, and R. J. Johnson. The information-theoretic approach to model selection: description and case study. In *Conference on Applied Statistics in Agriculture*, volume 14, pages 62–76, 2002.
- [34] A. Bollen. Grazing in wetlands: aboveground and belowground responses to herbivory. Master’s thesis, University of Utrecht, the Netherlands, 2013.
- [35] C. M. Bomske and A. A. Ahlers. How do muskrats ondatra zibethicus affect ecosystems? a review of evidence. *Mammal Review*, 51:40–50, 2021.
- [36] L. Bonesi and S. Palazon. The american mink in europe: Status, impacts, and control. *Biological Conservation*, 134:470–483, 2007.

- [37] L. Botton-Divet, R. Cornette, A. Houssaye, A. Fabre, and A. Herrel. Swimming and running: a study of the convergence in long bone morphology among semi-aquatic mustelids (carnivora: Mustelidae). *Biological Journal of the Linnean Society*, 121: 38–49, 2017.
- [38] V. Boucher-Lalonde and D. J. Currie. Spatial autocorrelation can generate stronger correlations between range size and climatic niches than the biological signal – a demonstration using bird and mammal range maps. *PLoS ONE*, 11:e0166243, 2016.
- [39] M. S. Boyce. Climatic variability and body size variation in the muskrats (*ondatra zibethicus*) of north america. *Oecologia*, 36:1–19, 1978.
- [40] P. Bridgewater and S. Aricò. Turbo-charging the ecohydrology paradigm for the anthropocene. *Ecohydrology & Hydrobiology*, 16:74–82, 2016.
- [41] J. M. Briggs, G. A. Hoch, and L. C. Johnson. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to juniperus virginiana forest. *Ecosystems*, 5:578–586, 2002.
- [42] J. M. Briggs, A. K. Knapp, and B. L. Brock. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist*, 147:287–294, 2002.
- [43] J. H. Brown and R. C. Lasiewski. Metabolism of weasels: the cost of being long and thin. *Ecology*, 53:939–943, 1972.
- [44] J. H. Brown and A. K. Lee. Bergmann’s rule and climatic adaptation in woodrats (*neotoma*). *Evolution*, 23:320–338, 1969.
- [45] C. L. Browne and C. A. Paszkowski. Hibernation sites of western toads (*anaxyrus boreas*): characterization and management implications. *Herpetological Conservation and Biology*, 5:49–63, 2010.

- [46] A. Brunke, A. Smetana, D. Carruthers-Lay, and J. Buffam. Revision of hemiquedius casey (staphylinidae, staphylininae) and a review of beetles dependent on beavers and muskrats in north america. *ZooKeys*, 702:27–43, 2017.
- [47] R. Bryce, R. van der Wal, R. Mitchell, and X. Lambin. Metapopulation dynamics of a burrowing herbivore drive spatio-temporal dynamics of riparian plant communities. *Ecosystems*, 16:1165–1177, 2013.
- [48] M. Brzeziński, J. Romanowski, M. Żmihorski, and K. Karowicz. Muskrat (ondata zibethicus) decline after the expansion of american mink (neovison vison) in poland. *European Journal of Wildlife Research*, 56:341–348, 2010.
- [49] A. G. Bunn, D. U. Urban, and T. H. Keitt. Landscape connectivity: a conservation application of graph theory. *Journal of Environmental Management*, 59:265–278, 2000.
- [50] A. D. Buren, M. Koen-Alonso, P. Pepin, F. Mowbray, B. Nakashima, G. Stenson, N. Ollerhead, and W. A. Montevecchi. Bottom-up regulation of capelin, a keystone forage species. *PLoS ONE*, 9:e87589, 2014.
- [51] K. P. Burnham and D. R. Anderson. *Model selection and multimodel inference: a practical information-theoretic approach*, volume 2nd ed. Springer, New York, United States of America, 2002.
- [52] K. P. Burnham, D. R. Anderson, and K. P. Huyvaert. Aic model selection and multimodel inference in behavioral ecology: some background, observations and comparisons. *Behavioral Ecology and Sociobiology*, 65:23–35, 2011.
- [53] R. M. Canals, V. Ferrer, A. Iriarte, S. Cárcamo, L. S. Emeterio, and E. Villanueva. Emerging conflicts for the environmental use of water in high-valuable rangelands. can livestock water ponds be managed as artificial wetlands for amphibians? *Ecological Engineering*, 37:1443–1452, 2011.
- [54] S. P. Castillo, R. D. Crego, J. E. Jiménez, and R. Rozzi. Native-predator invasive-prey

- trophic interactions in tierra del fuego: the beginning of biological resistance? *Ecology*, 98:2485–2489, 2017.
- [55] E. L. Charnov. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9:129–136, 1976.
- [56] A. S. Chavez and E. M. Gese. Food habits of wolves in relation to livestock depredations in northwestern minnesota. *American Midland Naturalist*, 154:253–263, 2005.
- [57] W. R. Clark. Habitat selection by muskrats in experimental marshes undergoing succession. *Canadian Journal of Zoology*, 72:675–680, 1994.
- [58] S. J. Coe field, M. J. Zwiernik, T. B. Fredricks, R. S. Seston, M. W. Nadeau, and D. L. Tazelaar. Great horned owl (*bubo virginianus*) dietary exposure to pcdd/df in the tittabawassee river floodplain in midland, michigan, usa. *Environmental Toxicology and Chemistry*, 29:2350–2362, 2010.
- [59] R. Conant. The reptiles of ohio. *American Midland Naturalist*, 20:1–200, 1938.
- [60] L. C. Connell, J. D. Scasta, and L. M. Porensky. Prairie dogs and wildfires shape vegetation structure in a sagebrush grassland more than does rest from ungulate grazing. *Ecosphere*, 9:e02390, 2018.
- [61] L. M. Connors, E. Kiviat, P. M. Groffman, and R. S. Ostfeld. Muskrat (*ondatra zibethicus*) disturbance to vegetation and potential net nitrogen mineralization and nitrification rates in a freshwater tidal marsh. *American Midland Naturalist*, 143: 53–63, 2000.
- [62] M. H. Cortez and J. S. Weitz. Coevolution can reverse predator-prey cycles. *PNAS*, 111:7486–7491, 2014.
- [63] L. A. Cotner and R. L. Schooley. Habitat occupancy by riparian muskrats reveals tolerance to urbanization and invasive vegetation. *Journal of Wildlife Management*, 75:1637–1645, 2011.

- [64] R. D. Crego, J. E. Jiménez, and R. Rozzi. 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, 2016.
- [65] J. G. Crockett, C. Brown, and B. D. Gerber. Muskrat occurrence in rhode island shows little evidence of land use change driving declines. *Journal of Wildlife Management*, 89:e22668, 2024.
- [66] K. Cuddington and A. Hastings. Invasive engineers. *Ecological Modelling*, 178:335–347, 2004.
- [67] K. Danell. Short-term plant successions following the colonization of a northern swedish lake by the muskrat, *ondatra zibethica*. *Journal of Applied Ecology*, 14:933–947, 1977.
- [68] K. Danell. Reduction of aquatic vegetation following the colonization of a northern swedish lake by the muskrat, *ondatra zibethica*. *Oecologia*, 38:101–106, 1979.
- [69] K. Danell. Introductions of aquatic rodents: lessons of the muskrat *ondatra zibethicus* invasion. *Wildlife Biology*, 2:213–220, 1996.
- [70] R. D. Davic. Linking keystone species and functional groups: a new operational definition of the keystone species concept. *Conservation Ecology*, 7:r11, 2003.
- [71] A. D. Davidson, J. K. Detling, and J. H. Brown. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world’s grasslands. *Frontiers in Ecology and the Environment*, 10:477–486, 2012.
- [72] A. F. DeBlase. *A Manual of Mammalogy: With Keys to Families of the World*. W. C. Brown: Dubuque, Iowa, 1981.
- [73] T. H. DeLuca and C. A. Zabinski. Prairie ecosystems and the carbon problem. *Frontiers in Ecology and the Environment*, 9:407–413, 2011.
- [74] P. K. Dayton. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at mcmurdo sound, antarctica. In *Proceedings*

- of the *Colloquium on Conservation Problems in Antarctica*, pages 81–96. Allen Press, Lawrence, Kansas, USA, 1972. B. C. Parker, ed.
- [75] C. R. Dickman. Rodent–ecosystem relationships: a review. In *Ecologically-based Management of Rodent Pests*, pages 113–133. ACIAR Monograph, 1999.
 - [76] T. P. Diggins and K. M. Stewart. Evidence of large change in unionid mussel abundance from selective muskrat predation, as inferred by shell remains left on shore. *International Review of Hydrobiology*, 85:505–520, 2000.
 - [77] S. I. Dodson. Complementary feeding niches sustained by size-selective predation. *Limnology and Oceanography*, 15:131–137, 1970.
 - [78] H. L. Dozier, M. H. Markley, and L. M. Llewellyn. Muskrat investigations on the blackwater national wildlife refuge, maryland. *Journal of Wildlife Management*, 12:177–190, 1948.
 - [79] A. J. Edelman, J. Moran, T. J. Garrabrant, and K. C. Vorreiter. Muskrat predation of native freshwater mussels in shoal creek, alabama. *Southeastern Naturalist*, 14:473–483, 2015.
 - [80] R. M. Elsey, M. Miller, D. LeJeune, and W. Selman. Commensal nesting of scincella lateralis (little brown skinks) in alligator mississippiensis (american alligator) nests and ondatra zibethicus (muskrat) houses in southwestern louisiana. *Southeastern Naturalist*, 15:653–668, 2016.
 - [81] J. Erb, M. S. Boyce, and N. C. Stenseth. Spatial variation in mink and muskrat interactions in canada. *Oikos*, 93:365–375, 2001.
 - [82] J. Erb, N. C. Stenseth, and M. S. Boyce. Geographic variation in population cycles of canadian muskrats (ondata zibethicus). *Canadian Journal of Zoology*, 78:1009–1016, 2000.

- [83] C. H. Ernst, R. W. Barbour, and J. E. Lovich. *Turtles of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., USA, 1994.
- [84] C. H. Ernst, R. T. Zappalorti, and J. E. Lovich. Overwintering sites and thermal relations of hibernating bog turtles, *clemmys muhlenbergii*. *Copeia*, 1989:761–764, 1989.
- [85] P. L. Errington. Reaction of muskrat populations to drought. *Ecology*, 20:168–186, 1939.
- [86] P. L. Errington. An analysis of mink predation upon muskrats in north-central united states. *Research Bulletin (Iowa Agriculture and Home Economics Experiment Station)*, 320:797–924, 1943.
- [87] P. L. Errington. Concerning fluctuations in populations of the prolific and widely distributed muskrat. *American Naturalist*, 85:273–292, 1951.
- [88] P. L. Errington. Of population cycles and unknowns. *Cold Spring Harbor Symposia on Quantitative Biology*, 22:287–300, 2007.
- [89] P. L. Errington. *Muskrats and Marsh Management*. University of Nebraska Press, Lincoln, Nebraska, USA, 1961.
- [90] P. L. Errington. *Muskrat Populations*. Iowa State University Press, Ames, Iowa, USA, 1963.
- [91] P. L. Errington, R. J. Siglin, and R. C. Clark. The decline of a muskrat population. *Journal of Wildlife Management*, 27:1–8, 1963.
- [92] B. M. Farina, S. Faurby, and D. Silvestro. Dollo meets bergmann: morphological evolution in secondary aquatic mammals. *Proceedings of the Royal Society B: Biological Sciences*, 290:20231099, 2023.
- [93] J. M. Farrell, B. A. Murry, D. J. Leopold, A. Halpern, M. B. Rippke, K. S. Godwin, and S. D. Hafner. Water-level regulation and coastal wetland vegetation in the upper

- st. lawrence river: inferences from historical aerial imagery, seed banks, and typha dynamics. *Hydrobiologia*, 647:127–144, 2010.
- [94] A. C. Ferregueti, C. L. Davis, W. M. Tomas, and H. G. Bergallo. Using activity and occupancy to evaluate niche partitioning: the case of two peccary species in the atlantic rainforest, brazil. *Hystrix, the Italian Journal of Mammalogy*, 29:168–174, 2018.
- [95] D. F. Fink and W. J. Mitsch. Seasonal and storm event nutrient removal by a created wetland in an agricultural watershed. *Ecological Engineering*, 23:313–325, 2004.
- [96] J. D. Fischer, S. C. Schneider, A. A. Ahlers, and J. R. Miller. Categorizing wildlife responses to urbanization and conservation implications of terminology: terminology and urban conservation. *Conservation Biology*, 29:1246–1248, 2015.
- [97] P. A. Fleming, H. Anderson, A. S. Prendergast, M. R. Bretz, V. L. Valentine, and G. E. St. J. Hardy. Is the loss of australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Review*, 44:94–108, 2014.
- [98] K. M. Fraley, T. B. Haynes, and J. A. López. Under-ice population density estimation of alaska blackfish. *North American Journal of Fisheries Management*, 38:454–461, 2018.
- [99] R. P. Freckleton, P. H. Harvey, and M. Pagel. Bergmann’s rule and body size in mammals. *The American Naturalist*, 161:821–825, 2003.
- [100] A. K. Fuller, D. W. Linden, and J. A. Royle. Management decision making for fisher populations informed by occupancy modeling. *Journal of Wildlife Management*, 80:794–802, 2016.
- [101] E. Gálvez-López, B. Kilbourne, and P. G. Cox. Cranial shape variation in mink: separating two highly similar species. *Journal of Anatomy*, 240:210–225, 2022.
- [102] A. Garibaldi and N. Turner. Cultural keystone species: implications for ecological conservation and restoration. *Ecology and Society*, 9:1, 2004.

- [103] W. Gearty, C. R. McClain, and J. L. Payne. Energetic tradeoffs control the size distribution of aquatic mammals. *PNAS*, 115:4194–4199, 2018.
- [104] K. Geluso, C. Kruse, and M. J. Harner. Wetland edge trampled by american bison (*bos bison*) used as basking site for painted turtles (*chrysemys picta*). *Transactions of the Nebraska Academy of Sciences and Affiliated Societies*, 40:39–44, 2020.
- [105] R. Gerell. Home ranges and movements of the mink *mustela vison schreber* in southern sweden. *Oikos*, 21:160–173, 1970.
- [106] X. Giroux-Bougard. Gene flow in an arctic wetland: modelling landscape effects on fine-scale genetic variation in an isolated muskrat (*ondatra zibethicus*) population. Master’s thesis, McGill University, Montréal, Canada, 2014.
- [107] J. E. Greenhorn, C. Sadowski, J. Holden, and J. Bowman. Coastal wetlands connected to lake ontario have reduced muskrat (*ondatra zibethicus*) abundance. *Wetlands*, 37: 339–349, 2017.
- [108] G. J. Gregory, R. Dibble, P. Daoust, and M. R. Van Den Heuvel. Declines in muskrat (*ondatra zibethicus*) population density in prince edward island, canada. *Canadian Wildlife Biology and Management*, 8:46–60, 2019.
- [109] J. L. Gutiérrez, C. G. Jones, and R. Sousa. Toward an integrated ecosystem perspective of invasive species impacts. *Acta Oecologica*, 54:131–138, 2014.
- [110] T. Guy-Haim, D. A. Lyons, J. Kotta, H. Ojaveer, A. M. Queirós, and E. Chatzinikolaou. Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: a global review and meta-analysis. *Global Change Biology*, 24:906–924, 2018.
- [111] N. Hagenah and N. C. Bennett. Mole rats act as ecosystem engineers within a biodiversity hotspot, the cape fynbos. *Journal of Zoology*, 289:19–26, 2013.

- [112] E. R. Hall. *The Mammals of North America: Second Edition. Volume I*. Wiley: New York, 1981.
- [113] R. G. Hamilton. Restoring heterogeneity on the tallgrass prairie preserve: applying the fire-grazing interaction model. In *Proceedings of the 23rd Tall Timbers Fire Ecology Conference: fire in grassland and shrubland ecosystems*, pages 163–169. Tall Timbers Research Station, Tallahassee, United States of America, 2007. R. E. Masters and K. E. M. Galley, eds.
- [114] W. J. Hamilton Jr. Habits of the star-nosed mole, *condylura cristata*. *Journal of Mammalogy*, 12:345–355, 1931.
- [115] B. Hamilton, W. Ostlie, G. Wingfield, J. Haferman, and D. Ladd. *Ecoregional conservation in the Osage Plains/Flint Hills prairie*. The Nature Conservancy, Minneapolis, United States of America, 2000.
- [116] A. Hartstone-Rose, I. Hertzog, and E. Dickinson. Bite force and masticatory muscle architecture adaptations in the dietarily diverse musteloidea (carnivora). *The Anatomical Record*, 302:2287–2299, 2019.
- [117] J. He, J. Tu, J. Yu, and H. Jiang. A global assessment of bergmann’s rule in mammals and birds. *Global Change Biology*, 29:5199–5210, 2023.
- [118] M. Heine and G. van der Velde. De muskusrat in de ooypolder bij nijmegen en zijn invloed op de nymphaeide vegetaties. *De Levende Natuur*, 81:122–128, 1978.
- [119] B. B. Hermosillo-Núñez, M. Ortiz, and F. A. Rodríguez-Zaragoza. Keystone species complexes in kelp forest ecosystems along the northern chilean coast (se pacific): improving multispecies management strategies. *Ecological Indicators*, 93:1101–1111, 2018.
- [120] K. A. Hersey, J. D. Clark, and J. B. Layzer. Consumption of freshwater bivalves by muskrats in the green river, kentucky. *American Midland Naturalist*, 170:248–259, 2013.

- [121] N. Hewitt and K. Miyanishi. The role of mammals in maintaining plant species richness in a floating typha marsh in southern ontario. *Biodiversity and Conservation*, 6:1085–1102, 1997.
- [122] C. W. Hibbard. A late illinoian fauna from kansas and its climatic significance. *Papers of the Michigan Academy of Science, Arts, and Letters*, 48:187–221, 1963.
- [123] C. W. Hibbard and D. W. Taylor. Two late pleistocene faunas from southwestern kansas. *Contributions from the Museum of Paleontology, University of Michigan*, 16: 1–223, 1960.
- [124] J. M. Hickey and R. A. Malecki. Nest site selection of the black tern in western new york. *Colonial Waterbirds*, 20:582–595, 1997.
- [125] C. Higgins and W. J. Mitsch. The role of muskrats (*ondata zibethicus*) as ecosystem engineers in created freshwater marshes. In *The Olentangy River Wetland Research Park Annual Report*, pages 81–86. Ohio State University, Columbus, Ohio, USA, 2001. W. J. Mitsch and L. Zhang, eds.
- [126] A. M. Holland, E. M. Schaubert, C. K. Nielsen, and E. C. Hellgren. Stream community richness predicts apex predator occupancy dynamics in riparian systems. *Oikos*, 127: 1422–1436, 2018.
- [127] A. M. Holland, E. M. Schaubert, C. K. Nielsen, and E. C. Hellgren. Occupancy dynamics of semi-aquatic herbivores in riparian systems in illinois, usa. *Ecosphere*, 10:e02614, 2019.
- [128] A. M. Holland, E. M. Schaubert, C. K. Nielsen, and E. C. Hellgren. River otter and mink occupancy dynamics in riparian systems. *Journal of Wildlife Management*, 83: 1552–1564, 2019.
- [129] N. Holmengen, K. L. Seip, M. Boyce, and N. C. Stenseth. Predator-prey coupling: interaction between mink *mustela vison* and muskrat *ondata zibethicus* across canada. *Oikos*, 118:440–448, 2009.

- [130] V. J. Horncastle, E. C. Hellgren, P. M. Mayer, A. C. Ganguli, D. M. Engle, and D. M. Leslie Jr. Implications of invasion by *juniperus virginiana* on small mammals in the southern great plains. *Journal of Mammalogy*, 86:1144–1155, 2005.
- [131] J. L. Isaac. Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review*, 35:101–115, 2005.
- [132] H. H. T. Jackson. *Mammals of Wisconsin*. University of Wisconsin Press, Madison, Wisconsin, USA, 1961.
- [133] S. M. Johnson-Bice, S. K. Windels, and K. L. Pilgrim. Observation and dna confirmation of a fisher (*pekania pennanti*) hunting and killing a muskrat (*ondatra zibethicus*). *Northeastern Naturalist*, 26:31–34, 2019.
- [134] C. E. Johnson. The muskrat in new york: its natural history and economics. *Roosevelt Wildlife Bulletin*, 3:199–320, 1925.
- [135] W. C. Johnson. Ecosystem services provided by prairie wetlands in northern rangelands. *Rangelands*, 41:44–48, 2019.
- [136] C. G. Jones. Ecosystem engineers and geomorphological signatures in landscapes. *Geomorphology*, 157–158:75–87, 2012.
- [137] C. G. Jones, J. L. Gutiérrez, J. E. Byers, J. A. Crooks, J. G. Lambrinos, and T. S. Talley. A framework for understanding physical ecosystem engineering by organisms. *Oikos*, 119:1862–1869, 2010.
- [138] C. G. Jones, J. H. Lawton, and M. Shachak. Organisms as ecosystem engineers. *Oikos*, 69:373, 1994.
- [139] R. H. Kadlec, J. Pries, and H. Mustard. Muskrats (*ondatra zibethicus*) in treatment wetlands. *Ecological Engineering*, 29:143–153, 2007.
- [140] P. C. Kangas and G. L. Hannan. Vegetation on muskrat mounds in a michigan marsh. *American Midland Naturalist*, 113:392–396, 1985.

- [141] D. W. Kaufman, G. A. Kaufman, and B. K. Clark. Small mammals in native and anthropogenic habitats in the lake wilson area of north-central kansas. *Southwestern Naturalist*, 45:45–60, 2000.
- [142] T. Keane. Flint hills farm ponds: good, bad, but rarely ugly. *Symphony in the Flint Hills Field Journal*, 8:80–85, 2018.
- [143] E. Kiviat. Vertebrate use of muskrat lodges and burrows. *Estuaries*, 1:196–200, 1978.
- [144] R. G. Klein. Carnivore size and quaternary climatic change in southern africa. *Quaternary Research*, 26:153–170, 1986.
- [145] A. K. Knapp and T. R. Seastedt. Detritus accumulation limits productivity of tallgrass prairie. *BioScience*, 36:662–668, 1986.
- [146] C. L. Knight, J. M. Briggs, and M. D. Nellis. Expansion of gallery forest on konza prairie research natural area, kansas, usa. *Landscape Ecology*, 9:117–125, 1994.
- [147] M. G. Knutson, W. B. Richardson, D. M. Reineke ..., and S. E. Weick. Agricultural ponds support amphibian populations. *Ecological Applications*, 14:669–684, 2004.
- [148] A. Kowarik and M. Templ. Imputation with the r package vim. *Journal of Statistical Software*, 74:1–16, 2016.
- [149] M. J. Lacki, W. T. Peneston, K. B. Adams, F. D. Vogt, and J. H. Houppert. Summer foraging patterns and diet selection of muskrats inhabiting a fen wetland. *Canadian Journal of Zoology*, 68:1163–1167, 1990.
- [150] S. Larivière. *Mustela vison*. *Mammalian Species*, 608:1–9, 1999.
- [151] M. R. Larreur, S. K. Windels, B. T. Olson, and A. A. Ahlers. Cross-scale interactions and non-native cattails influence the distributions of a wetland-obligate species. *Landscape Ecology*, 35:59–68, 2020.

- [152] S. Laurence, M. J. Smith, and A. I. Schulte-Hostedde. Effects of structural connectivity on fine scale population genetic structure of muskrat, *ondatra zibethicus*. *Ecology and Evolution*, 3:3524–3535, 2013.
- [153] A. Law. *Evaluation of the ecological impacts of beaver reintroduction on aquatic systems*. PhD thesis, University of Stirling, Scotland, UK, 2014.
- [154] C. J. Law. Evolutionary shifts in ant mustelid (mustelidae: Carnivora) cranial shape, body size and body shape coincide with the mid-miocene climate transition. *Biology Letters*, 15:20190155, 2019.
- [155] C. J. Law. Ecological drivers of carnivoran body shape evolution. *The American Naturalist*, 198:406–420, 2021.
- [156] J. D. Litzgus, J. P. Costanzo, R. J. Brooks, and R. E. Lee Jr. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. *Canadian Journal of Zoology*, 77:1348–1357, 1999.
- [157] A. Luati and T. Proietti. Hyper-spherical and elliptical stochastic cycles. *Journal of Time Series Analysis*, 31:169–181, 2010.
- [158] J. J. Lynch, T. O’Neil, and D. W. Lay. Management significance of damage by geese and muskrats to gulf coast marshes. *Journal of Wildlife Management*, 11:50–76, 1947.
- [159] R. H. MacArthur and E. O. Wilson. *The theory of island biogeography*. Princeton University Press, Princeton, United States of America, 1967.
- [160] R. A. MacArthur. Aquatic mammals in cold. In *Animal Adaptation to Cold. Advances in Comparative and Environmental Physiology 4*. Springer: Berlin, Heidelberg, 1989. L. C. H. Wang, ed.
- [161] R. A. MacArthur and K. L. Campbell. Heat increment of feeding and its thermoregulatory benefit in the muskrat (*ondatra zibethicus*). *Journal of Comparative Physiology B*, 164:141–146, 1994.

- [162] R. A. MacArthur, M. M. Humphries, and D. Jeske. Huddling behavior and the foraging efficiency of muskrats. *Journal of Mammalogy*, 78:850–858, 1997.
- [163] D. I. MacKenzie, J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*, volume 2nd ed. Academic Press, London, United Kingdom, 2018.
- [164] D. I. MacKenzie and J. A. Royle. Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, 42:1105–1114, 2005.
- [165] R. Maestri, L. L. Luza, L. D. Barros ..., and L. D. S. Duarte. Geographical variation of body size in sigmodontine rodents depends on both environment and phylogenetic composition of communities. *Journal of Biogeography*, 43:1192–1202, 2016.
- [166] K. H. Mann and P. A. Breen. The relation between lobster abundance, sea urchins, and kelp beds. *Journal of the Fisheries Research Board of Canada*, 29:603–605, 1972.
- [167] C. B. Marchbanks. Factors influencing muskrat (*ondata zibethicus*) choice of farm ponds in the flint hills. Master’s thesis, Emporia State University, Emporia, United States of America, 1992.
- [168] R. A. Martin. Body mass and correlated ecological variables in the north american muskrat lineage: evolutionary rates and the tradeoff of large size and speciation potential. *Historical Biology*, 31:631–643, 2019.
- [169] R. S. Matlack, D. W. Kaufman, and G. A. Kaufman. Influence of woody vegetation on small mammals in tallgrass prairie. *American Midland Naturalist*, 160:7–19, 2008.
- [170] B. R. Matykiewicz, S. K. Windels, B. T. Olson, R. T. Plumb, T. M. Wolf, and A. A. Ahlers. Assessing translocation effects on the spatial ecology and survival of muskrats *ondata zibethicus*. *Wildlife Biology*, 2021:wlb.00823, 2021.
- [171] B. McDonald. Distribution, abundance, and habitat affinities of oklahoma muskrats

- (*ondatra zibethicus*): new insight from trapper reports. *Proceedings of the Oklahoma Academy of Science*, 86:39–45, 2006.
- [172] B. R. McMillan, K. A. Pfeiffer, and D. W. Kaufman. Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. *American Midland Naturalist*, 165:60–73, 2011.
- [173] B. K. McNab. On the ecological significance of bergmann’s rule. *Ecology*, 52:845–854, 1971.
- [174] S. Meiri. Bergmann’s rule: what’s in a name? *Global Ecology and Biogeography*, 20: 203–207, 2011.
- [175] S. Meiri and T. Dayan. On the validity of bergmann’s rule. *Journal of Biogeography*, 30:331–351, 2003.
- [176] S. Meiri, Y. Yom-Tov, and E. Geffen. What determines conformity to bergmann’s rule? *Global Ecology and Biogeography*, 16:78–794, 2007.
- [177] R. L. Meeks and G. R. Ultsch. Overwintering behavior of snapping turtles. *Copeia*, 1990:880–884, 1990.
- [178] F. Messier and J. A. Virgl. Differential use of bank burrows and lodges by muskrats, *ondatra zibethicus*, in a northern marsh environment. *Canadian Journal of Zoology*, 70:1180–1184, 1992.
- [179] G. Middendorf, T. A. Becerra, and D. Cline. Transition and resilience in the kansas flint hills. *Online Journal of Rural Research & Policy*, 4:1–28, 2009.
- [180] J. E. Miller. Muskrats. *Wildlife Damage Management Technical Series*, 14:1–13, 2018.
- [181] L. S. Mills, M. E. Soulé, and D. F. Doak. The keystone-species concept in ecology and conservation. *BioScience*, 43:219–229, 1993.

- [182] D. R. Mitchell, E. Sherratt, and V. Weisbecker. Facing the facts: adaptive trade-offs along body size ranges determine mammalian craniofacial scaling. *Biological Reviews*, 99:496–524, 2024.
- [183] V. G. Monakhov and MJ. Hamilton. Trends in the size structure of pine marten *martes martes* linnaeus 1756 (mammalia: Mustelidae) within the species range. *Journal of Ecology*, 51:250–259, 2020.
- [184] P. J. Moors. Sexual dimorphism in the body size of mustelids (carnivora): the roles of food habits and breeding systems. *Oikos*, 34:147–158, 1980.
- [185] D. J. Morin, C. B. Yackulic, J. E. Diffendorfer ..., and E. M. Schaubert. Is your ad hoc selection strategy affecting your multimodel inference? *Ecosphere*, 11:e02997, 2020.
- [186] C. L. Mott, C. K. Bloomquist, and C. K. Nielsen. Within-lodge interactions between two ecosystem engineers, beavers (*castor canadensis*) and muskrats (*ondata zibethicus*). *Behaviour*, 150:1325–1344, 2013.
- [187] R. J. Naiman, C. A. Johnston, and J. C. Kelley. Alteration of north american streams by beaver. *BioScience*, 38:753–762, 1988.
- [188]
- [189] W. Nentwig, E. Kühnel, and S. Bacher. A generic impact-scoring system applied to alien mammals in europe. *Conservation Biology*, 24:302–311, 2010.
- [190] B. N. Ness and R. W. Klaver. Canada goose nest survival at rural wetlands in north-central iowa. *Wildlife Society Bulletin*, 40:705–713, 2016.
- [191] United States Geological Survey. National hydrography dataset. Reston, United States of America, 2021. NHD.
- [192] Multi-Resolution Land Characteristics Consortium. National land cover dataset. Research Triangle Park, United States of America, 2019. NLCD.

- [193] M. J. Noonan, P. J. Johnson, A. C. Kitchener ..., and D. W. Macdonald. Sexual size dimorphism in musteloids: an anomalous allometric pattern is explained by feeding ecology. *Ecology and Evolution*, 6:8495–8501, 2016.
- [194] P. Nummi, V.-M. Väänänen, and J. Malinen. Alien grazing: indirect effects of muskrats on invertebrates. *Biological Invasions*, 8:993–999, 2006.
- [195] M. A. Nuñez and D. Simberloff. Invasive species and the cultural keystone species concept. *Ecology and Society*, 10:r4, 2005.
- [196] O. Oskyrko, J. Liu, and W. Du. Is bergmann’s rule valid for terrestrial vertebrates? *Ecology*, 107:e70324, 2026.
- [197] C. T. Owen, M. A. McGregor, G. A. Cobbs, and J. E. Alexander Jr. Muskrat predation on a diverse unionid mussel community: impacts of prey species composition, size and shape. *Freshwater Biology*, 56:554–564, 2011.
- [198] C. E. Owensby, K. R. Blan, B. J. Eaton, and O. G. Russ. Evaluation of eastern redcedar infestations in the northern kansas flint hills. *Journal of Range Management*, 26:256–260, 1973.
- [199] K. A. Ozment, E. A. R. Welte, M. Shaffer, and M. Kaspari. Tracking nutrients in space and time: Interactions between grazing lawns and drought drive abundances of tallgrass prairie grasshoppers. *Ecology and Evolution*, 11:5413–5423, 2021.
- [200] R. T. Paine. Food web complexity and species diversity. *American Naturalist*, 100: 65–75, 1966.
- [201] R. T. Paine. A note on trophic complexity and community stability. *American Naturalist*, 103:91–93, 1969.
- [202] M. A. Parsons, T. C. Barkley, J. L. Rachlow, J. L. Johnson-Maynard, T. R. Johnson, C. R. Milling, J. H. Hammel, and I. Leslie. Cumulative effects of an herbivorous ecosystem engineer in a heterogeneous landscape. *Ecosphere*, 7:e01334, 2016.

- [203] G. R. Paulson. The mammals of the cudahy fauna. *Papers of the Michigan Academy of Science, Arts, and Letters*, 46:127–153, 1961.
- [204] T. Payne, S. Stevens, and W. Caire. Annotated checklist of the mammals of the tall-grass prairie preserve, osage county, oklahoma. *Proceedings of the Oklahoma Academy of Science*, 81:41–51, 2001.
- [205] W. T. Penfound and E. H. Hathaway. Plant communities in the marshlands of south-eastern louisiana. *Ecological Monographs*, 8:4–56, 1938.
- [206] M. C. Perry. Wetland habitats for wildlife of the chesapeake bay. In *Ecology of Wetlands and Associated Systems*, pages 332–349. Pennsylvania Academy of Science, Easton, Pennsylvania, USA, 1998. S. K. Majumdar, E. W. Miller, and F. B. Brenner, eds.
- [207] R. A. Powell and W. J. Zielinski. Competition and coexistence in mustelid communities. *Acta Zoology Fennica*, 174:223–227, 1983.
- [208] M. E. Power, D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, and L. S. Mills. Challenges in the quest for keystones. *BioScience*, 46:609–620, 1996.
- [209] H. Pöysä, J. Elmberg, G. Gunnarsson, S. Holopainen, P. Nummi, and K. Sjöberg. Habitat associations and habitat change: seeking explanation for population decline in breeding eurasian wigeon *anas penelope*. *Hydrobiologia*, 785:207–217, 2017.
- [210] R. M. Pringle, D. F. Doak, A. K. Brody, R. Jocqué, and T. M. Palmer. Spatial pattern enhances ecosystem functioning in an african savanna. *PLoS Biology*, 8:e1000377, 2010.
- [211] G. Proulx and F. F. Gilbert. The ecology of the muskrat, *ondata zibethicus*, at luther marsh, ontario. *Canadian Field-Naturalist*, 97:377–390, 1983.
- [212] L. R. Prugh and J. S. Brashares. Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. *Journal of Animal Ecology*, 81:667–678, 2012.

- [213] N. D. Pyenson and G. J. Vermeij. The rise of ocean giants: maximum body size in cenozoic marine mammals as an indicator for productivity in the pacific and atlantic oceans. *Biology Letters*, 12:20160186, 2016.
- [214] QGIS Association. Qgis geographic information system. version 3.16. qgis.org, 2021.
- [215] M. Quiroga-Carmona, P. Teta, and G. D’Elía. The skull variation of the olive field mouse *abrothrix olivacea* (cricetidae: Abrotrichini) is localized and correlated to the ecogeographic features of its geographic distribution. *PeerJ*, 11:e15200, 2023.
- [216] R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, 2025.
- [217] Z. Ratajczak, J. M. Briggs, D. G. Goodin ..., and B. Obermeyer. Assessing the potential for transitions from tallgrass prairie to woodlands: are we operating beyond critical fire thresholds? *Rangeland Ecology & Management*, 69:280–287, 2016.
- [218] Z. Ratajczak, J. B. Nippert, and S. L. Collins. Woody encroachment decreases diversity across north american grasslands and savannas. *Ecology*, 93:697–703, 2012.
- [219] X. Raynaud, C. G. Jones, and S. Barot. Ecosystem engineering, environmental decay and environmental states of landscapes. *Oikos*, 122:591–600, 2013.
- [220] S. A. Richards. Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, 86:2805–2814, 2005.
- [221] A. Riek and F. Geiser. Allometry of thermal variables in mammals: consequences of body size and phylogeny. *Biological Reviews*, 88:564–572, 2013.
- [222] PL. Risley. Observations in the natural history of the common musk turtle, *sternotherus odoratus* (latreille). *Papers of the Michigan Academy of Science, Arts, and Letters*, 17:685–711, 1933.
- [223] N. M. Roberts and S. M. Crimmins. Do trends in muskrat harvest indicate widespread population declines? *Northeastern Naturalist*, 17:229–238, 2010.

- [224] A. V. Rodrigues, L. A. Grossel ..., and A. F. Diniz-Filho. Habitat drives body size evolution in mustelidae (mammalia: Carnivora). *Evolutionary Biology*, 50:197–205, 2023.
- [225] M. Á. Rodríguez, M. Á. Olalla-Tárraga, and B. A. Hawkins. Bergmann’s rule and the geography of mammal body size in the western hemisphere. *Global Ecology and Biogeography*, 17:274–283, 2008.
- [226] F. Rosell, O. Bozser, P. Collen, and H. Parker. Ecological impact of beavers castor fiber and castor canadensis and their ability to modify ecosystems. *Mammal Review*, 35:248–276, 2005.
- [227] I. O. Rozhkova-Timina, V. K. Popkov, P. J. Mitchell, and S. N. Kirpotin. Beavers as ecosystem engineers – a review of their positive and negative effects. In *IOP Conference Series: Earth and Environmental Science*, volume 201, page 012015, 2018.
- [228] C. Sadowski and J. Bowman. Historical surveys reveal a long-term decline in muskrat populations. *Ecology and Evolution*, 11:7557–7568, 2021.
- [229] F. Samson and F. Knopf. Prairie conservation in north america. *BioScience*, 44: 418–421, 1994.
- [230] M. Sandell. Ecological energetics, optimal body size and sexual size dimorphism: a model applied to the stoat, mustela erminea l. *Functional Ecology*, 3:315–324, 1989.
- [231] D. Sanders, C. G. Jones, E. Thébault, T. B. Bouma, T. van der Heide, J. van Belzen, and S. Barot. Integrating ecosystem engineering and food webs. *Oikos*, 123:513–524, 2014.
- [232] J. M. Sarneel, N. Huig, G. F. Veen, W. Rip, and E. S. Bakker. Herbivores enforce sharp boundaries between terrestrial and aquatic ecosystems. *Ecosystems*, 17:1426–1438, 2014.

- [233] J. M. Sarneel, M. B. Soons, J. J. M. Geurts, B. Beltman, and J. T. A. Verhoeven. Multiple effects of land-use changes impede the colonization of open water in fen ponds: multiple factors impede floating fen vegetation. *Journal of Vegetation Science*, 22:551–563, 2011.
- [234] A. P. Saveljev, S. Shar, A. E. Scopin, M. Otgonbaatar, V. A. Soloviev, N. I. Putincev, and N. Lhamsuren. Introduced semiaquatic mammals in the uvs nuur hollow (current distribution and ecological vectors of naturalization). *Russian Journal of Biological Invasions*, 6:37–50, 2015.
- [235] R. L. Schooley and L. C. Branch. Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. *Ecosystems*, 10:846–853, 2007.
- [236] R. L. Schooley and L. C. Branch. Enhancing the area-isolation paradigm: habitat heterogeneity and metapopulation dynamics of a rare wetland mammal. *Ecological Applications*, 19:1708–1722, 2009.
- [237] R. L. Schooley and L. C. Branch. Habitat quality of source patches and connectivity in fragmented landscapes. *Biodiversity Conservation*, 20:1611–1623, 2011.
- [238] C. W. Schwartz and E. R. Schwartz. *The Wild Mammals of Missouri*. University of Missouri Press, Columbia, Missouri, USA, 1959.
- [239] R. P. Scofield and R. Reyes-Arriagada. A population estimate of the sooty shearwater *puffinus griseus* in the wollaston and hermite island groups, cape horn archipelago, chile, and concerns over conservation in the area. *Revía de Biología Marina y Oceanografía*, 48:623–628, 2013.
- [240] R. S. Sikes and The Animal Care and Use Committee of the American Society of Mammalogists. 2016 guidelines of the american society of mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97:663–688, 2016.
- [241] D. Simberloff. Rats are not the only introduced rodents producing ecosystem impacts on islands. *Biological Invasions*, 11:1735–1742, 2009.

- [242] G. G. Singh, R. W. Markel, R. G. Martone, A. K. Salomon, C. H. D. Harley, and K. M. A. Chan. Sea otters homogenize mussel beds and reduce habitat provisioning in a rocky intertidal ecosystem. *PLoS ONE*, 8:e65435, 2013.
- [243] G. Skyrienė and A. Paulauskas. Distribution of invasive muskrats (*ondata zibethicus*) and impact on ecosystem. *Ekologija*, 58:357–367, 2012.
- [244] V. V. Smirnov and K. Tretyakov. Changes in aquatic plant communities on the island of valaam due to invasion by the muskrat *ondata zibethicus* l. (rodentia, mammalia). *Biodiversity and Conservation*, 7:673–690, 1998.
- [245] S. V. Smith, W. H Renwick, J. D. Bartley, and R. W. Buddemeier. Distribution and significance of small, artificial water bodies across the united states landscape. *The Science of the Total Environment*, 299:21–36, 2002.
- [246] F. A. Smith and S. K. Lyons. How big should a mammal be? a macroecological look at mammalian body size over space and time. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366:2364–2371, 2011.
- [247] E. L. Smith, V. Rodd, B. McDonald ..., and M. Vankoughnett. Seasonal considerations for year-round operation of on-farm wetlands in temperate climates: a review. *Journal of Agricultural Science*, 13:1–20, 2021.
- [248] V. Soran, A. Ardelean, C. Bucsa, and C. Maior. Suitable method assessment the optimal size of natural biotic areas and nature reserves. *Transactions on Ecology and the Environment*, 16:147–154, 1997.
- [249] J. R. Speakman and E. Król. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, 79:726–746, 2010.
- [250] M. D. Starking-Szymanski, T. Yoder-Nowak, G. Rybarczyk, and H. A. Dawson. Movement and habitat use of headstarted blanding’s turtles in michigan. *Journal of Wildlife Management*, 82:1516–1526, 2018.

- [251] R. T. Stevens and M. L. Kennedy. Geographic variation in body size of american mink (*mustela vison*). *Mammalia*, 2006:145–152, 2006.
- [252] J. R. Straka, A. Antoine ..., and L. Wiltzen. “we used to say rats fell from the sky after a flood.”. *Arctic*, 71:218–228, 2018.
- [253] T. M. Swartz and J. R. Miller. Managing farm ponds as breeding sites for amphibians. *Ecological Applications*, 29:1–15, 2019.
- [254] T. M. Swartz and J. R. Miller. The american pond belt: an untold story of conservation challenges and opportunities. *Frontiers in Ecology and the Environment*, 19:501–509, 2021.
- [255] F. A. de Szalay and W. Cassidy. Effects of muskrat (*ondata zibethicus*) lodge construction on invertebrate communities in a great lakes coastal wetland. *American Midland Naturalist*, 146:300–310, 2001.
- [256] P. Teta, N. U. de la Sancha, G. D’Elía, and B. D. Patterson. Andean rain shadow effect drives phenotypic variation in a widely distributed austral rodent. *Journal of Biogeography*, 49:1767–1778, 2022.
- [257] M. D. Thom, L. A. Harrington, and D. W. Macdonald. Why are american mink sexually dimorphic? a role for niche separation. *Oikos*, 105:525–535, 2004.
- [258] M. J. Tilkens, C. Wall-Scheffler, T. D. Weaver, and K. Steudel-Numbers. The effects of body proportions on thermoregulation: an experimental assessment of allen’s rule. *Journal of Human Evolution*, 53:286–291, 2007.
- [259] J. Toner, J. M. Farrell, and J. V. Mead. Muskrat abundance responses to water level regulation within freshwater coastal wetlands. *Wetlands*, 30:211–219, 2010.
- [260] R. Tornberg and S. Haapala. The diet of the marsh harrier *circus aeruginosus* breeding on the isle of hailuoto compared to other raptors in northern finland. *Ornis Fennica*, 90:103–116, 2013.

- [261] E. J. Torres-Romero, I. Morales-Castilla, and M. Á. Olalla-Tárraga. Bergmann’s rule in the oceans? temperature strongly correlates with global interspecific patterns of body size in marine mammals. *Global Ecology and Biogeography*, 25:1206–1215, 2016.
- [262] M. A. Tucker and T. L. Rogers. Examining the prey mass of terrestrial and aquatic carnivorous mammals: minimum, maximum and range. *PLoS ONE*, 9:e106402, 2014.
- [263] C. K. Turner and T. C. Lantz. 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, 2018. With the Gwich’in Tribal Council Department of Cultural Heritage.
- [264] R. W. Tyndall. Long-term monitoring of two subpopulations of the federally threatened *aeschynomene virginica* (sensitive joint-vetch) in maryland. *Castanea*, 76:20–27, 2011.
- [265] M. Tyrrell and D. J. Hornbach. Selective predation by muskrats on freshwater mussels in 2 minnesota rivers. *Journal of the North American Benthological Society*, 17:301–310, 1998.
- [266] National Weather Service. Us climate data 3.0. Silver Spring, United States of America, 2021. US Climate Data.
- [267] A. Valladares-Gomez, F. Torres-Pérez, and R. E. Palma. Assessing ecogeographic rules in two sigmodontine rodents along an elevational gradient in central chile. *Animals*, 14:830, 2024.
- [268] A. E. J. Valenzuela, C. B. Anderson, L. Fasola, and J. L. Cabello. Linking invasive exotic vertebrates and their ecosystem impacts in tierra del fuego to test theory and determine action. *Acta Oecologica*, 54:110–118, 2013.
- [269] A. G. van der Valk and C. B. Davis. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*, 59:322–335, 1978.

- [270] J. E. Vermaat, B. Bos, and P. Van Der Burg. Why do reed beds decline and fail to re-establish? a case study of dutch peat lakes. *Freshwater Biology*, 61:1580–1589, 2016.
- [271] H. Viljugrein, O. C. Lingjaerde, N. C. Stenseth, and M. S. Boyce. Spatiotemporal patterns of mink and muskrat in canada during a quarter century. *Journal of Animal Ecology*, 70:671–682, 2001.
- [272] J. M. Visser, C. E. Sasser, and B. S. Cade. The effect of multiple stressors on salt marsh end-of-season biomass. *Estuaries and Coasts*, 29:328–339, 2006.
- [273] K. R. Wait, A. M. Ricketts, and A. A. Ahlers. Land-use change structures carnivore communities in remaining tallgrass prairie. *Journal of Wildlife Management*, 82:1491–1502, 2018.
- [274] V. J. Wainscott, C. Bartley, and P. Kangas. Effect of muskrat mounds on microbial density on plant litter. *American Midland Naturalist*, 123:399–401, 1990.
- [275] R. E. Walton, C. D. Sayer, H. Bennion, and J. C. Axmacher. Open-canopy ponds benefit diurnal pollinator communities in an agricultural landscape: implications for farmland pond management. *Insect Conservation and Diversity*, 14:501–509, 2021.
- [276] E. M. Ward and S. M. Gorelick. Drying drives decline in muskrat population in the peace-athabasca delta, canada. *Environmental Research*, 13:124026, 2018.
- [277] E. R. Wedel, J. B. Nippert, and D. C. Hartnett. Fire and browsing interact to alter intra-clonal stem dynamics of an encroaching shrub in tallgrass prairie. *Oecologia*, 196:1039–1048, 2021.
- [278] M. W. Weller and C. S. Spatcher. *Role of Habitat in the Distribution and Abundance of Marsh Birds*. Iowa State University of Science and Technology, Ames, Iowa, USA, 1965.
- [279] J. A. Wesson. A closed trapping season and subsequent muskrat harvests. *Wildlife Society Bulletin*, 5:194–196, 1977.

- [280] H. Wickham, R. François, L. Henry ..., and D. Vaughan. dplyr: A grammar of data manipulation. R package version 1.1.4, 2023.
- [281] A. H. Williams. The threespot damselfish: a noncarnivorous keystone species. *American Naturalist*, 116:138–142, 1980.
- [282] G. R. Willner, G. A. Feldhamer ..., and J. A. Chapman. Ondatra zibethicus. *Mammalian Species*, 141:1–8, 1980.
- [283] R. Williamson and J. D. Clark. Evaluating interactions between river otters and muskrats at bridge crossings in kentucky. *Journal of Mammalogy*, 92:1314–1320, 2011.
- [284] J. H. Wlosinski and L. B. Wlosinski. Muskrat harvests, water levels, and aquatic vegetation on the upper mississippi river national wildlife and fish refuge. Technical report, U.S. Geological Survey, USA, 1998. Project Status Report.
- [285] J. O. Wolff and R. D. Guthrie. Why are aquatic small mammals so large? *Oikos*, 45: 365–373, 1985.
- [286] S. N. Wood. *Generalized Additive Models: An Introduction with R*, volume 2nd edition. Chapman and Hall/CRC, 2017.
- [287] H. Xu, S. Qiang, Z. Han, J. Guo, Z. Huang, and H. Sun. The status and causes of alien species invasion in china. *Biodiversity and Conservation*, 15:2893–2904, 2006.
- [288] N. Yamaguchi and D. W. Macdonald. The burden of co-occupancy: intraspecific resource competition and spacing patterns in american mink, mustela vison. *Journal of Mammalogy*, 84:1341–1355, 2003.
- [289] Y. Yom-Tov, T. M. Heggberget ..., and S. Yom-Tov. Body size changes among otters, lutra lutra, in norway: the possible effects of food availability and global warming. *Oecologia*, 150:155–160, 2006.
- [290] Y. Yom-Tov, A. Roos ..., and T. M. Heggberget. Recent changes in body size of the eurasian otter lutra lutra in sweden. *AMBIO*, 39:496–503, 2010.

- [291] D. D. Young. The keystone species concept. *American Biology Teacher*, 42:312–324, 1980.
- [292] A. Zalewski and M. Bartoszewicz. Phenotypic variation of an alien species in a new environment: the body size and diet of american mink over time and at local and continental scales. *Biological Journal of the Linnean Society*, 105:681–693, 2012.
- [293] W. Zhang, Q. Yao, H. Tong, and N. Chr. Stenseth. Smoothing for spatiotemporal models and its application to modeling muskrat-mink interaction. *Biometrics*, 59: 813–821, 2003.
- [294] J. Zschille, N. Stier, M. Roth, and U. Berger. Dynamics in space use of american mink (neovison vison) in a fishpond area in northern germany. *European Journal of Wildlife Research*, 58:955–968, 2012.

Appendix A

Supplementary Material for Chapter 1

Table A.1: Table of all publications used in the review.

Context is the topical category of the publication and Focus denotes if the article dealt with muskrats as the primary focus. If muskrats were mentioned as ecosystem engineers or keystone species, the publication is denoted with EE or KS respectively in the third column. The fourth column, Status, specifies if the muskrats in the publication were native, introduced, or captive. We have abbreviated authors listed in the fifth column. We listed full publication references in the Comprehensive Bibliography. Lastly, we listed the type of publication – journal article, book chapter, scientific report, or a thesis (PhD or MSc) – in the final column.					
*Muskrats listed as "cultural keystone" species, but not in an ecological sense.					
Context	Focus	EE or KS	Status	Authors	Type
Disease	Other	No	Introduced	Adriana et al. (2016)	Article
Ecology	Muskrat	No	Native	Ahlers (2010)	Thesis
Management	Muskrat	No	Native	Ahlers and Heske (2017)	Article
Ecology	Muskrat	No	Native	Ahlers et al. (2010a)	Article
Ecology	Muskrat	No	Native	Ahlers et al. (2010b)	Article
Physiology	Muskrat	No	Native	Ahlers et al. (2011)	Article
Ecology	Muskrat	No	Native	Ahlers et al. (2015a)	Article
Disease	Muskrat	No	Native	Ahlers et al. (2015b)	Article
Management	Muskrat	No	Native	Ahlers et al. (2016a)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Other	No	Native	Ahlers et al. (2016b)	Article
Physiology	Other	No	Native	Aigeldinger and Fish (1995)	Article
Physiology	Other	No	Native	Allers and Culik (1997)	Article
Ecology	Other	No	Native	Andersen and Shafroth (2010)	Article
Ecology	Other	No	Native	Anderson and Mitsch (2005)	Article
Ecology	Other	No	Native	Anderson et al. (2005)	Article
Ecology	Other	No	Introduced	Anderson et al. (2006)	Article
Disease	Other	No	Native	Antonation et al. (2015)	Article
Physiology	Other	No	Introduced	Antonova et al. (2017)	Article
Disease	Other	No	Introduced	Aviat et al. (2009)	Article
Disease	Other	No	Introduced	Bagrade et al. (2016)	Article
Ecology	Muskrat	No	Introduced	Bakker and Bos (2019)	Article
Ecology	Other	No	Native	Baldwin (2004)	Article
Ecology	Other	No	Native	Baldwin and Pendleton (2003)	Article
Ecology	Other	No	Native	Barthelmess (2014)	Article
Ecology	Other	EE	Native	Batzer et al. (2006)	Chapter
Physiology	Muskrat	No	Native	Belant (1995)	Article
Physiology	Muskrat	No	Native	Belant (1996)	Article
Ecology	Other	No	Native	Beltaos (2014)	Article
Management	Other	No	Native	Beltaos et al. (2006a)	Article
Management	Other	No	Native	Beltaos et al. (2006b)	Article
Ecology	Other	No	Native	Bernal and Mitsch (2013)	Article
Ecology	Other	No	Native	Beutel et al. (2014)	Article
Disease	Other	No	Native	Bitto and Aldras (2009)	Article
Ecology	Other	No	Introduced	Bobrov et al. (2008)	Article
Ecology	Other	No	Native	Bollen (2013)	Thesis
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Physiology	Muskrat	No	Native	Borucinska et al. (1996)	Article
Disease	Muskrat	No	Native	Borucinska et al. (1997)	Article
Disease	Muskrat	No	Captive	Borucinska et al. (2001)	Article
Management	Muskrat	No	Introduced	Bos and Ydenberg (2011)	Article
Ecology	Other	No	Native	Brandt et al. (2015)	Article
Ecology	Other	No	Native	Bridges et al. (2007)	Article
Ecology	Other	EE	Native	Bridgewater and Aricò (2016)	Article
Ecology	Muskrat	No	Native	Britzke (2015)	Article
Ecology	Other	No	Native	Browne and Paszkowski (2010)	Article
Ecology	Muskrat	KS	Native	Brunke et al. (2017)	Article
Ecology	Muskrat	No	Introduced	Brzezinski et al. (2010)	Article
Physiology	Other	No	Native	Butler and Jones (1997)	Article
Physiology	Muskrat	No	Native	Campbell and MacArthur (1994)	Article
Ecology	Muskrat	No	Native	Campbell and MacArthur (1996a)	Article
Ecology	Muskrat	No	Native	Campbell and MacArthur (1996b)	Article
Physiology	Muskrat	No	Native	Campbell and MacArthur (1997)	Article
Physiology	Muskrat	No	Native	Campbell and MacArthur (1999)	Article
Physiology	Muskrat	No	Native	Campbell et al. (1998)	Article
Physiology	Other	No	Native	Campbell et al. (2000)	Article
Physiology	Muskrat	No	Captive	Cao et al. (2015)	Article
Ecology	Muskrat	No	Introduced	Castillo et al. (2017)	Article
Ecology	Other	No	Native	Cepek et al. (2004)	Article
Disease	Muskrat	No	Introduced	Charante et al. (1998)	Article
Ecology	Other	No	Native	Chavez and Gese (2005)	Article
Ecology	Muskrat	No	Native	Clark (1994)	Article
Ecology	Other	No	Native	Cofield et al. (2010)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Muskrat	No	Native	Connors et al. (2000)	Article
Ecology	Other	No	Native	Cortez and Weitz (2014)	Article
Ecology	Muskrat	No	Native	Cotner and Schooley (2011)	Article
Ecology	Other	No	Native	Cott et al. (2008)	Article
Ecology	Muskrat	No	Introduced	Crego et al. (2016)	Article
Ecology	Muskrat	No	Introduced	Danell (1977)	Article
Ecology	Muskrat	No	Introduced	Danell (1979)	Article
Ecology	Muskrat	KS	Introduced	Danell (1996)	Article
Disease	Other	No	Introduced	Danisova et al. (2017)	Article
Physiology	Muskrat	No	Native	Darby et al. (2016)	Article
Ecology	Other	No	Native	Das et al. (2015)	Article
Physiology	Other	No	Native	De Leeuw (1996)	Article
Physiology	Other	No	Native	De Leeuw et al. (1998)	Article
Ecology	Muskrat	No	Native	De Szalay and Cassidy (2001)	Article
Ecology	Muskrat	No	Introduced	Deferrari (2007)	Thesis
Ecology	Other	No	Introduced	Dell’Arte et al. (2007)	Article
Disease	Muskrat	No	Native	Detwiler et al. (2012)	Article
Management	Other	No	Native	Dickins et al. (1999)	Article
Ecology	Other	No	Native	Dickman (1999)	Article
Ecology	Muskrat	No	Native	Diggins and Stewart (2000)	Article
Ecology	Muskrat	No	Introduced	Ecke et al. (2014)	Article
Ecology	Muskrat	No	Native	Edelman et al. (2015)	Article
Ecology	Other	No	Native	Elsey et al. (2015)	Article
Ecology	Muskrat	No	Native	Elsey et al. (2016)	Article
Management	Muskrat	No	Introduced	Engeman and Whisson (2003)	Article
Management	Muskrat	No	Native	Erb et al. (1999)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Muskrat	No	Native	Erb et al. (2000)	Article
Ecology	Muskrat	No	Native	Erb et al. (2001)	Article
Ecology	Other	No	Native	Ernst et al. 1989	Article
Ecology	Other	No	Native	Ernst et al. 1994	Chapter
Management	Muskrat	No	Native	Estay et al. (2011)	Article
Ecology	Muskrat	No	Native	Falcone (2015)	Thesis
Ecology	Other	No	Native	Faller and McCleery (2017)	Article
Ecology	Muskrat	No	Native	Fan et al. (2003)	Article
Disease	Other	No	Native	Farid (2013)	Article
Ecology	Other	EE	Native	Farrell and Distler (2012)	Report
Ecology	Other	No	Native	Farrell et al. (2010)	Article
Ecology	Other	No	Native	Fink and Mitsch (2004)	Article
Physiology	Other	No	Native	Fish (1993)	Article
Physiology	Other	No	Native	Fish (1994)	Article
Ecology	Other	No	Native	Fish (1996)	Article
Physiology	Other	No	Native	Fish (2000)	Article
Physiology	Other	No	Native	Fish and Baudinette (1999)	Article
Physiology	Other	No	Captive	Fish and Baudinette (2008)	Article
Physiology	Other	No	Native	Fish et al. (1997)	Article
Management	Other	No	Native	Fraley et al. (2018)	Article
Ecology	Other	No	Native	Fretueg et al. (2015)	Article
Ecology	Other	No	Native	Froda and Colavita (2005)	Article
Disease	Other	No	Native	Fuehrer (2014)	Article
Disease	Other	No	Native	Gabriele-Rivet et al. (2016)	Article
Physiology	Other	No	Captive	Galewski et al. (2006)	Article
Physiology	Other	No	Native	Gamberg et al. (2005)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Other	No	Native	Gleason et al. (2005)	Article
Ecology	Other	No	Native	Gordon et al. (2016)	Article
Ecology	Other	No	Introduced	Gorgadze (2013)	Article
Ecology	Other	No	Native	Gori et al. (2014)	Report
Physiology	Other	No	Native	Gorini et al. (2009)	Article
Ecology	Other	No	Native	Gough and Grace (1998)	Article
Ecology	Muskrat	EE	Native	Greenhorn et al. (2016)	Article
Management	Muskrat	No	Native	Gregory et al. (2019)	Article
Management	Muskrat	No	Native	Gross et al. (2017)	Article
Disease	Muskrat	No	Introduced	Gulyaeva et al. (2017)	Article
Ecology	Muskrat	No	Native	Haas (2002)	Article
Physiology	Muskrat	No	Captive	Han et al. (2017)	Article
Ecology	Other	No	Native	Hanlon and Levine (2004)	Article
Disease	Other	No	Introduced	Hanosset et al. (2008)	Article
Ecology	Other	No	Native	Hartman (1994)	Article
Disease	Other	No	Introduced	Hartskeerl and Terpstra (1996)	Article
Physiology	Other	No	Native	Haukisalmi et al. (2006)	Article
Ecology	Muskrat	No	Native	Haydon et al. (2001)	Article
Ecology	Other	No	Native	Hazelton et al. (2014)	Article
Ecology	Muskrat	No	Introduced	Heine and van der Velde (1978)	Article
Disease	Other	No	Introduced	Hejlícek et al. (1997)	Article
Ecology	Muskrat	No	Native	Hersey et al. (2013)	Article
Ecology	Other	No	Native	Hewitt and Miyanishi (1997)	Article
Ecology	Other	No	Native	Hickey and Malecki (1997)	Article
Ecology	Muskrat	EE	Native	Higgins (2002)	Thesis
Ecology	Muskrat	EE	Native	Higgins and Mitsch (2001)	Chapter
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Physiology	Muskrat	No	Native	Hindle et al. (2006)	Article
Ecology	Other	No	Native	Hoggarth et al. (1995)	Article
Ecology	Other	No	Native	Holland (2016)	Thesis
Ecology	Other	No	Native	Holland et al. (2018)	Article
Ecology	Muskrat	No	Native	Holland et al. (2019)	Article
Ecology	Muskrat	No	Native	Holmengen and Seip (2009)	Article
Ecology	Muskrat	No	Native	Holmengen et al. (2009b)	Article
Ecology	Other	No	Native	Hood and Larson (2014)	Article
Ecology	Other	No	Introduced	Hulme et al. (2010a)	Chapter
Ecology	Other	No	Introduced	Hulme et al. (2010b)	Chapter
Disease	Muskrat	No	Introduced	Hurd et al. (2017)	Article
Management	Other	No	Introduced	Jamrozy (2008)	Article
Disease	Other	No	Native	Jiang et al. (2005)	Article
Disease	Other	No	Native	John and Smith (1997)	Article
Ecology	Other	No	Native	Johnson-Bice et al. 2019)	Article
Ecology	Muskrat	No	Native	Jokela and Mutikainen (1995)	Article
Ecology	Muskrat	No	Native	Juhlin and Halbrook (1997)	Article
Ecology	Muskrat	No	Native	Kadlec et al. (2007)	Article
Ecology	Other	No	Native	Kadlec et al. (2010)	Article
Ecology	Other	No	Native	Kadlec et al. (2012a)	Article
Ecology	Other	No	Native	Kadlec et al. (2012b)	Article
Ecology	Other	No	Native	Kanda and Fuller (2004)	Article
Ecology	Muskrat	No	Native	Kangas and Hannan (1985)	Article
Disease	Muskrat	No	Introduced	Karan et al. (2014)	Article
Physiology	Other	No	Native	Kaseloo and Lovvorn (2005)	Article
Disease	Muskrat	No	Native	Keulen et al. (1998)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Muskrat	No	Native	Kiviat (1978)	Article
Management	Other	No	Introduced	Kloskowski (2011)	Article
Ecology	Other	No	Native	Kratzer (2014)	Thesis
Physiology	Other	No	Native	Kuhn and Meyer (2009)	Article
Ecology	Muskrat	No	Native	Lacki et al. (1990)	Article
Ecology	Other	No	Native	Landriault et al. (2009)	Article
Ecology	Other	No	Native	Larkin et al. (2012)	Article
Ecology	Muskrat	EE	Native	Larreur (2018)	Thesis
Ecology	Muskrat	EE	Native	Larreur et al. (2019)	Article
Ecology	Other	No	Introduced	Latham et al. (2017)	Article
Physiology	Muskrat	No	Native	Laurence et al. (2009)	Article
Physiology	Muskrat	No	Native	Laurence et al. (2011)	Article
Ecology	Muskrat	No	Native	Laurence et al. (2013)	Article
Ecology	Other	KS	Introduced	Law (2014)	Thesis
Ecology	Other	No	Introduced	Law et al. (2014a)	Article
Ecology	Other	No	Introduced	Law et al. (2014b)	Article
Physiology	Muskrat	No	Introduced	Legendre and Makarenkov (2002)	Article
Ecology	Other	No	Introduced	Leppakoski (2004)	Chapter
Disease	Muskrat	No	Native	Levesque et al. (1995)	Article
Paleontology	Muskrat	No	Extinct	Lewis and Johnson (2002)	Article
Physiology	Muskrat	No	Native	Lewis et al. (2002)	Article
Physiology	Muskrat	No	Captive	Li et al. (2011)	Article
Physiology	Muskrat	No	Captive	Li et al. (2017a)	Article
Physiology	Muskrat	No	Captive	Li et al. (2017b)	Article
Ecology	Other	No	Native	Litzgus et al. (1999)	Article
Physiology	Other	No	Captive	Lovvorn (2007)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Physiology	Muskrat	No	Captive	Lu et al. (2014)	Article
Ecology	Other	No	Native	Luati and Proietti (2010)	Article
Disease	Other	No	Native	Lujan-Vega et al. (2018)	Article
Physiology	Muskrat	No	Captive	Ma et al. (2011)	Article
Physiology	Muskrat	No	Native	MacArthur and Campbell (1994)	Article
Physiology	Muskrat	No	Native	MacArthur and Humphries (1999)	Article
Physiology	Muskrat	No	Native	MacArthur et al. (1997)	Article
Physiology	Muskrat	No	Native	MacArthur et al. (2001)	Article
Physiology	Muskrat	No	Native	MacArthur et al. (2003)	Article
Ecology	Other	No	Introduced	Magnusdottir et al. (2012)	Article
Ecology	Other	No	Introduced	Manchester and Bullock (2000)	Article
Paleontology	Other	No	Extinct	Maridet et al. (2014)	Article
Ecology	Muskrat	No	Native	Marinelli and Messier (1995)	Article
Physiology	Muskrat	No	Native	Marinelli et al. (1997)	Article
Physiology	Muskrat	No	Native	Marti et al. (2011)	Article
Disease	Other	No	Native	Marti et al. (2013)	Article
Paleontology	Other	No	Extinct	Martin (2009)	Article
Physiology	Muskrat	No	Native	Mayack and Loukmas (2001)	Report
Disease	Muskrat	No	Introduced	Mazur and Fomina (2014)	Article
Physiology	Other	No	Native	McCulloch (2005)	Article
Physiology	Other	No	Native	McCulloch (2012)	Article
Physiology	Other	No	Native	McCulloch et al. (1997)	Article
Ecology	Muskrat	No	Native	McDonald (2010)	Article
Physiology	Other	No	Native	McIntyre et al. (2002)	Article
Physiology	Other	No	Native	McPhail and Jones (1999)	Article
Ecology	Other	No	Native	Meeks and Ultsch (1990)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Muskrat	No	Native	Messier and Virgle 1992)	Article
Paleontology	Muskrat	No	Extinct	Mihlbachler (2012)	Article
Paleontology	Muskrat	No	Extinct	Mihlbachler et al. (2002)	Article
Paleontology	Other	No	Extinct	Miller et al. (2014)	Article
Ecology	Other	No	Native	Mitsch and Zhang (2004)	Chapter
Ecology	Other	No	Native	Mitsch et al. (2005a)	Chapter
Ecology	Other	No	Native	Mitsch et al. (2005b)	Article
Disease	Other	No	Introduced	Moinet et al. (2010)	Article
Disease	Other	No	Introduced	Mori et al. (2015)	Article
Ecology	Muskrat	EE	Native	Mott et al. (2013)	Article
Management	Other	No	Introduced	Mougenot and Roussel (2005)	Article
Ecology	Other	No	Native	Muhametsafina et al. (2014)	Article
Physiology	Muskrat	No	Introduced	Mychajliw and Harrison (2014)	Article
Ecology	Muskrat	No	Native	Nadeau et al. (1995)	Article
Disease	Muskrat	No	Native	Naem and Smythe (2015)	Article
Ecology	Other	No	Introduced	Nentwig et al. (2010)	Article
Ecology	Other	No	Native	Ness and Klaver (2016)	Article
Ecology	Other	No	Native	Nkuruniziza (2008)	Article
Ecology	Other	No	Native	Nkurunziza (2009)	Article
Ecology	Other	No	Native	Nolet and Rosell (1994)	Article
Ecology	Other	No	Introduced	Novillo and Ojeda (2008)	Article
Ecology	Muskrat	KS	Introduced	Nummi et al. (2006)	Article
Ecology	Other	No	Native	Nyman et al. (2013)	Article
Disease	Other	No	Introduced	Oksanen et al. (2016)	Article
Ecology	Muskrat	No	Introduced	Otgonbaatar et al. (2018)	Article
Ecology	Muskrat	No	Native	Owen et al. (2011)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Disease	Other	No	Introduced	Pannekoek et al. (2010)	Article
Physiology	Other	No	Native	Panneton et al. (2010)	Article
Physiology	Muskrat	No	Native	Parker (2004)	Article
Ecology	Other	No	Native	Pascoe and DalSoglio (1994)	Article
Physiology	Other	No	Native	Patrick et al. (2016)	Article
Ecology	Other	No	Native	Perry (1998)	Chapter
Ecology	Other	No	Native	Perry and Atkinson (2009)	Article
Ecology	Other	No	Native	Perry et al. (2001)	Article
Disease	Other	No	Native	Perz and Blancq (2001)	Article
Disease	Other	No	Native	Poulin (2003)	Article
Ecology	Other	No	Native	Powell (2017)	Report
Ecology	Other	No	Introduced	Poysa et al. (2017)	Article
Management	Other	No	Native	Premo and Premo (2009)	Report
Disease	Other	No	Native	Prendergast and Jensen (2011)	Article
Ecology	Muskrat	No	Native	Prendergast and Jensen (2012)	Article
Ecology	Other	No	Native	Prepas et al. (1997)	Article
Management	Other	No	Native	Pritchard et al. (2006)	Article
Ecology	Muskrat	No	Native	Proulx and Gilbert (1983)	Article
Disease	Other	No	Native	Rhodes and Kator (1999)	Article
Management	Muskrat	No	Native	Roberts and Crimmins (2010)	Article
Management	Other	No	Introduced	Robertson et al. (2017)	Article
Ecology	Other	No	Native	Rosell et al. (2005)	Article
Physiology	Other	No	Native	Rosen et al. (2007)	Article
Ecology	Other	No	Native	Ross and Murkin (2009)	Chapter
Disease	Other	No	Native	Ruecker et al. (2007)	Article
Disease	Other	No	Native	Ruecker et al. (2012)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Disease	Other	No	Introduced	Runge et al. (2013)	Article
Ecology	Other	No	Introduced	Ruys et al. (2111)	Article
Disease	Other	No	Introduced	Ruzek et al. (2010)	Article
Ecology	Other	No	Native	Sabelli and Kovacevic (2008)	Article
Disease	Other	No	Native	Santin et al. (2010)	Article
Ecology	Other	No	Introduced	Sarneel et al. (2111)	Article
Ecology	Other	No	Native	Sarneel et al. (2014)	Article
Ecology	Other	No	Introduced	Saveljev et al. (2015)	Article
Ecology	Other	No	Native	Schooley and Branch (2009)	Article
Ecology	Other	No	Native	Schooley and Branch (2011)	Article
Ecology	Other	No	Native	Schooley et al. (2012)	Article
Paleontology	Other	No	Extinct	Schultz (2010)	Article
Ecology	Other	No	Introduced	Schuttler et al. (2008)	Article
Ecology	Other	No	Introduced	Schuttler et al. (2010)	Article
Ecology	Other	No	Introduced	Schuttler et al. (2018)	Article
Ecology	Other	No	Introduced	Scofield and Reyes-Arriagada (2013)	Article
Ecology	Other	No	Native	Sears et al. (2003)	Article
Physiology	Other	No	Native	Segade (2003)	Article
Physiology	Muskrat	No	Introduced	Sergina et al. (2015)	Article
Ecology	Muskrat	No	Native	Shier and Boyce (2009)	Article
Ecology	Muskrat	No	Native	Sietman et al. (2003)	Article
Ecology	Other	No	Introduced	Silva and Saavedra (2008)	Article
Ecology	Other	No	Introduced	Simberloff (2009)	Article
Disease	Other	No	Introduced	Simpson et al. (2008)	Article
Management	Other	No	Introduced	Singleton et al. (2007)	Article
Ecology	Other	No	Introduced	Singleton et al. (2008)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Other	No	Native	Sinkins (2008)	Thesis
Management	Muskrat	No	Native	Skinner and Skinner (2008)	Article
Ecology	Muskrat	No	Introduced	Skyriene and Paulauskas (2012)	Article
Management	Muskrat	No	Native	Sleeman et al. (1997)	Article
Ecology	Muskrat	No	Introduced	Smirnov and Tretyakov (1998)	Article
Disease	Other	No	Native	Smith and Frenkel (1995)	Article
Physiology	Other	No	Introduced	Spataru et al. (2013)	Article
Management	Other	No	Native	Starking-Szymanski et al. (2018)	Article
Ecology	Other	No	Native	Stoffyn-Egli and Willison (2111)	Article
Physiology	Muskrat	No	Native	Streeby and McKean (1994)	Article
Physiology	Other	No	Native	Sulaiman et al. (2003a)	Article
Physiology	Other	No	Native	Sulaiman et al. (2003b)	Article
Ecology	Other	No	Native	Sundaram et al. (2013)	Article
Ecology	Other	No	Native	Swanson and Johnson (1999)	Article
Ecology	Other	No	Native	Swarth et al. (2013)	Article
Management	Other	No	Native	Takacs et al. (2001)	Article
Ecology	Other	No	Native	Tapisso et al. (2013)	Article
Physiology	Muskrat	No	Native	Tasikas et al. (2009)	Article
Ecology	Other	No	Native	Taylor et al. (2009)	Article
Ecology	Other	No	Native	Timoney et al. (1997)	Article
Ecology	Muskrat	EE	Native	Toner et al. (2010)	Article
Ecology	Other	No	Introduced	Tornberg and Haapala (2013)	Article
Disease	Muskrat	No	Introduced	Tsoi et al. (2008)	Article
Management	Muskrat	No*	Native	Turner et al. (2018)	Article
Management	Muskrat	No	Introduced	Tuytens and Stuyck (2002)	Article
Ecology	Other	No	Native	Tyndall (2011)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Ecology	Muskrat	No	Native	Tyrrell and Hornbach (1998)	Article
Disease	Muskrat	No	Introduced	Umhang et al. (2013)	Article
Ecology	Other	No	Introduced	Valenzuela et al. (2013)	Article
Ecology	Other	No	Introduced	Valenzuela et al. (2014)	Article
Ecology	Other	No	Native	Van Den Wyngaert and Bobbink (2009)	Chapter
Ecology	Other	No	Native	Van der Valk and Davis (1978)	Article
Ecology	Other	No	Introduced	Van Erp et al. (2018)	Chapter
Management	Muskrat	No	Introduced	Van Loon et al. (2017)	Article
Ecology	Other	No	Introduced	Vermaat et al. (2016)	Article
Ecology	Other	No	Introduced	Vila et al. (2010)	Article
Ecology	Muskrat	No	Native	Viljugrein et al. (2001)	Article
Ecology	Muskrat	No	Native	Virgl and Messier (1997)	Article
Ecology	Muskrat	No	Native	Virgl and Messier (2000)	Article
Ecology	Other	No	Native	Visser et al. (2006)	Article
Ecology	Other	No	Native	Voslamber and Vulink (2010)	Article
Ecology	Muskrat	No	Native	Wainscott et al. (1990)	Article
Ecology	Muskrat	No	Native	Ward and Gorelick (2018)	Article
Disease	Muskrat	No	Native	Webb and Woods (2001)	Article
Management	Muskrat	No	Native	Wesson (1977)	Article
Ecology	Other	No	Native	Whigham et al. (2009)	Chapter
Ecology	Other	No	Native	Whyte et al. (2008)	Article
Disease	Other	No	Native	Wilkes et al. (2013)	Article
Ecology	Muskrat	No	Native	Williamson and Clark (2011)	Article
Management	Muskrat	No	Native	Wlosinski and Wlosinski (1998)	Report
Disease	Other	No	Native	Wobeser et al. (2009)	Article
Management	Other	No	Native	Wywialowski (1999)	Article
Continued on next page...					

Table A.1 – Continued from previous page

Context	Focus	EE or KS	Status	Authors	Type
Physiology	Muskrat	No	Native	Xie et al. (2019)	Article
Management	Other	No	Introduced	Xu et al. (2006)	Article
Ecology	Muskrat	No	Native	Yao et al. (2000)	Article
Ecology	Muskrat	No	Introduced	Zachos et al. (2007)	Article
Ecology	Other	No	Native	Zadnik et al. (2009)	Article
Ecology	Other	No	Introduced	Zalewski and Bartoszewicz (2012)	Article
Ecology	Other	No	Introduced	Zalewski et al. (2111)	Article
Ecology	Muskrat	No	Native	Zhang et al. (2003)	Article
Physiology	Muskrat	No	Captive	Zhang et al. (2016)	Article
Physiology	Muskrat	No	Captive	Zhang et al. (2016b)	Article
Physiology	Muskrat	No	Captive	Zhang et al. (2017a)	Article
Physiology	Muskrat	No	Captive	Zhang et al. (2017b)	Article
Physiology	Muskrat	No	Captive	Zhang et al. (2017c)	Article
Physiology	Muskrat	No	Native	Zhao et al. (2018)	Article
Disease	Other	No	Native	Zhou et al. (2004)	Article
Physiology	Other	No	Native	Zuercher et al. (1999)	Article

Appendix B

Supplementary Material for Chapter 2

Table B.1: Complete model set for muskrat and mink occupancy and detection

The complete model set for single-season models for detection and wetland occupancy probabilities of muskrats (<i>Ondatra zibethicus</i>) and American mink (<i>Neogale vison</i>) in Kansas, USA, from 2019–2020. ΔAICc (Akaike’s information criterion corrected for small sample sizes) = difference between the model of interest and the model with the lowest AICc value, w = model weight, $-2l = -2(\text{Log likelihood})$, and K = number of parameters in each model. Detection covariates included ‘Observer’ (three covariates, one for each observer compared to a baseline observer), ‘Date’ (day of year, out of 365), ‘Year’ (2019 and 2020), and ‘Precipitation’ (total amount of rain [cm] seven days prior to survey). Occupancy covariates included ‘SHDI’ (Shannon diversity index of wetland plants), ‘Size’ (PCA for wetland surface area and depth), ‘Wood’ (percent cover of woody vegetation), ‘Watershed’ (area of wetland-specific watershed [ha]), ‘Distance’ (distance to nearest permanent waterbody [m]), ‘Agriculture’ (proportion of row-crop agriculture landcover within a 5 km circular buffer), ‘Prairie’ (proportion of tallgrass prairie within a 5 km circular buffer), and ‘Forest’ (proportion of forest landcover within a 5 km circular buffer).						
Species	Type	Model	ΔAICc	w	-2l	K
Muskrat	Detection	Observer + Date*	0.00	0.24	345.30	6
		Observer + Date + Year	0.89	0.16	344.19	7
		Observer + Date + Precipitation	1.00	0.15	344.30	7
		Observer	1.39	0.12	348.69	5
		Observer + Date + Year + Precipitation	1.73	0.10	343.03	8
		Observer + Precipitation	2.04	0.09	347.34	6
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		Observer + Year	3.07	0.05	348.37	6
		Observer + Precipitation + Year	3.58	0.04	346.88	7
		Date	5.28	0.02	356.58	3
		Date + Precipitation	6.29	0.01	355.59	4
		Date + Year	7.28	0.01	356.58	4
		Date + Precipitation + Year	8.28	0.00	355.58	5
		Null	8.68	0.00	361.98	2
		Year	8.82	0.00	360.12	3
		Precipitation	8.91	0.00	360.21	3
		Precipitaition + Year	9.49	0.00	358.79	4
Muskrat	Occupancy	SHDI + Size + Watershed	0.00	0.24	306.21	9
		SHDI + Size + Watershed + Distance	1.05	0.14	305.26	10
		SHDI + Size + Watershed + Agriculture	1.40	0.12	305.61	10
		SHDI + Size + Watershed + Prairie	1.74	0.10	305.95	10
		SHDI + Size + Watershed + Forest	1.85	0.09	306.06	10
		SHDI + Size	2.62	0.06	310.83	8
		SHDI + Size + Agriculture	3.13	0.04	309.34	9
		SHDI + Size + Distance	3.54	0.04	309.75	9
		SHDI + Size + Prairie	3.63	0.03	309.84	9
		SHDI + Size + Agriculture + Distance	4.30	0.02	308.51	10
		SHDI + Watershed	4.32	0.02	312.53	8
		SHDI + Size + Forest	4.44	0.02	310.65	9
		SHDI + Size + Distance + Prairie	4.60	0.02	308.81	10
		SHDI + Size + Agriculture + Forest	5.05	0.02	309.26	10
		SHDI + Watershed + Distance	6.74	0.01	310.95	10
SHDI + Watershed + Distance + Agriculture	7.11	0.01	311.32	10		
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		SHDI + Watershed + Distance + Prairie	7.27	0.01	311.48	10
		SHDI + Watershed + Forest + Prairie	7.47	0.01	311.68	10
		SHDI + Watershed + Forest + Agriculture	7.50	0.01	311.71	10
		SHDI	11.09	0.00	321.30	7
		SHDI + Forest	11.69	0.00	319.90	8
		SHDI + Distance	11.72	0.00	319.93	8
		SHDI + Agriculture	11.97	0.00	320.18	8
		SHDI + Forest + Distance	12.75	0.00	318.96	9
		SHDI + Prairie	12.82	0.00	321.03	8
		SHDI + Distance + Agriculture	12.86	0.00	319.07	9
		SHDI + Forest + Agriculture	13.43	0.00	319.64	9
		SHDI + Distance + Prairie	13.49	0.00	319.70	9
		SHDI + Forest + Prairie	13.62	0.00	319.83	9
		SHDI + Forest + Distance + Agriculture	14.51	0.00	318.72	10
		SHDI + Forest + Distance + Prairie	14.68	0.00	318.89	10
		Size + Watershed	19.05	0.00	327.26	8
		Size + Watershed + Forest	19.81	0.00	326.02	9
		Size + Watershed + Agriculture	20.25	0.00	326.46	9
		Size + Watershed + Distance	20.35	0.00	326.56	9
		Size + Watershed + Prairie	21.03	0.00	327.24	9
		Size + Watershed + Forest + Distance	21.34	0.00	325.55	10
		Size + Watershed + Forest + Agriculture	21.68	0.00	325.89	10
		Size + Watershed + Agriculture + Distance	21.68	0.00	325.89	10
		Size + Watershed + Forest + Prairie	21.81	0.00	326.02	10
		Size + Watershed + Distance + Prairie	22.32	0.00	326.53	10
		Size	22.59	0.00	332.80	7
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		Size + Agriculture	22.70	0.00	330.91	8
		Watershed + Forest	23.36	0.00	331.57	8
		Size + Forest	23.50	0.00	331.71	8
		Size + Distance	23.90	0.00	332.11	8
		Watershed	23.92	0.00	334.13	7
		Size + Prairie	24.08	0.00	332.29	8
		Size + Agriculture + Distance	24.18	0.00	330.39	9
		Size + Agriculture + Forest	24.55	0.00	330.76	9
		Watershed + Forest + Distance	24.93	0.00	331.14	9
		Watershed + Forest + Prairie	25.04	0.00	331.25	9
		Watershed + Distance	25.15	0.00	333.36	8
		Size + Forest + Prairie	25.19	0.00	331.40	9
		Watershed + Forest + Agriculture	25.31	0.00	331.52	9
		Size + Distance + Prairie	25.36	0.00	331.57	9
		Watershed + Agriculture	25.53	0.00	333.74	8
		Watershed + Prairie	25.81	0.00	334.02	8
		Size + Forest + Distance	25.90	0.00	332.11	9
		Size + Agriculture + Forest + Distance	26.09	0.00	330.30	10
		Watershed + Forest + Distance + Prairie	26.61	0.00	330.82	10
		Size + Forest + Distance + Prairie	26.69	0.00	330.90	10
		Watershed + Distance + Agriculture	26.86	0.00	333.07	9
		Watershed + Forest + Distance + Agriculture	26.86	0.00	333.07	10
		Watershed + Distance + Prairie	27.04	0.00	333.25	9
		Forest	32.16	0.00	342.37	7
		Null	33.09	0.00	345.30	6
		Agriculture	33.59	0.00	343.80	7
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		Forest + Distance	33.77	0.00	341.98	8
		Forest + Agriculture	34.00	0.00	342.21	8
		Forest + Prairie	34.16	0.00	342.37	8
		Distance	34.32	0.00	344.53	7
		Agriculture + Distance	34.98	0.00	343.19	8
		Prairie	35.01	0.00	345.22	7
		Forest + Distance + Agriculture	35.61	0.00	341.82	9
		Forest + Distance + Prairie	35.77	0.00	341.98	9
		Distance + Prairie	36.22	0.00	344.43	8
Mink	Detection	Precipitation + Date	0.00	0.59	505.25	4
		Precipitation + Date + Year	1.29	0.31	504.54	5
		Precipitation + Date + Observer	4.36	0.07	503.61	7
		Precipitation + Date + Year + Observer	5.91	0.03	503.16	8
		Precipitation + Year	13.43	0.00	518.68	4
		Precipitation	14.45	0.00	521.70	3
		Precipitation + Observer	15.22	0.00	516.47	6
		Precipitation + Year + Observer	17.22	0.00	516.47	7
		Date + Year	37.49	0.00	542.74	4
		Date	37.85	0.00	545.10	3
		Date + Observer	40.87	0.00	542.12	6
		Date + Year + Observer	42.34	0.00	541.59	7
		Year	71.55	0.00	578.80	3
		Observer	74.03	0.00	577.28	5
		Year + Observer	75.67	0.00	576.92	6
		Null	80.36	0.00	589.61	2
Mink	Occupancy	Distance + Forest + Prairie	0.00	0.10	495.13	7
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAIC_c	w	-2l	K
		Distance + Forest + Prairie + Wood	0.43	0.08	493.56	8
		Distance + Forest + Prairie + SHDI	1.68	0.04	494.81	8
		Distance + Forest + Prairie + Size	1.99	0.04	495.12	8
		Distance + Forest + Wood	2.08	0.04	497.21	7
		Distance + Forest	2.08	0.04	499.21	6
		Wood + Forest + Prairie	2.13	0.04	497.26	7
		Forest + Prairie	2.25	0.03	499.38	6
		Distance + Prairie	3.16	0.02	500.29	6
		Wood + Forest	3.20	0.02	500.33	6
		Distance + Prairie + Wood	3.42	0.02	498.55	7
		Distance + Forest + Agriculture	3.45	0.02	498.58	7
		Distance + Wood	3.54	0.02	500.67	6
		Distance	3.57	0.02	502.70	5
		Wood	3.58	0.02	502.71	5
		Wood + Prairie	3.60	0.02	500.73	6
		Distance + Forest + Wood + Agriculture	3.61	0.02	496.74	8
		Forest	3.77	0.02	502.90	5
		Distance + Forest + SHDI	3.80	0.02	498.93	7
		Prairie	3.83	0.02	502.96	5
		Distance + Forest + Size	3.91	0.01	499.04	7
		Distance + Forest + Wood + SHDI	3.98	0.01	497.11	8
		Forest + Prairie + SHDI	4.07	0.01	499.20	7
		Distance + Forest + Wood + Size	4.07	0.01	497.20	8
		Wood + Forest + Prairie + SHDI	4.07	0.01	497.20	8
		Wood + Forest + Prairie + Size	4.07	0.01	497.20	8
		Null	4.12	0.01	505.25	4
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		Forest + Prairie + Size	4.24	0.01	499.37	7
		Distance + Prairie + Size	4.77	0.01	499.90	7
		Wood + Forest + Agriculture	4.81	0.01	499.94	7
		Distance + Size	4.98	0.01	502.11	6
		Distance + Prairie + SHDI	5.00	0.01	500.13	7
		Wood + Forest + SHDI	5.17	0.01	500.30	7
		Distance + Forest + Agriculture + SHDI	5.18	0.01	498.31	8
		Wood + Forest + Size	5.20	0.01	500.33	7
		Forest + Agriculture	5.21	0.01	502.34	6
		Distance + Prairie + Wood + Size	5.32	0.01	498.45	8
		Distance + Wood + Size	5.34	0.01	500.47	7
		Distance + Prairie + Wood + SHDI	5.37	0.01	498.50	8
		Distance + Forest + Agriculture + Size	5.37	0.01	498.50	8
		Distance + SHDI	5.43	0.01	502.56	6
		Distance + Wood + Agriculture	5.44	0.01	500.57	7
		Wood + Size	5.48	0.01	502.61	6
		Distance + Wood + SHDI	5.50	0.01	500.63	7
		Distance + Agriculture	5.52	0.01	502.65	6
		Prairie + Size	5.53	0.01	502.66	6
		Wood + Agriculture	5.54	0.01	502.67	6
		Wood + Prairie + Size	5.56	0.01	500.69	7
		Wood + SHDI	5.57	0.01	502.70	6
		Wood + Prairie + SHDI	5.58	0.01	500.71	7
		Forest + Size	5.62	0.01	502.75	6
		Forest + SHDI	5.62	0.01	502.75	6
		Size	5.66	0.01	504.79	5
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAIC_c	w	-2l	K
		Distance + Forest + SHDI + Size	5.66	0.01	498.79	8
		Prairie + SHDI	5.74	0.01	502.87	6
		SHDI	6.05	0.01	505.18	5
		Forest + Prairie + SHDI + Size	6.06	0.01	499.19	8
		Agriculture	6.11	0.00	505.24	5
		Distance + Prairie + Size + SHDI	6.65	0.00	499.78	8
		Wood + Forest + Agriculture + SHDI	6.77	0.00	488.90	8
		Wood + Forest + Agriculture + Size	6.81	0.00	499.94	8
		Distance + Size + SHDI	6.87	0.00	502.00	7
		Distance + Size + Agriculture	6.91	0.00	502.04	7
		Forest + Agriculture + SHDI	7.05	0.00	502.18	7
		Forest + Agriculture + Size	7.14	0.00	502.27	7
		Wood + Forest + SHDI + Size	7.17	0.00	500.30	8
		Distance + Wood + Size + Agriculture	7.23	0.00	500.36	8
		Distance + Wood + Size + SHDI	7.31	0.00	500.44	8
		Distance + SHDI + Agriculture	7.37	0.00	502.50	7
		Distance + Wood + Agriculture + SHDI	7.40	0.00	500.53	8
		Wood + Size + Agriculture	7.43	0.00	502.56	7
		Wood + Size + SHDI	7.47	0.00	502.60	7
		Prairie + Size + SHDI	7.47	0.00	502.60	7
		Forest + SHDI + Size	7.50	0.00	502.63	7
		Wood + Agriculture + SHDI	7.53	0.00	502.66	7
		Wood + Prairie + Size + SHDI	7.55	0.00	500.68	8
		Size + SHDI	7.61	0.00	504.74	6
		Size + Agriculture	7.64	0.00	504.77	6
		SHDI + Agriculture	8.04	0.00	505.17	6
Continued on next page...						

Table B.1 – Continued from previous page

Species	Type	Model	ΔAICc	w	-2l	K
		Distance + Size + SHDI + Agriculture	8.80	0.00	501.93	8
		Forest + Agriculture + SHDI + Size	9.00	0.00	502.13	8
		Wood + Size + Agriculture + SHDI	9.43	0.00	502.56	8
		Size + SHDI + Agriculture	9.59	0.00	504.72	7