

SEASONAL MOVEMENT, SPACE USE, AND MORTALITY OF GRAY WOLVES, MOOSE,
AND WHITE-TAILED DEER IN NORTHEASTERN MINNESOTA

By

Nathaniel H. Wehr

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife – Doctor of Philosophy

2023

ABSTRACT

Background

The Anishinaabe people of the Grand Portage Band of Lake Superior Chippewa manage for subsistence moose (mooz; *Alces alces*) and white-tailed deer (waawaashkeshi; *Odocoileus virginianus*) harvests and conservation of gray wolves (ma'iingan; *Canis lupus*) within the 1854 Ceded Territory in northeastern Minnesota, USA. Prey, such as moose and deer, vulnerability varies seasonally. Predators, such as wolves, may respond to increased prey vulnerability by shifting their space use to match prey via migratory coupling and ecological seasonality.

Methods

We assessed seasonal space use of gray wolves, moose, and white-tailed deer as well as seasonal mortality of moose and deer on and around GPIR. We analyzed GPS collar data collected by the Grand Portage Band and the National Park Service during 2008–2022. We used Brownian bridge movement models in Migration Mapper to estimate individual- and population-level occurrence distributions and determine the status and timing of range shifts; we estimated the proportion of wolf utilization distributions overlapping moose and deer occurrence distributions. We used cluster and principal component analyses to estimate timing and drivers of seasonal changes in space use among populations, and we used weighted autocorrelated kernel density estimation for weighted resource selection functions to assess seasonal habitat selection for each population. Finally, we estimated mortality timing using time-to-event models informed by weather data and population-level species space use.

Results

Our analyses identified a single migration corridor through which white-tailed deer synchronously departed GPIR. Gray wolf utilization distributions overlapped the deer migration corridor similarly across seasons, but wolves altered within-range space use seasonally in response to prey distributions. Seasonal space use shifts by wolves resulted in greater overlap with deer during fall migration and greater overlap with moose during summer. Space use shifts followed a two-season pattern with transitions between seasons coinciding with changing weather and deer migration. Moose mortality peaked during pre-parturition transitions between seasons and during the summer–winter transition. Deer mortality peaked during spring migration in late winter and during fall migration in late summer.

Conclusions

Gray wolves did not increase their use of the white-tailed deer migration corridor but shifted spatially within their territories in response to seasonal variations in prey distributions. Seasonal space use among all populations was likely due to deer migration. Our findings suggest ecological seasonality of predators is linked to prey via seasonal space use dynamics but was not associated with parturition. Our results indicate mortality timing coincided with transitions between seasonal space use states suggesting ungulates are at greater mortality risk during these periods. Our results can be used to improve management including sampling schedules, population modeling, and harvest regulations on GPIR under Anishinaabe principles of seventh-generation conservation.

To my wife, who put her dreams on hold while I chased mine.
To my family, who loved unconditionally and instilled my persistence.
To God, whose countenance and mercy guided each step of my journey.

ACKNOWLEDGEMENTS

The presented work was developed collaboratively, and I am extremely grateful to each person who contributed. Firstly, I thank my advisor, Dr. Jerry Belant, who provided the opportunity to pursue my degree and has facilitated my continued success and development as an academician; his extensive and immediate support regarding project development, writing critiques, and professional guidance were invaluable to the completion of my dissertation. Second, I thank the Grand Portage Band of Lake Superior Chippewa and their biologists, Dr. Seth Moore and E.J. Isaac, who went out of their way to include me in their community and provide the necessary logistical support to facilitate diverse field skill development and the completion of these manuscripts. Third, I thank Dr. Ken Kellner who provided consistent and thorough feedback on my statistical analyses and whose expertise and patience when teaching statistics and programing were vital to the completion of my work. Finally, I thank Dr. Todd Kautz, Dr. Josh Millspaugh, and Mark Romanski for their respective contributions to my work including many helpful conversations on mammal ecology and the analysis thereof.

I am also grateful to the numerous people who supported this work behind the scenes. I thank Roger “Poe” Deschampe for his willingness to answer any question and his guidance on Indigenous natural resource management. I thank Dr. Scott Winterstein for serving on my dissertation committee. I thank Jacob Bonessi, Yvette Chenaux-Ibrahim, Dr. Beth Orning, and Lynette Potvin for assistance with data collection and curation. I thank my fellow Belant Lab members including Hailey Boone, Nick Fowler, Joe Goergen, Dan Li, Ashley Lutto, Merijn van den Bosch, and Ale Zubiria Perez for their friendship and guidance in all things science. I also thank the members of my foster lab at the State University of New York College of Environmental Science and Forestry including but not limited to Dr. Elie Gurarie, Chloe

Beaupré, Mel Berger, Dr. Ophélie Couriot, Dr. Stephanie Cunningham, Katya Khadonova, Megan Perra, and Georgi Silveira for their friendship and support.

This research was made possible by cooperation among individuals from Michigan State University, State University of New York College of Environmental Science and Forestry, Grand Portage Band of Lake Superior Chippewa, National Park Service, and many other agencies, and while I cannot include all their names here, I thank them for their efforts supporting these projects and for the positive interactions with which I was consistently blessed. Financial support for this dissertation and its associated endeavors was provided by the Boone and Crockett Program in Wildlife Conservation at Michigan State University, Camp Fire Conservation Fund, Edna Bailey Sussman Fund, Grand Portage Band of Lake Superior Chippewa, Isle Royale National Park, Michigan Technological University, Moore Family Fund for Wildlife Conservation, National Parks of Lake Superior Foundation, State University of New York College of Environmental Science and Forestry, and The Wildlife Society.

TABLE OF CONTENTS

RECOGNIZING PLACE.....	1
INTRODUCTION	3
CHAPTER 1: SPATIAL OVERLAP OF GRAY WOLVES AND UNGULATE PREY CHANGES SEASONALLY CORRESPONDING TO PREY MIGRATION	7
CHAPTER 2: GRAY WOLVES ALTER SPACE USE SEASONALLY IN RESPONSE TO MIGRATORY PREY	35
CHAPTER 3: MOOSE AND WHITE-TAILED DEER MORTALITY PEAKS IN FALL AND LATE WINTER.....	62
BIBLIOGRAPHY.....	86
APPENDIX A: CHAPTER 1 SUPPLEMENTARY MATERIALS	104
APPENDIX B: CHAPTER 3 SUPPLEMENTARY MATERIALS.....	116

RECOGNIZING PLACE

We conducted these studies in and around Gichi Onigaming (the great carrying place) on the ancestral and present homelands of the Anishinaabeg (the people). Also known as the Grand Portage Indian Reservation (GPIR), Minnesota, USA, Gichi Onigaming is the present home of the Grand Portage Band of Lake Superior Chippewa, a federally recognized sovereign nation within the United States. In 1854, the Lake Superior Chippewa signed a treaty ceding lands in northeastern Minnesota to the United States. Under the 1854 Treaty, members of the Grand Portage, Fond du Lac, and Bois Forte bands of Lake Superior Chippewa can exercise their usufructuary rights to hunt, fish, and gather throughout the 1854 Ceded Territory which spans northeastern Minnesota from Grand Portage to Moose Lake to Crane Lake (Thompson 2020; 1854 Treaty Authority 2023). These practices cannot be regulated by Minnesota state law, but may be governed by United States federal law, such as the Endangered Species Act. Within Gichi Onigaming, resource harvest (e.g., wild fish and game, timber, and manoomin [wild rice; *Zizania palustris*]) is managed by the elected Tribal Council of the Grand Portage Band. Recently, Minong (the good place), also known as Isle Royale National Park, Michigan, USA, was recognized as a Traditional Cultural Property of the Grand Portage Band (National Park Service 2022). The Chapter 2 study area was expanded to include Minong.

Our research emphasized three culturally important species to Anishinaabe seventh-generation environmental stewardship: mooz (moose; *Alces alces*), waawaashkeshi (white-tailed deer; *Odocoileus virginianus*), and ma'iingan (gray wolf; *Canis lupus*). Mooz populations in northeastern Minnesota are declining (Severud et al. 2022). These declines are concerning because mooz remain a primary subsistence species for the Anishinaabe people. Waawaashkeshi are also an important subsistence species for the Anishinaabe people. Waawaashkeshi

populations are growing in northeastern Minnesota, but an increased presence of waawaashkeshi may negatively influence mooz populations (Oliveira-Santos et al. 2021; Severud et al. 2023). Ma'iingan are integral to the Anishinaabe creation story, which establishes ma'iingan as kin to Anishinaabe people (Gilbert et al. 2022). Gichi Onigaming is one of the only places in the conterminous United States where ma'iingan were never extirpated (Boitani 2003), and the Anishinaabe people were integral to the recent introduction of wolves to Minong (Romanski et al. 2020). Mooz and waawaashkeshi are primary prey of ma'iingan in Gichi Onigaming and Minong (Chenaux-Ibrahim 2015; Sovie et al. 2023). The Grand Portage Band conducts predator-prey research to improve their understanding of ecosystem health, which set the context for this dissertation.

INTRODUCTION

Observations of seasonally variable ecology predate formal scientific inquiry. Numerous modern examinations demonstrate this variability on large (e.g., wildebeest [*Connochaetes taurinus*] migrations [Hopcraft et al. 2014]) and small scales (e.g., roe deer [*Capreolus capreolus*] resource selection [Couriot et al. 2018]). Supported by these observations, ecological theory describes these patterns at broad scales. Migratory coupling describes the spatial adaptation of predators to seasonal availability of migratory prey as exhibited among grizzly bears (*Ursus arctos*) and cheetahs (*Acinonyx jubatus*) (Deacy et al. 2016; Furey et al. 2018; Broekhuis et al. 2021). Ecological seasonality describes seasons based on animal ecology influenced by community dynamics, such as seasonal responses of Hector's dolphins (*Cephalorhynchus hectori*) and lions (*Panthera leo*) to prey habitat selection (Bräger et al. 2003; Basille et al. 2013; Schooler et al. 2022). Mortality seasons describe reoccurring annual peaks in mortality as exhibited among caribou (*Rangifer tarandus*) and hen harriers (*Circus cyaneus*) (Gurarie et al. 2020; Kelly 2020; Ewing et al. 2023). Migratory coupling, ecological seasonality, and mortality seasons are based on more established ecological concepts such as game theory, encounter theory, leapfrog effect, and resource dispersion (Macdonald 1984; Sih 1998; Mitchell and Lima 2002; Gurarie and Ovaskainen 2013).

In this dissertation, we tested these newer ecological concepts (i.e., migratory coupling, ecological seasonality, mortality seasons) using gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) as a model predator-prey system. We used GPS collar data collected from these species on and around the Grand Portage Indian Reservation (GPIR), Minnesota, USA from 2008–2022 (Oliveira-Santos et al. 2021). Wolf management in this region has been dynamic, with historical overharvest leading to wolves being listed on the

Endangered Species Act (ESA) of 1973 and thereafter intermittently removed from and relisted under the ESA following population increases and controversial harvests (Erb et al. 2018; Gilbert et al. 2022). Regional moose populations have recently declined resulting in efforts to conserve and restore moose and their habitats (Severud et al. 2022). Comparatively, deer populations are increasing, but their expansion increases the risk of disease transmission to moose (Oliveira-Santos et al. 2021; Severud et al. 2023).

In Chapter 1, we examined migratory coupling of gray wolves to white-tailed deer using seasonal wolf, moose, and deer movements. We used Brownian bridge movement models in Migration Mapper to estimate individual- and population-level occurrence distributions and determine the status and timing of range shifts as corroborated by mechanistic range shift analyses (Nielson et al. 2013; Gurarie et al. 2017; Merkle et al. 2022; Michelot et al. 2023). We then estimated the proportion of wolf utilization distributions overlapping moose and deer occurrence distributions and tested for differences among seasons and populations. We identified a single migration corridor through which deer synchronously departed to (April) and returned from (October–November) their summer ranges. Though wolves did not increase their use of the deer migration corridor seasonally, they shifted spatially within their territories in response to seasonal variations in prey distributions. This pattern was exhibited by 1.8–2.1 times greater wolf overlap with deer in fall and 1.6–2.7 times greater wolf overlap with moose in summer. Potential drivers of these increases included summer moose calf vulnerability, summer co-occurrence with American beaver (*Castor canadensis*), and seasonal variation in deer abundance associated with migration.

In Chapter 2, we examined ecological seasonality of gray wolves, moose, and white-tailed deer by comparing seasonal space use between communities with and without deer by

using Isle Royale National Park (IRNP), Michigan, USA as a simplified system to compare against GPIR. We used cluster and principal component analyses (PCA) to estimate timing and drivers of seasonal space use states (Basille et al. 2013). We then used weighted autocorrelated kernel density estimation (wAKDE) for weighted resource selection functions (wRSFs) to assess habitat selection for each population within their respective seasonal space use states (Alston et al. 2022a). Mainland populations on and around GPIR generally exhibited two seasonal space use states with transitions between states coinciding with changing weather and white-tailed deer migration. Selection for landscape attributes varied among seasonal space use states for all mainland populations (e.g., increased use of south-facing slopes in winter). In contrast, island wolves and moose did not display seasonal space use states, and their resource selection differed from mainland populations. The occurrence and lack of seasonal space use states among mainland and island populations, respectively, was likely due to the migration of mainland deer. Our findings suggest ecological seasonality of predators is linked to prey via seasonal space use dynamics but was not associated with parturition.

In Chapter 3, we estimated mortality seasons of moose and white-tailed deer using time-to-event models informed by population-level space use metrics and weather data. Mean annual moose survival was 83.2% with mortality peaking during late winter (about 25 April) and during fall (about 8 October). In total, we recorded 42 moose mortalities including 17 health-related, 8 predation, 4 harvest, and 13 unknown. Mean annual deer survival was 48.0% with increased winter severity predicting decreased survival. Deer mortality peaked during late winter (about 25 March) and during fall (about 11 November). We recorded 49 total deer mortalities including 26 predation, 13 harvest, 4 other, and 6 unknown. Our results indicate mortality timing coincided with transitions between seasonal space use states suggesting ungulates are at greater mortality

risk during these periods. Our moose and deer survival estimates were similar to prior work and support recent population estimates suggesting regional moose population declines (Hauge and Keith 1981; Nelson and Mech 1986; Brinkman et al. 2004; Severud et al. 2022).

Wildlife biologists and managers require precise estimates of seasonal ecology including movement, space use, and mortality rates to effectively estimate and manage wildlife populations (Gurarie et al. 2020). Supporting these objectives, sampling schedules incorporating seasonal ecology can improve scientific insights and management applications (Basille et al. 2013). We demonstrated gray wolves responding to seasonal prey distributions in an area with white-tailed deer migration (Chapter 1). We furthered this observation by determining wolf and moose seasonal responses were altered in the presence of migratory deer (Chapter 2). Finally, we found that mortality of moose and deer coincided with transitions between these seasonal space use states (Chapter 3). Collectively, these results support the use of species-defined sampling schedules in ecological research. For example, if surveys of predation pressure (Chapter 1), habitat suitability (Chapter 2), or survival (Chapter 3) were scheduled during periods of relative ecological stability, researchers could minimize the interannual variability in their estimates. Additionally, our results provide insights into ecological theory that may be used in the continued scientific understanding of predator-prey interactions in natural settings. Specifically, we suggest migratory coupling may only be possible among non-territorial predators (Chapter 1), ecological seasonality appears in part dependent on predator-prey community dynamics (Chapter 2), and seasonal mortality is likely directly related to ecological seasonality (Chapter 3).

CHAPTER 1:

SPATIAL OVERLAP OF GRAY WOLVES AND UNGULATE PREY CHANGES

SEASONALLY CORRESPONDING TO PREY MIGRATION

Abstract

Background

Prey are often more vulnerable during migration due to decreased familiarity with their surroundings and spatially concentrated movements. Predators may respond to increased prey vulnerability by shifting their ranges to match prey via migratory coupling. Moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) are primary prey of gray wolves (*Canis lupus*) and important subsistence species for Indigenous communities. We hypothesized wolves would increase use of ungulate migration corridors during migrations, and we predicted wolf distributions would overlap with primary available prey.

Methods

We examined seasonal movements of gray wolves, moose, and white-tailed deer on and near the Grand Portage Indian Reservation, Minnesota, USA. We analyzed GPS collar data during 2012–2021 using Brownian bridge movement models in Migration Mapper and mechanistic range shift analysis to estimate individual- and population-level occurrence distributions and determine the status and timing of range shifts. We estimated the proportion of wolf utilization distributions overlapping moose and deer occurrence distributions and tested for differences among seasons and populations.

Results

We identified a single migration corridor through which white-tailed deer synchronously departed their winter ranges in April and asynchronously returned from their summer ranges in

October–November. Gray wolf utilization distributions overlapped the deer migration corridor similarly across seasons, but wolves altered within-range distributions seasonally corresponding to prey distributions. Seasonal spatial shifts by wolves resulted in 1.8–2.1 times greater overlap with deer during fall migration (10 October–28 November) and 1.6–2.7 times greater overlap with moose during summer (3 May–9 October).

Conclusions

Gray wolves did not increase their use of the white-tailed deer migration corridor but shifted spatially within their territories in response to seasonal prey distributions. Greater overlap of wolves and deer in fall may be due to greater predation success facilitated by asynchronous deer movements during migration. Greater summer overlap between wolves and moose may be linked to moose calf vulnerability, co-occurrence with American beaver (*Castor canadensis*), and reduced deer abundance associated with seasonal migration. Our results suggest potential increases in predation pressure on deer in fall and moose in summer, which can be used to inform Indigenous conservation efforts. We observed seasonal plasticity of wolf spatial distributions suggestive of prey switching; that wolves did not exhibit migratory coupling was likely due to spatial constraints resulting from wolf territoriality.

Background

Recognizing place

The Grand Portage Band of Lake Superior Chippewa is a federally recognized sovereign nation of Anishinaabe people with jurisdiction over the Grand Portage Indian Reservation (Gichi Onigaming), Minnesota, USA. The Grand Portage Band exercises its usufructuary rights to food sovereignty through subsistence hunting, fishing, and gathering throughout the 1854 Ceded Territory (Thompson 2020). Moose (mooz; *Alces alces*) and white-tailed deer (waawaashkeshi:

Odocoileus virginianus) are primary subsistence species of Anishinaabe people. Gray wolves (ma'iingan; *Canis lupus*) are culturally and environmentally important to their seventh-generation planning philosophy of environmental stewardship (Grand Portage Band of Lake Superior Chippewa 2023). The Grand Portage Band conducts predator-prey research to improve their understanding of ecosystem health, which set the context for this study.

Migratory coupling

A primary assumption of predator-prey movement modeling is that predators have good spatial memories, otherwise prey could remain in high quality patches indefinitely because predators would not concentrate space use in these areas (Sih 1998; Mitchell and Lima 2002). Prey are therefore less likely to be depredated if their movements among resource patches are unpredictable (Mitchell and Lima 2002). However, seasonal migrations can reduce variation in inter-individual movements, resulting in predictable population-level responses (Grigg 2007; White et al. 2010; Sawyer et al. 2019). When seasonal second-order habitat selection (i.e., home range selection [Johnson 1980]) by predators matches these predictable prey movements, migratory coupling occurs (Furey et al. 2018). Predator home range shifts considered migratory coupling can vary from fine-scale shifts (e.g., seasonal use of migratory bottlenecks or feeding grounds) to complete migration by predators to follow prey (Furey et al. 2018). These shifts generally lead to increased predation risk among migrating prey (Furey et al. 2018).

Evolutionarily, prey should not migrate if the costs outweigh the benefits (Avgar et al. 2014). Two primary benefits of migration are increased forage opportunities and decreased seasonal predation risk (Fryxell and Sinclair 1988; Bergerud et al. 1990; Hebblewhite and Merrill 2009; Avgar et al. 2014). Migrating to match available forage is common across taxa (Avgar et al. 2014); olive ridley sea turtles (*Lepidochelys olivacea*) (Whiting et al. 2007), water

pythons (*Liasis fuscus*) (Madsen and Shine 1996), common eiders (*Somateria mollissima*) (Guillemette 2001), and bats (order Chiroptera) (Ahlén et al. 2009) demonstrate migratory behavior for foraging. Though more difficult to identify, migrating to reduce seasonal predation risk also occurs across taxa (e.g., common roach fish [*Rutilus rutilus*] [Brönmark et al. 2008], baleen whales [parvorder Mysticeti] [Corkeron and Connor 1999], and bighorn sheep [*Ovis canadensis*] [Festa-Bianchet 1988]) (Avgar et al. 2014).

Despite the benefits, migration often increases predation risk for prey. Juvenile sockeye salmon (*Onorhynchus nerka*) exhibited poor survival during migration (< 70%) despite rapid downstream movements that overwhelmed predators (Furey et al. 2016). Predation risk of migrating wildebeest (*Connochaetes taurinus*) increased during migration due to foregoing predator avoidance in favor of high quality forage (Hopcraft et al. 2014), and pronghorn (*Antilocapra americana*) experienced increased predation risk from mountain lions (*Puma concolor*) when migrating through typically unused and narrow forest corridors (Barnowe-Meyer et al. 2009). Prey communities must respond to tradeoffs between predation risk and improved forage access to maintain the benefits of migration (Avgar et al. 2014).

Gray wolves are obligate carnivores (Newsome et al. 2016; Middleton et al. 2021) whose space use can alter predation risk and increase mortality of migrating prey. Caribou (*Rangifer tarandus*) predation by wolves in Finland increased during their migrations (Kojola et al. 2004). Migratory elk (*Cervus canadensis*) in Yellowstone National Park, USA decreased predation risk by migrating but were about 1.7 times more likely to be depredated during migration, and 63% of migratory elk deaths occurred during or immediately before or after migration (Hebblewhite 2006; Hebblewhite and Merrill 2007). Non-territorial wolves in tundra ecosystems exhibited migratory coupling by following caribou populations during their seasonal migrations (Walton et

al. 2001; Musiani et al. 2007; Michelot et al. 2023). Wolves in boreal ecosystems maintain territories year-round (Mech and Boitani 2003; Musiani et al. 2007) but may alter second-order habitat selection in response to seasonal prey space use (Anderson 2014).

Despite predation risk generally increasing during migration in the presence of territorial predators (Kojola et al. 2004; Robinson et al. 2010; White et al. 2014), the spatial response of territorial predators to prey migration remains less understood (Furey et al. 2018). Ungulates (i.e., moose and white-tailed deer) are primary gray wolf prey (Newsome et al. 2016) and invaluable subsistence species for Indigenous peoples. The Grand Portage Band of Lake Superior Chippewa has been conducting predator-prey research toward effective stewardship of subsistence resources (Oliveira-Santos et al. 2021; Wolf et al. 2021; Van de Vuurst et al. 2022). We furthered this research by investigating the response of a territorial predator, wolves, to migration and seasonally shifting spatial distributions of prey. We hypothesized wolves would shift their ranges to increase use of ungulate migration corridors during migrations as predicted by migratory coupling (Furey et al. 2018). We predicted seasonal wolf movements would overlap with primary available ungulate prey.

Methods

Study area

The Grand Portage Indian Reservation is in northeastern Minnesota, USA (47.9614° N, 89.7594° W). The reservation borders Lake Superior to the southeast, Ontario, Canada to the north, and U.S. federal, state, and private properties to the west. Our approximately $1,200 \text{ km}^2$ study area included the reservation and mainland areas within 30 km (Figure 1.1). Elevations are 183–674 m above sea level with broad valleys between steep ridges (USGS 2020). The area contains 11% coniferous forest, 17% deciduous forest, 44% mixed forest, 9% shrubland, 7%

wetland, and 5% open water (CCRS et al. 2020). Temperatures within the study area (Cook County, Minnesota, USA) during 2009–2019 ranged from mean daily minima of -17.8 ± 3.5 C° (mean \pm SD) in January to mean daily maxima of 23.3 ± 1.7 C° in July; annual precipitation included 281.9 ± 11.7 cm of rainfall and 351.6 ± 80.8 cm of snowfall (NOAA 2022).

The primary prey of gray wolves in the western Great Lakes region are white-tailed deer, moose, and American beaver (*Castor canadensis*) (Vucetich et al. 2012; Chenaux-Ibrahim 2015). About 80–95% of the region’s deer migrate and exhibit winter and summer range fidelity (Nelson and Mech 1981; Mech and Barber-Meyer 2020). Moose in the region are semi-nomadic with about 20% migrating between summer and winter ranges while the remainder maintain a single year-round home range or shift among multiple ranges without clear patterns (Phillips et al. 1973). Wolves could be legally harvested in Ontario during the study period (OMNRF 2023), but legal harvest in Minnesota occurred only during 2012–2014 (Erb et al. 2018). Deer and moose could also be legally harvested, but after 2013, only Indigenous band members could harvest moose in Minnesota (1854 Treaty Authority 2023; MNDNR 2023a). Wolves were not harvested by Grand Portage Band members when legal.

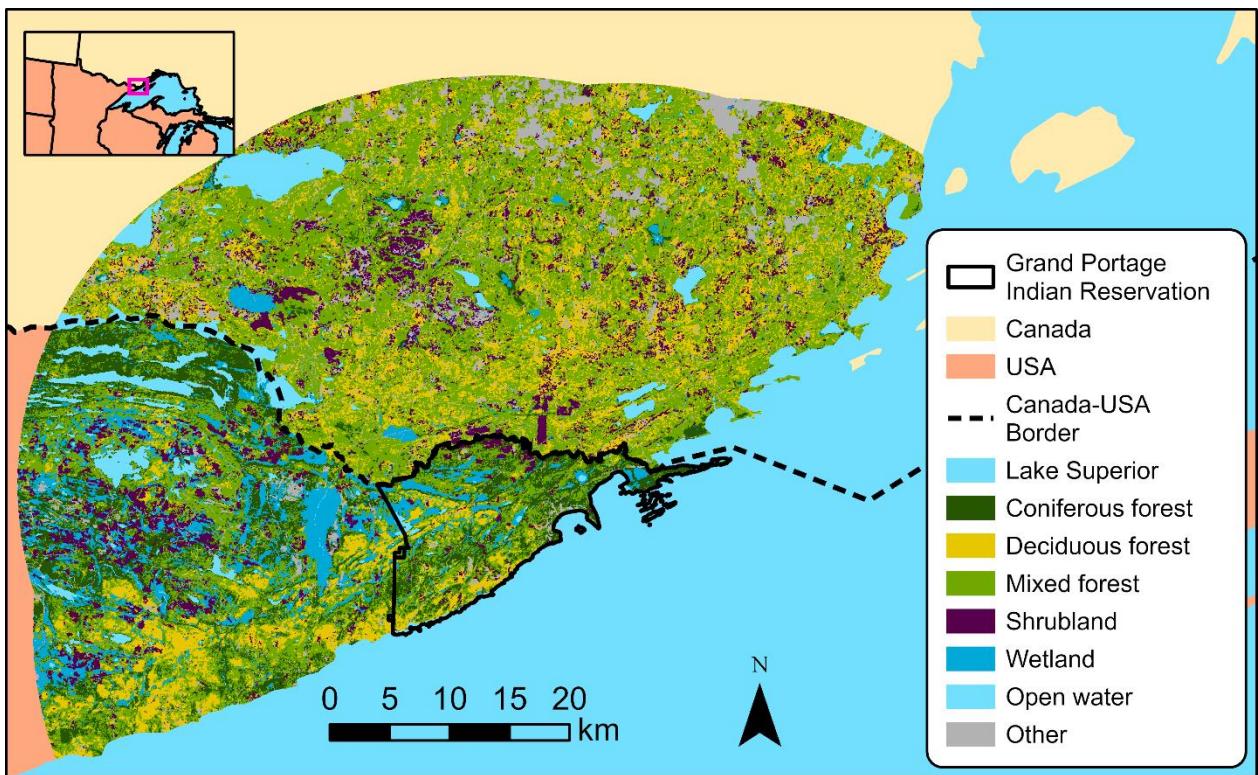


Figure 1.1. Study area on and near the Grand Portage Indian Reservation, Minnesota, USA and adjacent portions of Ontario, Canada. Land cover data is from the Commission for Environmental Cooperation 30-m land cover map of North America (CCRS et al. 2020).

Analytical approach

We tested our hypothesis that gray wolves would shift their ranges to increase use of migration corridors during migration and our prediction that wolves would concentrate movements on seasonally available prey in three stages. First, we determined home ranges, movement strategies, movement timing, seasonal population-level occurrence distributions, and locations of migration corridors using Brownian bridge movement models (BBMMs) in Migration Mapper (v3.0) (Merkle et al. 2022). Potential movement strategies included resident (single year-round home range), migratory (seasonally shifting between 2 or 3 home ranges), nomadic (shifting among ≥ 4 home ranges), or unknown (movement strategy could not be assessed). We recorded movement timing as the dates during which animals moved between seasonal home ranges. Population-level occurrence distributions are estimates of where a population is likely to be in a given time period based on individual-level occurrence distributions, but they do not represent home ranges (Alston et al. 2022b). Second, we reassessed whether wolves exhibited home range shifts and, if so, the timing and duration of those home range shifts using mechanistic range shift analysis (MRSA) to corroborate our Migration Mapper results (Gurarie et al. 2017). Third, we calculated individual-level utilization distributions (UDs) for wolves and overlap of these UDs with population-level occurrence distributions of prey and their migration corridors.

We used GPS location data from gray wolves, moose (each monitored October 2012–December 2021), and white-tailed deer (monitored March 2016–December 2021) collared during research conducted by the Grand Portage Band of Lake Superior Chippewa Department of Biology and Environment (Oliveira-Santos et al. 2021). Wolves were captured using foothold traps (Frame and Meier 2007), moose using aerial darting (Barros et al. 2018), and deer using

clover traps (VerCauteren et al. 1999). Capture and handling protocols were approved by the Grand Portage Band of Lake Superior Chippewa Tribal Council, Michigan State University institutional animal care and use committee (IACUC) (PROTO202200266), and State University of New York College of Environmental Science and Forestry IACUC (210702). Collar relocation data was obtained via satellite or, upon retrieval, downloaded from the collar. Minimum relocation intervals of wolf, moose, and deer collars were 3.25–4.5 h (depending on estimated collar longevity), 0.25–4 h (depending on time of year), and 4 h, respectively. We resampled moose locations to 4-h intervals using the R package *padr* (Theon 2022) to make them similar to wolf and deer relocation intervals. We excluded from analyses individuals that dispersed from the study area.

Migration Mapper

Migration Mapper is a software application that allows users to analyze GPS location data using six modules in a web browser interface while underlying calculations occur in the R statistical platform (Merkle et al. 2022; R Core Team 2023). We used Migration Mapper to determine home ranges, movement strategies, and timing as well as population-level occurrence distributions and migration corridors for gray wolves, moose, and white-tailed deer. We used default settings unless otherwise stated.

In Module 1, we censored aberrant locations from our dataset. Migration Mapper identified potentially aberrant locations using movement distances < 50 m in 48 hours as these locations were considered post-mortem. However, we retained these locations because we censored post-mortem locations before data were imported to Migration Mapper. We censored locations identified as aberrant due to movement speeds > 10.8 km/h between consecutive 4-h relocations as we considered these locations implausible. We manually inspected remaining

locations using first passage time (i.e., the time an animal requires to cross a circle of defined radius, which describes the relative use of an area [Fauchald and Tveraa 2003]) and relative turning angle, and we censored locations exhibiting small first passage time values (< 1, indicating rare usage [Fauchald and Tveraa 2003]) and tight turning angles (179–181°, indicating direct routes to and from the location) because these locations were likely anomalous.

In Module 2, we visually identified home ranges, migratory movements between them, and migration timing using maps of locations and temporal graphs of net squared displacement and movement speed. We set the beginning of the ecological year to 13 February (the earliest capture date for white-tailed deer); if an individual was monitored for more than one year, its movement status was aggregated across all monitored years. When individuals moved between winter and summer ranges multiple times, we considered individuals to have migrated during the movement period associated with the longest transitional occurrence in either range. We assessed migratory status following examples from Migration Mapper (Merkle et al. 2022). We considered stopover events (i.e., animals stopping in a single concentrated area along their migration route for < 1 month) part of the migration event, and we considered individuals nomadic, but not migratory, if they moved among ≥ 4 distinct home ranges at irregular intervals. If an individual was not monitored long enough (the duration of one migration season for individuals with typical movements) to visually assess its movement status due to collar failure or mortality, we considered its movement status unknown. If an individual was migratory, we recorded the displacement (i.e., Euclidian distance) between the arithmetic centroids of its winter and summer home ranges; if an individual did not exhibit range fidelity, we averaged its displacement measures.

In Module 3, we categorized location data into seasons using animal movements. We considered spring and fall migration to occur from the first quartile date migratory white-tailed deer departed for their new seasonal range to the third quartile date migratory deer arrived in their new seasonal range (Table 1.1). We defined summer and winter as the periods between spring and fall migration. We used the same seasons (winter, spring migration, summer, and fall migration) for all species to compare population-level occurrence distributions. We used deer migrations to define seasons because gray wolves and moose did not exhibit seasonally-defined movements (see results).

In Module 4, we used BBMMs from the R package *BBMM* (Nielson et al. 2013) to generate individual-level occurrence distributions for compilation into population-level occurrence distributions for each season in Module 5. We allowed *BBMM* to calculate movement variance instead of manually selecting a movement variance value. We specified a 50-m resolution for distributions estimated by *BBMM* (default = 500-m resolution) to enhance occurrence distribution resolutions, and we increased the maximum lag time (i.e., the time interval between relocations) to 9 h to allow for a single missed relocation.

In Module 5, we merged individual-level occurrence distributions to form seasonal population-level occurrence distributions. We compiled a model for each season for gray wolves, moose, and three subsets of white-tailed deer: migratory individuals only, resident individuals only, and all individuals combined (the composite population). This hierarchical process produced 20 population-level seasonal occurrence distributions representing the four seasons and five populations. We produced population-level distributions by (1) calculating mean distributions of individuals during given seasons by merging their individual-level distributions from Module 4, (2) calculating mean annual population distributions by merging mean

distributions of all individuals monitored each year, and (3) calculating final population-level occurrence distributions by merging mean annual distributions from all monitoring years. We generated one additional model to represent the deer migration corridor by (1) calculating mean distributions of individuals during spring or fall migration by merging their individual-level distributions from Module 4 during their migration movements, (2) calculating mean spring and fall migration distributions by merging the mean distributions of all migratory individuals monitored during the respective migration periods, and (3) calculating the final population-level migration corridor occurrence distribution by merging the mean spring and fall migration distributions. We merged the spring and fall migration corridors as they were highly similar (93.5% overlap; calculated following Cardillo and Warren [2016]). Unlike seasonal population-level distributions, we treated the migration corridor distribution as a single distribution that did not change seasonally. Finally, we exported the 21 resultant 95% population-level occurrence distributions from Migration Mapper as shapefiles. We used Module 6 for data visualization throughout the process.

Table 1.1. Timing of annual migrations by white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2021.

Migration event	5% start migrating	25% start migrating	Average migration start	Average migration finish	75% finish migrating	95% finish migrating
Spring	2 April	4 April	19 April	28 April	2 May	2 June
Fall	11 August	10 October	28 October	8 November	28 November	13 January

Mechanistic range shift analysis (MRSA)

We tested if gray wolves shifted their home ranges using MRSA in the *marcher* package (Gurarie et al. 2017; Gurarie and Cheraghi 2017) in R (v4.2.1) (R Core Team 2023) to corroborate results from Migration Mapper. The utility of MRSA is the statistical validation of the occurrence of range shift behaviors. We visually searched the movements of each wolf for temporal differences in latitude and longitude and applied a 3-cluster means process including three of the four seasons observed to identify potential home range shifts (Gurarie et al. 2017; Gurarie and Cheraghi 2017). We then fit a migratory white noise range shift model using maximum likelihood and tested for statistical significance ($p < 0.05$) (Gurarie et al. 2017; Gurarie and Cheraghi 2017). If a model identified a home range shift, we recorded the estimates of range shift timing and duration with 95% confidence intervals (CI).

Overlap calculations

We assessed whether gray wolves switched prey seasonally by calculating spatial overlap of wolves with prey. We calculated wolf utilization distributions using kernel BBMMs (Horne et al. 2007). We excluded wolves if < 5% of recorded locations were within the 95% white-tailed deer migration corridor occurrence distribution boundary due to territorial boundaries of adjacent packs or dispersal. We subset remaining wolf locations into the four seasons defined using Migration Mapper (winter, spring migration, summer, and fall migration). We removed wolf-seasons with < 50 locations, which represented one week of monitoring and the approximate minimum time required by wolves to traverse their home ranges several times as determined visually using variograms in the R package *ctmm* (Fleming and Calabrese 2022b; Fleming and Calabrese 2022a). We calculated the outer boundary of 95% kernel BBMM UD for each wolf-season in the R package *adehabitatHR* (Calenge 2006; Michelot et al. 2023). We calculated the

percentage of the area within those boundaries overlapping the corresponding population-level seasonal prey occurrence distributions and the deer migration corridor (hereafter, percent overlap) in the R package *sf* (Pebesma 2018; Michelot et al. 2023). Finally, we calculated the mean and 95% CI of percent overlap of wolf-seasons. Because percent overlap was not normally distributed, we used nonparametric Kruskal-Wallis tests to identify populations with differences in percent overlap between seasons and Dunn tests to identify specific seasons with greater overlap (Potvin and Roff 1993; Dinno 2015). We used Mann-Whitney tests to identify differences in percent overlap with wolves between populations during given seasons (Potvin and Roff 1993).

We repeated the above steps for Migration Mapper and overlap calculations using 50% UDs and 50% occurrence distributions to represent the core areas of spatial distributions and determine if seasonal patterns in percent overlap varied between spatial scales.

Results

Movement Status

We obtained location data from 45 gray wolves (median = 623 locations per individual; range = 7–2,721), 135 moose (median = 2,541; range = 6–16,042), and 72 white-tailed deer (median = 1,363; range = 6–8,497). Of these, we assessed seasonal movement status of 35 wolves, 106 moose, and 63 deer. We monitored 3 wolves for 2 years, 85 moose for 2–10 years, and 35 deer for 2–5 years. We did not assess the movement status of 9 wolves, 29 moose, and 9 deer that dispersed from the study area or were not monitored long enough to assess movement status due to mortality or collar failure.

No wolves exhibited range shifts or were migratory. Among moose, 58 (54.7%) were nomadic, 11 (10.4%) migrated, and 37 (34.9%) maintained a single home range. Median

displacement between migratory moose winter and summer home ranges was 5.0 km (range = 1.5–20.0 km), but we did not identify a moose migration corridor. Among white-tailed deer, 42 (66.7%) migrated and 21 (33.3%) maintained a single home range. We identified 62 spring and 46 fall deer migration events from 42 individuals including 15 individuals monitored for 2–5 years exhibiting migration each year. Spring migration by deer primarily occurred synchronously in April, and fall migration primarily occurred asynchronously during October–November (Table 1.1; Figure A.1; Figure A.2). Migratory deer followed a single migration corridor between their winter and summer ranges (Figure 1.2). Median displacement between migratory deer winter and summer home ranges was 16.8 km (range = 3.5–33.0 km).

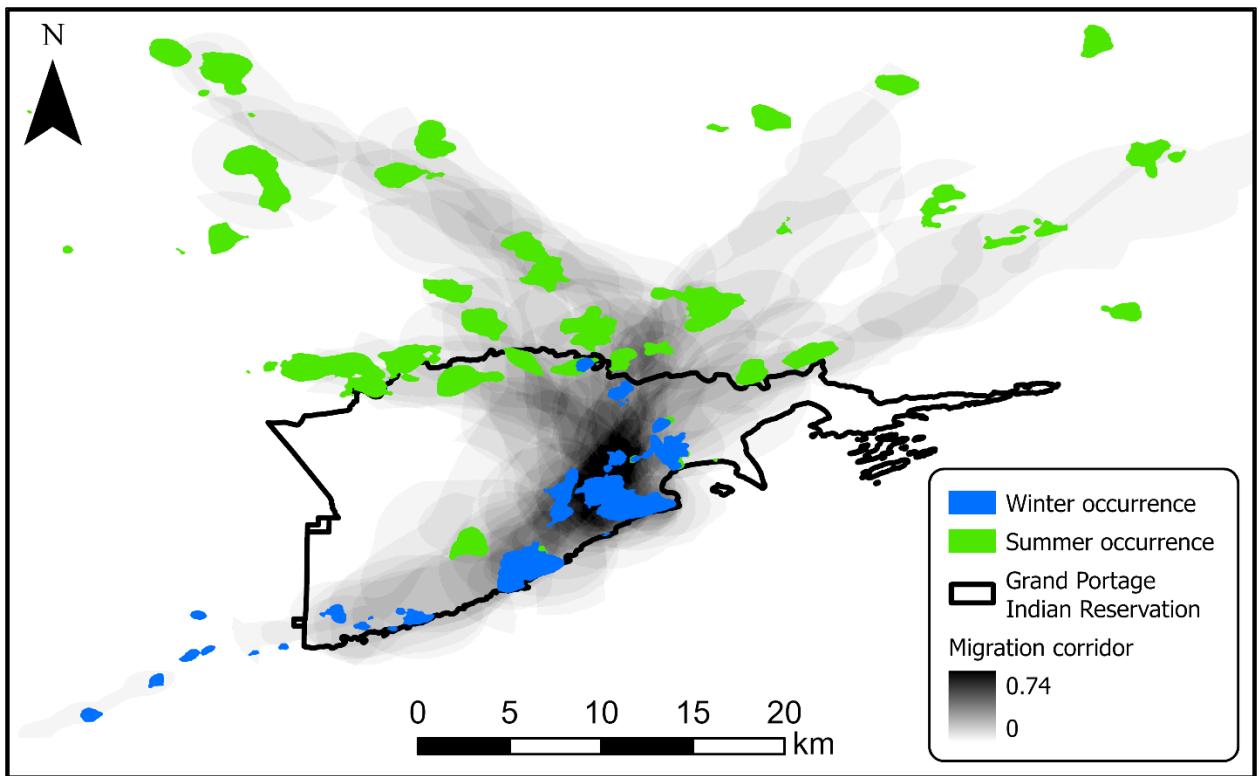


Figure 1.2. White-tailed deer (*Odocoileus virginianus*) migration corridor on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2021. Blue and green polygons represent 95% occurrence distributions of the migratory deer population during winter and summer, respectively; gray-scale overlapping polygons represent the proportion of migratory deer using a given area during their spring and fall migration movements.

Seasonal overlap

We calculated population-level occurrence distributions for moose-seasons and white-tailed deer-seasons as well as separate distributions for migratory and resident deer during winter (214 moose, 45 deer [32 migratory, 13 resident]), spring migration (268 moose, 104 deer [69 migratory, 35 resident]), summer (256 moose, 96 deer [67 migratory, 29 resident]), and fall migration (213 moose, 73 deer [55 migratory, 18 resident]). We calculated individual-season models for gray wolves during winter ($n = 33$), spring migration ($n = 11$), summer ($n = 25$), and fall migration ($n = 32$). We excluded from our individual-season models 3 wolves with too few locations and 7 wolves because < 5% of their total recorded locations were within the deer migration corridor of which 6 dispersed from the study area.

Here, we present results from calculating percent overlap of gray wolf 95% UD s with prey 95% occurrence distributions (Figure 1.3; Table 1.2; Table 1.3), which were similar to respective calculations of percent overlap of wolf 50% UD s with prey 50% occurrence distributions (Figure A.3; Tables A.1–A.4). Percent overlap of wolf UD s and the white-tailed deer migration corridor differed marginally among seasons ($\chi^2 = 7.81$, $p = 0.05$), with overlap greater during fall migration than spring migration ($Z = 2.72$, $p = 0.04$). Overlap of wolf UD s with moose distributions differed among seasons and was 1.6–2.7 times greater during summer. Overlap of wolf UD s with composite deer distributions changed seasonally and was 1.7–2.1 times greater during fall migration. Overlap of wolf UD s with composite deer distributions was greater than that of wolves with moose during fall migration. Percent overlap of wolf UD s with only migratory deer occurrence distributions changed seasonally and was 1.7–2.1 times greater during fall migration. Overlap of wolves with only resident deer distributions did not change

seasonally. Overlap of wolves with only migratory deer was greater than overlap with only resident deer during summer, fall migration, and winter.

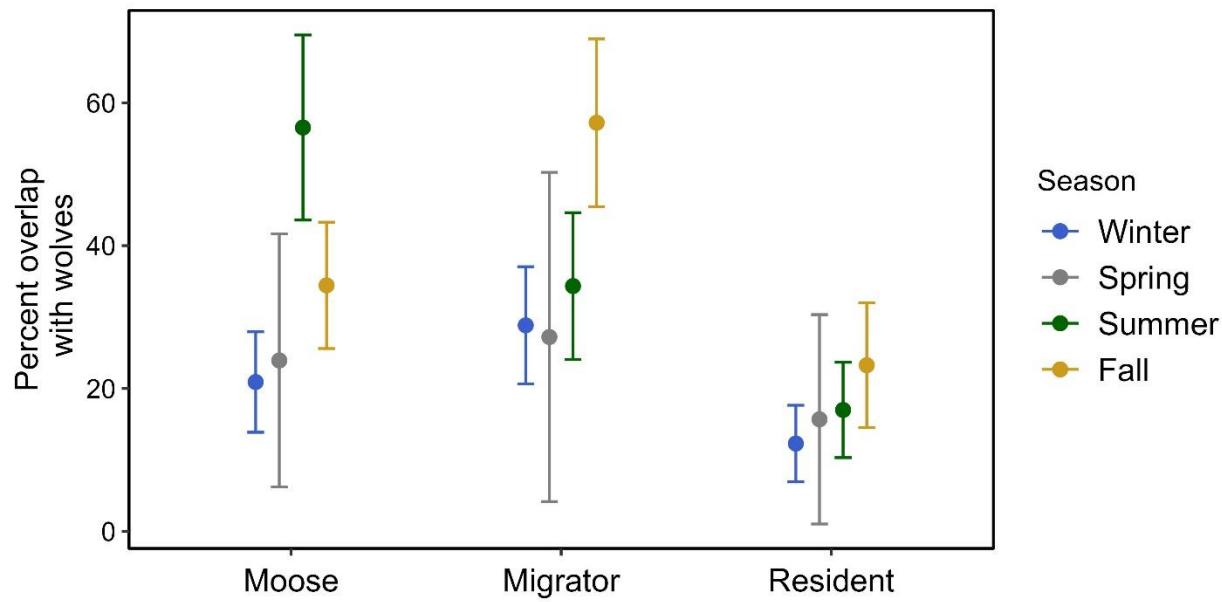


Figure 1.3. Seasonal percent overlap of gray wolves (*Canis lupus*) with prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Percent overlap was calculated using 95% wolf UD s and 95% occurrence distributions of moose (*Alces alces*), migratory white-tailed deer (*Odocoileus virginianus*), and resident deer. Points represent means with 95% CI. Spring and fall represent the deer migration period.

Table 1.2. Kruskal-Wallis tests for differences in seasonal percent overlap of gray wolves (*Canis lupus*) with prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Comparisons of percent overlap of individual-level wolf 95% UD with population-level 95% occurrence distributions of moose (*Alces alces*), the white-tailed deer (*Odocoileus virginianus*) migration corridor, the composite deer population, migratory deer only, or resident deer only are presented. A significant test ($p < 0.05$) indicates percent overlap of wolves with the indicated population changed seasonally. Dunn tests identify seasons during which overlap differed.

Population	χ^2	p-value	Dunn test
Moose	20.09	< 0.01	Table S3
Deer migration corridor	7.81	0.05	N/A
Composite deer	12.88	< 0.01	Table S4
Migratory deer	14.22	< 0.01	Table S4
Resident deer	3.50	0.32	N/A

Table 1.3. Mann-Whitney tests for differences in percent overlap of gray wolves (*Canis lupus*) with prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Population comparisons represent percent overlap of individual-level wolf 95% UD (n) with population-level 95% occurrence distributions of moose- (*Alces alces*) seasons (N) and resident-, migratory-, and composite- white-tailed deer (*Odocoileus virginianus*) seasons (N). A significant test ($p < 0.05$) indicates percent overlap of wolves with specified populations differed during the specified season; the population with greater overlap is designated in the final column.

n (wolves)	Population 1 (N)	Population 2 (N)	Season	W	p-value	Greater overlap
33	Composite deer (45)	Moose (214)	Winter	673	0.10	N/A
11	Composite deer (104)	Moose (268)	Spring	64	0.84	N/A
25	Composite deer (96)	Moose (256)	Summer	217	0.06	N/A
32	Composite deer (73)	Moose (213)	Fall	743	< 0.01	Composite deer
33	Resident deer (13)	Migratory deer (32)	Winter	794	< 0.01	Migratory deer
11	Resident deer (35)	Migratory deer (69)	Spring	76	0.32	N/A
25	Resident deer (29)	Migratory deer (67)	Summer	431	0.02	Migratory deer
32	Resident deer (18)	Migratory deer (55)	Fall	795	< 0.01	Migratory deer

Discussion

We did not find support for our hypothesis that gray wolves would increase their use of migration corridors during white-tailed deer migration. Wolves in our study also did not exhibit home range shifts or migratory coupling (Gurarie et al. 2017; Furey et al. 2018), though this phenomena has occurred among non-territorial migratory wolves pursuing migratory caribou (Ballard et al. 1997; Musiani et al. 2007; Michelot et al. 2023). Non-migratory wolves, like those in our study, are territorial and defend their home ranges year-round (Mech and Boitani 2003; Musiani et al. 2007). Spatial constraints due to intra-specific territoriality likely explain why wolves in our study did not shift their ranges seasonally (Figure A.4). Migratory coupling has only been reported among non-territorial (e.g., grizzly bear [*Ursus arctos*] [Servheen 1983; Deacy et al. 2016]), semi-territorial (e.g., cheetah [*Acinonyx jubatus*] [Melzheimer et al. 2018; Broekhuis et al. 2021]), or seasonally territorial (e.g., red knot [*Calidris canutus*] [Reneerkens et al. 2002; Buehler and Piersma 2008]) predators (Furey et al. 2018). This pattern indicates territorial predators may not exhibit migratory coupling as proposed by Furey et al. (2018). An exception may occur among territorial wolves whose ranges were seasonally limited by elevation-mediated snow depths (Anderson 2014), but this requires further examination.

In contrast to our hypothesis, gray wolf distributions overlapped the migration corridor similarly year-round. Migratory corridors typically follow least-cost paths that facilitate animal movement (Nuñez et al. 2022), and wolves select for least-cost paths to increase prey encounters (Kittle et al. 2017; Clare et al. 2023). Though we did not assess landscape resistance, wolves could be using the corridor year-round to optimize foraging. Alternatively, resource dispersion hypothesis posits predators should defend the minimum amount of territory necessary to support themselves when prey are least available, which may include maintaining access to migration corridors even when prey are not migrating (Macdonald 1984). Wolves, cheetahs, and African

lions (*Panthera leo*) exhibited such behavior despite territorial limitations (Brandell et al. 2021; Broekhuis et al. 2021). Wolves may therefore maintain access to the migration corridor year-round to access increased prey availability during migrations (Macdonald 1984) or to facilitate improved mobility in all seasons (Gurarie and Ovaskainen 2013; Kittle et al. 2017).

Though we did not observe home range shifts or migratory coupling, our prediction that gray wolves would adapt to seasonal prey availability was supported as wolves altered their within-range spatial distributions in concert with seasonal prey distributions. This result contrasts assertions that wolves alter prey distributions rather than responding to them (Oliveira-Santos et al. 2021). A possible explanation is that both patterns occur simultaneously; we used prey to describe wolf movement whereas Oliveira-Santos et al. (2021) used wolves to describe prey movement. We observed greater overlap of wolves with migratory white-tailed deer during fall migration as well as with moose during summer. This outcome suggests a spatial response to memories of predation success and biased movements towards available prey in support of prey switching under alternative prey hypothesis (Lack 1954; Mitchell and Lima 2002; Tschanz et al. 2007; Vijayan et al. 2019; Brandell et al. 2021). Seasonal prey switching in response to relative prey availability is common among predators (Tschanz et al. 2007; Xavier et al. 2018; Moorhouse-Gann et al. 2020). In our study area, migratory deer were present in winter while moose were present year-round. Further, fall migration by deer is protracted and asynchronous while spring migration is brief and synchronous. Analogous to prey switching, wolves should concentrate their spatial distributions on the more functionally available deer in fall and winter then switch to the best alternatives in summer when deer are less abundant (Tschanz et al. 2007). This pattern is supported by the greater proportions of deer in wolves' winter diets and of beaver and moose calves in summer diets in this region (Chenauix-Ibrahim 2015; Severud et al. 2019b;

Sovie et al. 2023) as well as increased deer mortality during fall migration due to wolf predation (Chapter 3).

Migratory white-tailed deer in our study experienced the greatest overlap with gray wolves during fall migration. Prey migration is risky due to decreased vigilance and lessened familiarity with areas traversed (Hebblewhite and Merrill 2007; Hopcraft et al. 2014; Forrester et al. 2015; Gehr et al. 2020); however, migration to reduce predation risk or seek better forage is common (Avgar et al. 2014). Though overlap may not equate to risk (Hebblewhite et al. 2005; Suraci et al. 2022), deer in our study are likely most vulnerable during fall migration because their asynchronous and predictable movements could facilitate higher predation success (Mitchell and Lima 2002; Vijayan et al. 2019). Deer may also exhibit reduced predator avoidance behaviors (e.g., more diurnal activity) during the rut, which coincides with fall migration (Nelson and Mech 1981; Clare et al. 2023), though male ungulates may exhibit greater vigilance during this period (Quenette 1990). Comparatively, spring deer migration was synchronous, which may have limited wolves' ability to respond to spring migration movements (Nelson and Mech 1991). Wolves also reduce movements during denning and parturition, which occurred during spring deer migration (Fuller 1989; Benson et al. 2015) potentially explaining marginally lower overlap of wolves with the migration corridor during this period. We suggest increased overlap of wolves with migratory deer during fall is a consequence of increased predation success due to greater deer vulnerability and increased availability of deer carcass remains from hunter harvest. Supporting our conclusions, deer and caribou experienced greater mortality during fall migration than during spring migration (Nelson and Mech 1991; Kojola et al. 2004; Chapter 3), and wolves used anthropogenic sources of carrion (Gable et al. 2018; Petroelje et al. 2019). Our models, however, may not have identified complete patterns as wolves

could have pursued unmonitored deer whose fall migrations were not examined or corridor distributions may have been too coarse due to the 4–8-h relocation intervals used in our analyses (Merkle et al. 2022).

Compared to fall migration, white-tailed deer exhibited lower overlap with gray wolves during winter suggesting potential predator avoidance when they are in poorest condition (Kautz et al. 2020; Vindenes et al. 2023). The corresponding lower overlap of wolves and deer during summer relative to winter, however, is likely an artifact of monitored migratory deer leaving the ranges of monitored wolves and entering the ranges of unmonitored wolves. Migratory deer also experienced greater overlap with wolves year-round than resident deer. Migratory barnacle geese (*Branta leucopsis*) foraged for longer durations than residents (Boom et al. 2023), and migratory elk increased predation risk to obtain greater summer forage while resident elk exhibited the opposite (Hebblewhite and Merrill 2009; Hebblewhite and Merrill 2011). Migratory deer in our study may do the same and exhibit increased predator avoidance in winter and forage seeking in summer (Avgar et al. 2014; Clare et al. 2023). Resident deer in our study remained closer to Lake Superior shoreline habitats that receive less snowfall and have greater human activity (Sanderson et al. 2002; MNDNR 2023b). These factors may reduce risk through increased deer mobility and human shield effect (Pearson et al. 1995; Berger 2007) and may explain why a lower percentage of deer in our study were migratory than in nearby inland populations (Nelson and Mech 1981; Mech and Barber-Meyer 2020).

We observed an increase in gray wolf and moose overlap during summer despite the relative year-round range stability of these species. There are several possible explanations for this response. First, many white-tailed deer, which are wolves' primary prey (Latham et al. 2013; Chenaux-Ibrahim 2015), are absent from the core of our study area during summer. Second,

moose calves are spatially concentrated in predictable landscape-level patterns during summer, more vulnerable to depredation, and have high mortality rates due largely to wolf depredation (Severud et al. 2015; Severud et al. 2019b; Van de Vuurst et al. 2022). Third, American beaver account for up to one third of summer wolf biomass consumption (Latham et al. 2013; Chenaux-Ibrahim 2015), and resource selection by wolves suggests selection for beaver habitat (Latham et al. 2013; Benson et al. 2015). Finally, wolves select for flatter slopes in mid- to late summer when pups are immature and less mobile (Anderson 2014; Benson et al. 2015). This combination of decreased deer availability, high moose calf vulnerability, increased beaver availability, and limited wolf pup mobility likely explains the greater spatial overlap of wolves and moose in summer.

Management implications

Moose populations are declining throughout their southern range including the 1854 Ceded Territory (Ruprecht et al. 2016; Severud et al. 2022). The Grand Portage Band desires to increase moose abundance and conducts management to limit population declines. For example, implementing spring black bear (*Ursus americanus*) harvests appear to have improved moose recruitment (Grand Portage Band of Lake Superior Chippewa, *unpublished data*). Our results and previous work indicate moose likely experience greater gray wolf predation pressure during summer when calves are more vulnerable (Severud et al. 2015; Wolf et al. 2021). If management goals include further increases in moose calf recruitment, management actions to reduce wolf predation of calves could be implemented (Hayes et al. 2003; Adams et al. 2019), though Indigenous constituents' opinions should also be considered (Gilbert et al. 2022).

Conclusions

Our work is among the first to use season-specific population-level occurrence distributions for analysis of predator-prey interactions (Alston et al. 2022b; Michelot et al. 2023). Gray wolves seasonally altered their within-range spatial distributions supporting prey switching. We also demonstrate spatial plasticity of predators in response to spatially dynamic prey, which is well-studied among non-territorial predator populations (Furey et al. 2018) but warrants further consideration among territorial and semi-territorial species (Brandell et al. 2021; Broekhuis et al. 2021). Wolves in our study did not, however, exhibit home range shifts or migratory coupling in response to white-tailed deer migration. Because wolves in the western Great Lakes region are territorial with little available space between packs (Mech 1977; Mech and Boitani 2003), even subtle range shifts between seasons may be inhibited. We suggest territorial predator populations can exhibit within-territory shifts in spatial distributions but not migratory coupling as originally postulated by Furey et al. (2018), though an exception may occur among territorial predators whose ranges are seasonally limited by weather conditions (e.g., snow depth) (Anderson 2014).

CHAPTER 2:

GRAY WOLVES ALTER SPACE USE SEASONALLY IN RESPONSE TO MIGRATORY PREY

Abstract

Ecological seasonality describes the dynamic adaptation of species to changes in the biotic community of their environment and suggests predators will alter space use synchronously with seasonal prey availability. We assessed ecological seasonality using seasonal space use states (i.e., periods of similar movement and resource use). We compared seasonal space use of mainland gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA against island populations of wolves and moose on nearby Isle Royale National Park, Michigan, USA. We hypothesized mainland wolves would alter their seasonal space use states in response to variations in prey availability corresponding to seasonal migration but island wolves would not because primary prey are non-migratory. We also hypothesized that reproduction would influence seasonal space use states in both systems. We used GPS collar locations from mainland wolves (beginning in 2008), moose (2010), and deer (2016) plus island wolves (2018) and moose (2019) recorded through 2021. We used cluster and principal component analyses (PCA) to temporally define seasonal space use states among populations. We used weighted autocorrelated kernel density estimation (wAKDE) for weighted resource selection functions (wRSFs) to assess habitat selection during seasonal space use states for each population. Mainland populations generally exhibited two seasonal space use states with transitions between seasons coinciding with changing weather and deer migration. Selection for landscape attributes varied among seasonal space use states for all mainland populations (e.g., increased use of south-facing slopes

in winter). In contrast, island wolves and moose did not alter their space use states seasonally, and their resource selection differed from mainland populations. The occurrence and lack of seasonal space use states exhibited by mainland and island populations, respectively, was likely due to the migration of mainland deer. Our findings suggest ecological seasonality of predators is linked to prey via seasonal space use dynamics, but seasonal space use states were not associated with parturition.

Context

The Grand Portage Band of Lake Superior Chippewa is a federally recognized sovereign nation of Anishinaabe people whose home is on the Grand Portage Indian Reservation, Minnesota, USA (Gichi Onigaming). Band members exercise their usufructuary rights to food sovereignty through subsistence hunting, fishing, and gathering in the 1854 Ceded Territory (Thompson 2020). Recently, Isle Royale National Park, Michigan, USA (Minong) was recognized as a Traditional Cultural Property of the Grand Portage Band (National Park Service 2022). Moose (mooz; *Alces alces*) and white-tailed deer (waawaashkeshi; *Odocoileus virginianus*) are primary subsistence species of Anishinaabe people in the 1854 Ceded Territory. Gray wolves (ma'iingan; *Canis lupus*) are kin to the Anishinaabe people and environmentally important to their seventh-generation approach to ecosystem stewardship (Gilbert et al. 2022; Grand Portage Band of Lake Superior Chippewa 2023). Predator-prey research is conducted by the Grand Portage Band to improve their understanding of ecosystem health, which set the context for this study.

Introduction

Habitat selection is ultimately influenced by cost–benefit tradeoffs that maximize fitness (Mayor et al. 2009). For predators, optimal habitat selection depends on matching prey habitat

selection across space and time (Mitchell and Lima 2002). Predator adaptations may therefore correspond to seasonal variability in prey abundance following optimal foraging theory and alternative prey hypothesis (Lack 1954; Werner and Hall 1974; Tschanz et al. 2007). Gentoo penguins (*Pygoscelis papua*), for example, switch between zooplankton (*Themisto gaudichaudii*) and krill (*Euphausia superba*) when krill abundance increases during late winter (Xavier et al. 2018), and Eurasian otters (*Lutra lutra*) consume more amphibians in winter when density is greater (Moorhouse-Gann et al. 2020).

Ecological seasonality is based on animal ecology and can be influenced by biotic (e.g., available forage or reproductive cycles) or abiotic (e.g., weather) factors, as opposed to calendar-derived seasons of fixed duration such as solstices or seasons determined using a single variable such as migration timing (Basille et al. 2013). Combined with existing predator-prey theory (Lack 1954; Werner and Hall 1974; Mitchell and Lima 2002), predators should alter space use across ecological seasons corresponding with extrinsic changes in the prey community (Furey et al. 2018). Basking sharks (*Cetorhinus maximus*) (Sims et al. 2003) and Hector's dolphins (*Cephalorhynchus hectori*) (Bräger et al. 2003) demonstrate seasonal changes in space use by using shallower habitats in summer and deeper habitats in winter when shallow-water prey are scarce. Lions (*Panthera leo*) alter space use between wet and dry seasons in response to spatial concentrations of prey around water sources (Kittle et al. 2016; Schooler et al. 2022).

Though optimal space use by predators is primarily determined by prey consumption, reproduction also influences space use. Male bottlenose dolphins (*Tursiops aduncus*) select prey-rich offshore embankments except when females enter estrus; male dolphins then switch to sheltered habitats used by females forfeiting higher prey abundances (O'Brien et al. 2020). Steller sea lion (*Eumetopias jubatus*) (Sinclair and Zeppelin 2002) and mountain lion (*Puma*

concolor) (Smereka et al. 2020) females select habitats that decrease predation of their dependent young in lieu of habitats with higher prey concentrations, thereby conceding prey encounters.

These space use changes suggest a balance between food consumption and sexual reproduction.

Gray wolf (*Canis lupus*) space use is influenced by prey availability and reproduction.

Where wolves' primary prey are migratory, they alter space use to match prey distributions.

Wolves migrated between winter and summer ranges following caribou (*Rangifer tarandus*) migrations (Walton et al. 2001) and followed elevation-mediated ungulate habitat selection associated with decreased snow-depths and increased forage (Anderson 2014). In contrast, wolves pursuing non-migratory ungulates did not alter space use seasonally (Roffler et al. 2018). Wolves also switch between prey seasonally according to relative availability, such as consuming more American beaver (*Castor canadensis*) and caribou in summer when these species are more vulnerable (Latham et al. 2013). Reproduction also influences wolf space use; wolves contract their space use to remain closer to den sites and pups following parturition (Walton et al. 2001; Benson et al. 2015; Roffler and Gregovich 2018).

Defined in the context of ecological seasonality, seasonal space use states are time periods identified by population-level space use patterns (i.e., movements and resource selection) resulting from species-specific responses to changing biotic and abiotic conditions (e.g., available forage, reproductive activities, snowfall). We examined how annual reproduction and prey availability affected gray wolf space use by assessing wolves' seasonal space use states in two environmentally similar systems with disparate prey communities. We hypothesized space use by wolves would differ temporally in the presence of migratory prey due to altered prey availability but remain largely unchanged where prey were non-migratory and present year round. We hypothesized wolf space use would be defined by spatial limitations during

parturition but would otherwise reflect habitats used by primary available prey regardless of prey migration.

Material and methods

Study area

We conducted our study on and near the Grand Portage Indian Reservation (GPIR), Minnesota, USA (47.9614° N, 89.7594° W) and Isle Royale National Park (IRNP), Michigan, USA (47.9959° N, 88.9093° W) (Figure 2.1). The GPIR study area comprised about $1,200 \text{ km}^2$ including GPIR and mainland areas $\leq 30 \text{ km}$ from GPIR (i.e., areas within the migratory range of our study species [Chapter 1]) including portions of Ontario, Canada to the north and U.S. federal, state, and private land within the 1854 Ceded Territory to the west. This mainland study area is characterized by steep ridges and broad valleys with elevations 183–674 m above sea level (USGS 2020). The mainland area contains 44% mixed forest, 17% deciduous forest, 11% coniferous forest, 9% shrubland, 7% wetland, and 5% open water (CCRS et al. 2020). Mean daily temperatures during 2009–2019 ranged from minima of $-17.8 \pm 3.5 \text{ }^{\circ}\text{C}$ (mean \pm SD) in January to maxima of $23.3 \pm 1.7 \text{ }^{\circ}\text{C}$ in July, with $281.9 \pm 11.7 \text{ cm}$ of rainfall and $351.6 \pm 80.8 \text{ cm}$ of snowfall annually (NOAA 2022). Gray wolves could be legally harvested in Ontario during our study, but legal harvest in Minnesota occurred only during 2012–2014 (Erb et al. 2018). Migratory white-tailed deer (*Odocoileus virginianus*), non-migratory moose (*Alces alces*), and beaver are the primary prey of wolves in the area (Chenauix-Ibrahim 2015; Chapter 1). Deer and moose could be harvested throughout Ontario and Minnesota, but after 2012, only indigenous band members could harvest moose in Minnesota (1854 Treaty Authority 2023).

An approximately 534 km^2 archipelago of over 450 islands, IRNP is a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Biosphere Reserve with no

roads in northwestern Lake Superior about 22 km from mainland Minnesota and Ontario. This island study area contains elevations 183–429 m above sea level with rocky terrain, steep parallel ridges, and low-lying areas containing inland lakes (USGS 2020). Land cover of IRNP is 49% mixed forest, 23% wetland, 9% deciduous forest, 8% coniferous forest, 8% open water, and 2% shrubland (CCRS et al. 2020). During 2009–2019, IRNP had mean January daily minima of -13.4 ± 3.1 C° and mean July daily maxima of 24.2 ± 1.8 C° (NOAA 2022). Non-migratory moose are the only ungulate on IRNP and the principal prey of gray wolves along with beaver (Tischler et al. 2022; Sovie et al. 2023). Harvest of moose and wolves in IRNP is prohibited.

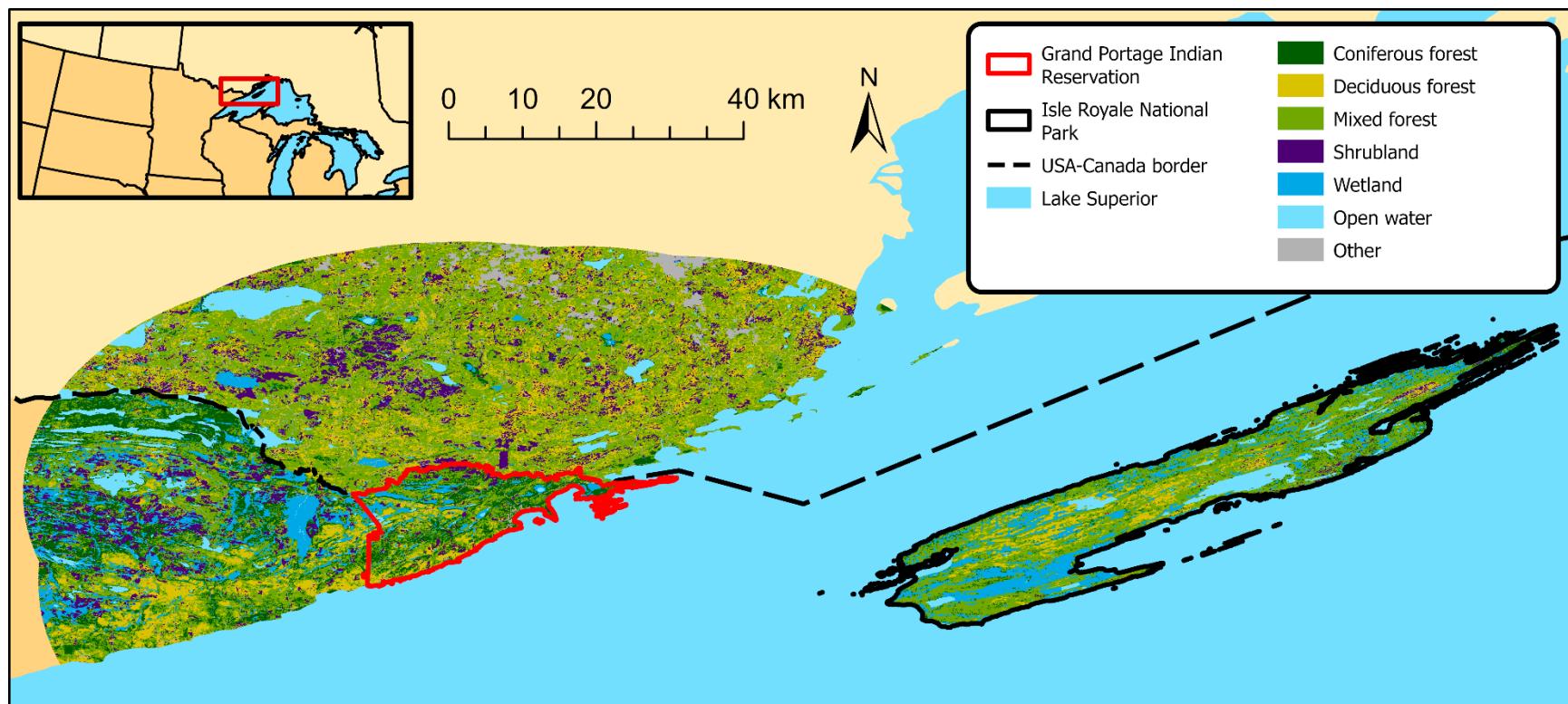


Figure 2.1. Study area including areas on and near the Grand Portage Indian Reservation, Minnesota, USA and Isle Royale National Park, Michigan, USA. Land cover data was obtained from the Commission for Environmental Cooperation 30-m land cover map of North America (CCRS et al. 2020).

Data collection

We used data collected by the Grand Portage Band of Lake Superior Chippewa and National Park Service (NPS) through 31 December 2021. Mainland gray wolves (beginning in 2008), moose (2010), and white-tailed deer (2016) were captured and affixed with GPS collars each year. Capture methods included foothold traps for wolves (Frame and Meier 2007), aerial darting for moose (Barros et al. 2018), and clover traps for deer (VerCauteren et al. 1999). Capture and handling protocols were approved by the Grand Portage Band of Lake Superior Chippewa Tribal Council, Michigan State University institutional animal care and use committee (IACUC) (PROTO202200266), and State University of New York College of Environmental Science and Forestry IACUC (210702),

From September 2018 to September 2019, 19 gray wolves were captured, fitted with GPS collars, and introduced to the island where two wolves were already present (Romanski et al. 2020). Five additional wolves born on the island were captured using foothold traps in May 2021 (Hoy et al. 2022). Moose on the island were captured in February 2019 and March 2020 using aerial darting (Barros et al. 2018). All suitable captured individuals were affixed with GPS collars following methods approved by the NPS IACUC (MWR_ISRO_Romanski_Wolves_2018.A3; MWR_ISRO_Hoy_Moose_2018.A3).

In both study areas, most collar data was obtained via satellite when collars were active; remaining data were downloaded directly from the hardware upon retrieval. Minimum relocation intervals of gray wolf and white-tailed deer collars were 3.25–4.5 h (based on intended collar longevity), and minimum relocation intervals of moose collars were 0.25–4 h (based on time of year). We excluded location data within seven days of capture or mortality to account for capture myopathy and our inability to determine exact mortality dates (Northrup et al. 2014).

We produced raster maps of aspect, slope, distance to Lake Superior, distance to roads (mainland only), distance to trails (island only), and land cover using ArcGIS Pro (v3.0.3, Esri, Redlands, California, USA). We derived aspect and slope from the United States Geological Survey (USGS) 1 arc-second (about 30-m resolution) digital elevation models (USGS 2020). We used the *Euclidian distance* tool to calculate the nearest distance from each 30-m cell to Lake Superior as defined by the National Oceanic and Atmospheric Administration (NOAA) digital shoreline (NOAA 2000), to roads demarcated by the United States Census Bureau (USCB) or Ontario Road Network (USCB 2021; OMNRF 2022), and to trails using a NPS database (Isle Royale National Park, *unpublished data*). We used the Commission for Environmental Cooperation (CEC) 30-m resolution land cover map of North America to determine land cover (CCRS et al. 2020). We considered agriculture and grassland part of the shrubland category for our analyses because these three categories were frequently misidentified as one another as determined during qualitative field assessments and because agriculture and grassland each composed < 2% of land cover.

We obtained weather data from the NOAA Climate Data Online tool as the daily average of data recorded from weather stations in Cook County, Minnesota, USA during 2008–2021 (NOAA 2022). We calculated average daily change in growing degree days (ΔGDD) from mean daily temperatures using a latitudinal correction (van Wijk et al. 2012).

Seasonal space use states

To test our hypothesis that space use would change temporally, we first determined the occurrence and timing of seasonal space use states for each population (i.e., mainland gray wolves, moose, and white-tailed deer; island wolves and moose) using cluster analyses in R (v4.2.1) with the R packages *clusterSim* and *fpc* (Basille et al. 2013; Hennig 2020; Walesiak and

Dudek 2021; R Core Team 2023). Cluster analyses are used to group data points with similar characteristics and can be applied to any vector of measurements describing a study object (i.e., daily space use) (Frades and Matthiesen 2010; Basille et al. 2013). We ran cluster analyses using year-round data and did not limit resultant clusters to any specific timeframes.

To determine daily space use, we resampled collar locations to 12 ± 2 h relocation intervals to reduce biases resulting from relocation intervals varying across individuals and seasons using R package *amt* (Signer et al. 2019). We calculated step-length and turning angle of GPS collar movement data for each location. Step-length was the distance between the prior and current locations, and turning angle was the angle formed by the prior, current, and subsequent locations. We extracted landscape covariate values for each location then calculated the daily population average for each landscape covariate from all available locations for each ordinal day. We assessed normality of daily averages using quantile–quantile plots and made square root or center and scale transformations as necessary (Fox 2015; Kassambra 2023). We checked daily averages of landscape covariates for multicollinearity using Pearson’s product-moment correlation coefficient (r), assumed influential when $|r| \geq 0.70$ (Dormann et al. 2013). The output of these steps was a matrix of daily space use averages for each population comprised of individual movements and habitat use (hereafter, daily space use matrix). We also generated daily space use matrices for subsets of island gray wolves monitored before and after the first denning event by introduced wolves (considered 15 April 2019) to account for potential variability in pack stability following introduction (Romanski et al. 2020).

We used the daily space use matrices to conduct cluster analyses. We first generated heuristic identification of noisy variables (HINoV) models in R package *clusterSim* to determine the inclusion and exclusion of space use metrics (Carmone Jr. et al. 1999; Walesiak and Dudek

2021). The HINoV process assesses which variables contain little clustering information so they can be removed from analyses to reduce the production of misleading results (Carmone Jr. et al. 1999). We used one-way analysis of variance (ANOVA) to identify variables whose distributions differed ($\alpha < 0.05$) and removed those variables (Carmone Jr. et al. 1999). We determined the number of clusters (k) to be considered using the elbow method in R package *factoextra* (Kassambra and Mundt 2020) and the silhouette method via manual programming (de Amorim and Hennig 2015). The elbow and silhouette methods allow for visual determination of the appropriate number of clusters (de Amorim and Hennig 2015; Kassambra and Mundt 2020).

We used a k-means cluster analysis to determine cluster assignments for each day in our daily space use matrices. The k-means process assigned each day to a cluster while minimizing the mean squared distance from each day's space use vector to the center of k clusters in the model. We completed our cluster analysis in R package *fpc* with 5,000 bootstrap replicates for each of ten random number seeds for the range of the number of clusters considered (k) (Hennig 2020). To improve robustness of inference, if clusters from any of the ten seeds were unstable per Jaccard similarity index ($\gamma < 0.75$), we considered cluster formation not possible (Hennig 2007). If all ten clusters were stable, we assigned the cluster values from the first seed to each day and transposed daily cluster assignments as the mode of a 5-day moving window centered on each ordinal day (Basille et al. 2013). We calculated transition dates between seasonal space use states (i.e., clusters) as the average date between eight consecutive days of cluster assignments occurring in a newly assigned category chronologically and reverse-chronologically rounded to the nearest day. We used this approach to overcome selection biases resulting from moving windows and to account for daily cluster assignments occurring outside final assigned seasonal space use states (Basille et al. 2013). Using the assigned dates and daily space use matrices, we

applied principal component analyses (PCA) to visualize and identify differences between clusters (Frades and Matthiesen 2010).

Resource selection

To assess space use differences between seasonal space use states, we used weighted autocorrelated kernel density estimation (wAKDE) for weighted resource selection functions (wRSFs) to characterize habitat use for each population within each seasonal space use state delineated by the cluster analyses (Alston et al. 2022a). Using wAKDE accounts for spatial and temporal auto-correlation when generating home range estimates, and using wRSFs accounts for model fits across individuals to generate population-level estimates (Alston et al. 2022a). This hierarchical approach accounts for pseudoreplication across individuals generally present in traditional resource selection functions and typically generates broader confidence intervals, which produces more robust results (Alston et al. 2022a).

We standardized relocation intervals across populations and seasonal space use states by resampling moose collar data at 4-h intervals using R package *padr* (Theon 2022). We used smaller relocation intervals for our wRSFs than our cluster analyses because the hierarchical approach allowed for increased resolution without inducing biases due to relocation interval frequency (Alston et al. 2022a). We subset location data by population, individual, seasonal space use state, and year resulting in individual-space use states as our sample units. If an individual was monitored during the same seasonal space use state across multiple years, we considered the individual-space use states separately. We excluded location data collected within two weeks of a transition date to help account for the presence of daily cluster assignments occurring outside assigned seasonal space use states (Basille et al. 2013). We excluded individual-space use states with < 50 locations, a threshold representing the approximate

minimum time required by gray wolves to traverse their home ranges several times as determined visually using variograms in R package *ctmm* (Fleming and Calabrese 2022b; Fleming and Calabrese 2022a).

For each individual-space use state, we generated a wAKDE utilization distribution (UD) using *ctmm* (Fleming et al. 2015; Alston et al. 2022a; Fleming and Calabrese 2022a). We fit a wRSF for each individual-space use state at core (50% UD) and home range (95% UD) levels (Alston et al. 2022a). Finally, we estimated population-level models weighted using Akaike information criterion for small samples (AIC_c) (Alston et al. 2022a), which weighted each individual-space use state's resource selection parameters by the model AIC_c then calculated the arithmetic mean of the parameters. We used landscape variables (i.e., aspect, slope, distance to Lake Superior, distance to roads [mainland only], distance to trails [island only], and land cover [with open water as the reference category]) as predictors. We determined continuous variables had statistically significant effects on habitat selection if the 95% confidence intervals of the associated parameters did not overlap zero.

Results

Mainland populations

We obtained data from 45 mainland gray wolves (35,670 total locations), but six dispersed from the study area and were excluded from analyses. Per our cluster analysis, wolves formed seasonal space use state clusters during summer (10 April–7 November) and winter (8 November–9 April). The first two principal components of these clusters described 30.6% of variation between seasons with winter defined by shorter step-lengths and more locations nearer Lake Superior, on south-facing slopes, and in coniferous forests compared to summer (Figure 2.2; Table 2.1). We analyzed 40 mainland wolf-summers and 35 mainland wolf-winters using

wRSFs. Our results indicated wolves selected for wetlands, shrublands, and deciduous forests during summer and for south-facing slopes during winter at the home range level (Figure 2.3). Landscape variables did not predict patterns of core range resource selection, and step-lengths did not vary seasonally.

We obtained data from 135 mainland moose (2,179,502 locations). Cluster analysis indicated two space use clusters for moose resulting in four seasonal space use states: summer (7 May–17 October), winter (18 October–10 March), spring shift (11 March–13 April), and pre-parturition shift (14 April–6 May). The first two principal components accounted for 36.4% of variation, and moose exhibited shorter step-lengths, tighter turning angles, more locations nearer to Lake Superior and in coniferous forests, and fewer locations in shrublands during winter compared to other seasons (Figure 2.2; Table 2.1). Moose used deciduous forests more during spring and pre-parturition shifts and used mixed forests less during summer and winter. We analyzed 263 moose-summers and 228 moose-winters using wRSFs; we did not analyze resource use during spring or pre-parturition shifts because too few locations were available for analysis. Moose selected for flatter slopes in core ranges year round and in summer home ranges (Figure 2.3). Within winter core ranges, moose selected for shrublands, nearer to roads, farther from Lake Superior, and south-facing slopes as well as having shorter step-lengths.

We obtained data from 74 mainland white-tailed deer (139,634 locations), but we excluded two deer that dispersed from the study area. Deer formed summer (24 April–18 November) and winter (19 November–23 April) seasonal space use states as determined by cluster analysis. The first two principal components described 41.2% of variation between clusters. Summer was defined by longer step-lengths, more northerly-facing and steeper slopes, distances farther from Lake Superior, and greater use of deciduous forests and shrublands

compared to winter (Figure 2.2; Table 2.1). We analyzed 90 deer-summers and 100 deer-winters using wRSFs; results indicated deer selected for shrublands in summer core ranges and deciduous forests in summer home ranges. Deer also selected for steeper slopes in winter home ranges and had shorter step-lengths (Figure 2.3). Landscape variables did not predict patterns of winter core range resource selection.

Transitions from winter to spring or summer for all mainland populations coincided with the onset of GDD accumulation and snow melt (Δ GDD and snow depth were negatively correlated [$t = -33.33$, $p < 0.01$]), white-tailed deer migration, and parturition timing of respective species (Figure 2.4). The gray wolf transition from summer to winter occurred 20 days after moose and 12 days before deer; the wolf transition from winter to summer occurred 14 days before deer. Because of their two additional transitional seasons in spring, the moose transition from winter to summer was offset from wolves and deer but encompassed wolf and deer seasonal transitions. Deer transitions between ecological seasons occurred near the ends of their seasonal migrations.

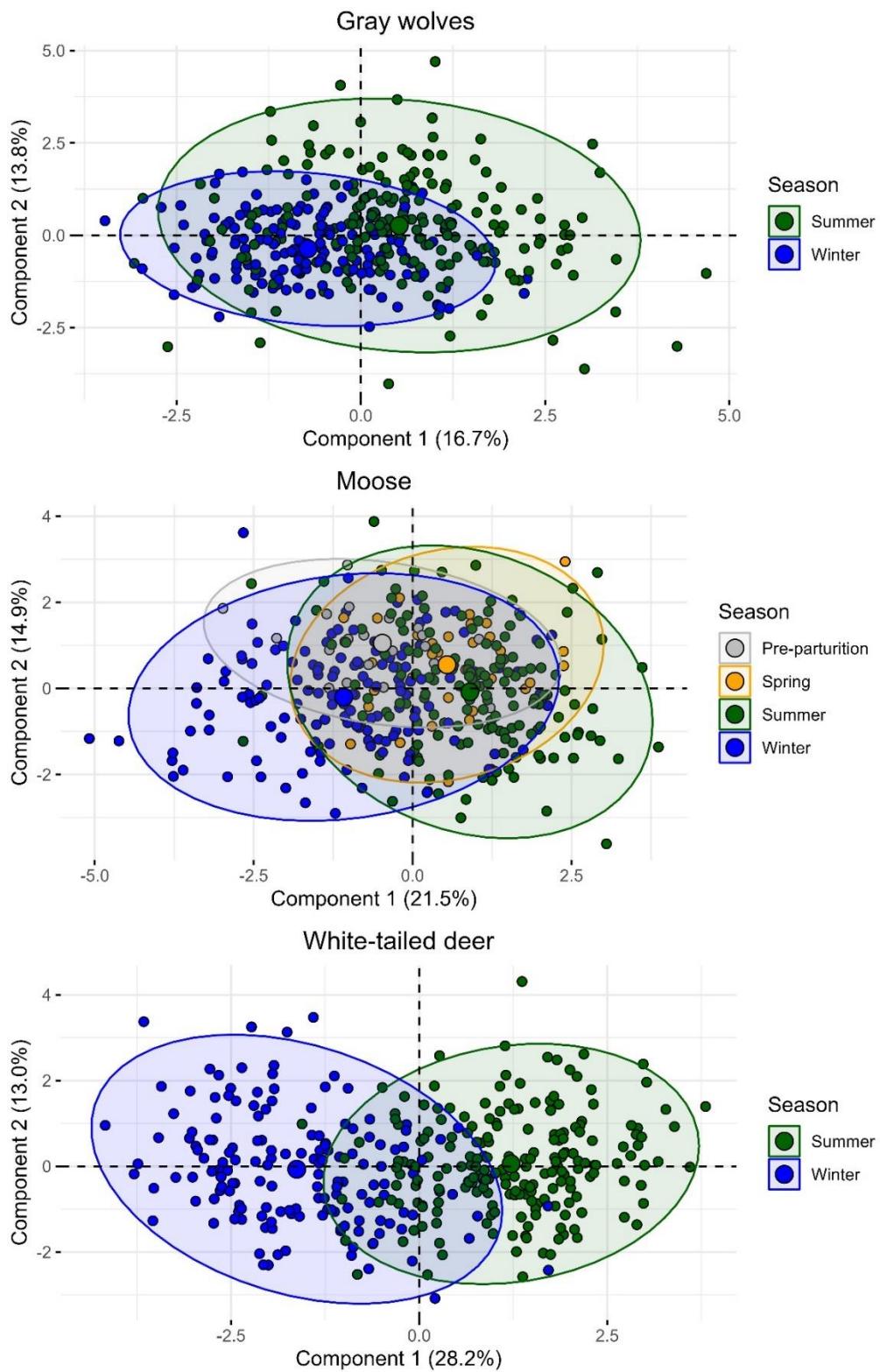


Figure 2.2. Two-dimensional representation of daily space use variation across seasonal space use states for mainland gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer

Figure 2.2 (cont'd)

(*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. Points represent population-level space use for each ordinal date, and shaded polygons represent population-level space use of all ordinal dates comprising a space use state. Component percentages of variation described are included parenthetically. Wolf components were influenced by step-length, distance to Lake Superior, aspect, and coniferous forests (Table 2.1). Moose components were influenced by step-length, turning angle, distance to Lake Superior, coniferous forests, and shrublands. Deer components were influenced by step-length, aspect, slope, distance to Lake Superior, deciduous forests, and shrublands.

Table 2.1. Principle component analysis (PCA) loadings describing daily space use variation across seasonal space use states for mainland gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. Loadings represent the direction and strength of a covariate's influence on space use in two dimensions (Component 1, Component 2). Differences between seasonal space use were best described by components 1 and 2 combined for wolves and component 1 only for moose or deer (Figure 2.2).

Covariate	Wolves		Moose		Deer	
	Component 1 (16.7%)	Component 2 (13.8%)	Component 1 (21.5%)	Component 2 (14.9%)	Component 1 (28.2%)	Component 2 (13.0%)
Step-length	0.143	0.160	0.304	0.348	0.452	-
Turning angle	-	-	-0.287	-0.131	-	-0.254
Aspect	0.400	0.317	0.276	-0.136	0.298	-
Slope	-0.508	-	-0.361	0.432	-0.116	-0.410
Distance to Lake Superior	0.226	0.462	-0.140	-0.516	0.493	-
Distance to roads	-	-	0.304	-0.275	0.251	-0.425
Coniferous forest	-0.366	-0.248	0.236	0.385	-0.468	0.125
Deciduous forest	0.231	-0.424	-	0.211	0.321	0.224
Mixed forest	-0.326	0.587	-0.243	-	-	-0.571
Shrubland	0.108	-	-0.428	-0.192	0.226	-
Wetland	0.441	-0.212	0.457	0.285	-	0.414

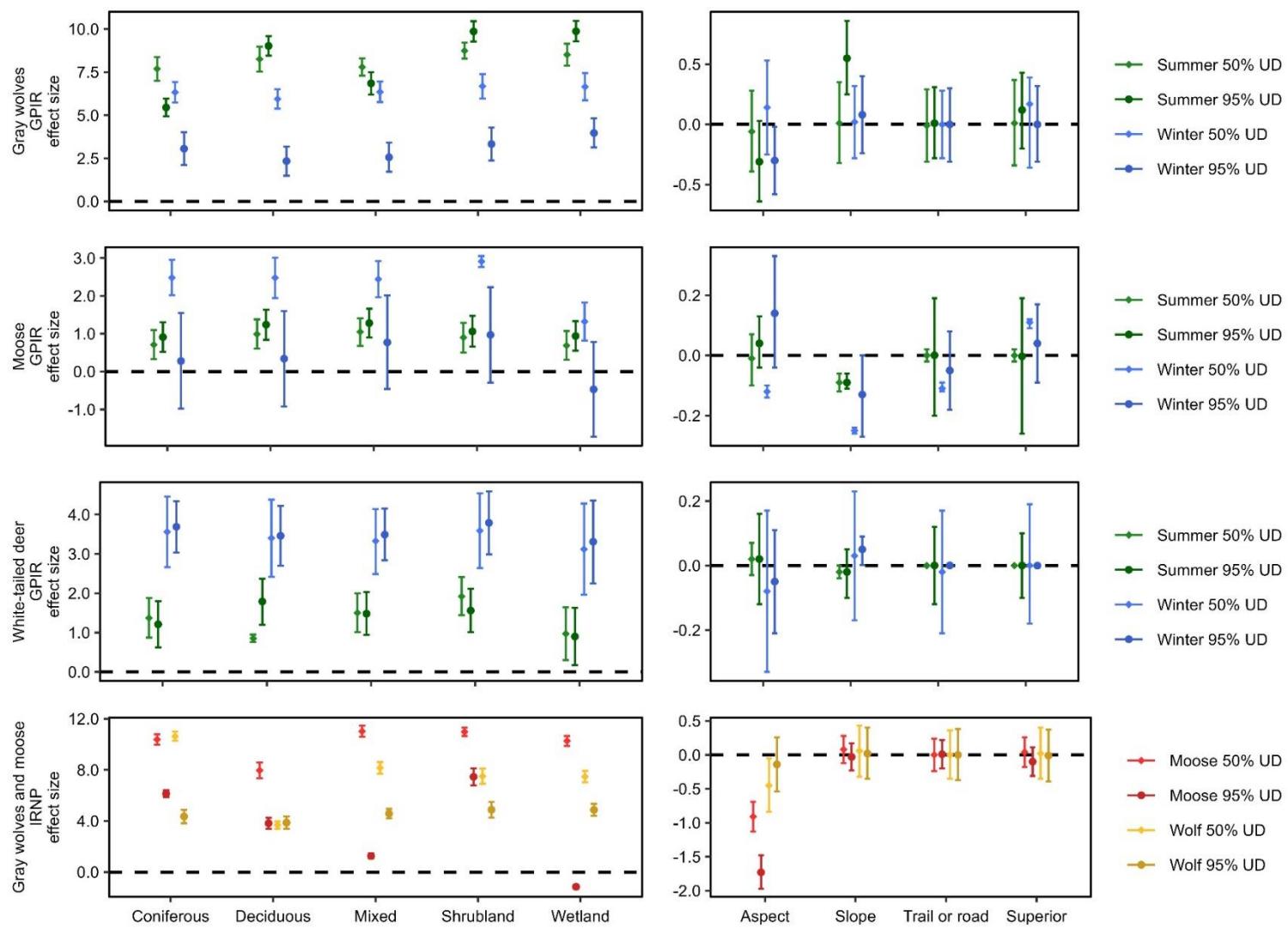


Figure 2.3. Effect size mean with 95% confidence intervals for predictor variables used in weighted resource selection functions for mainland gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) on and near the Grand

Figure 2.3 (cont'd)

Portage Indian Reservation (GPIR), Minnesota, USA, 2010–2021 and island wolves and moose on Isle Royale National Park (IRNP), Michigan, USA, 2018–2021. The left panel column represents land cover as a categorical variable where open water was the reference category. The right panel column represents continuous predictor variables aspect (negative values represent south), slope, distance to nearest trail (island only) or road (mainland only), and distance to Lake Superior. The top three panel rows display seasonal selection, and the bottom panel row displays annual selection.

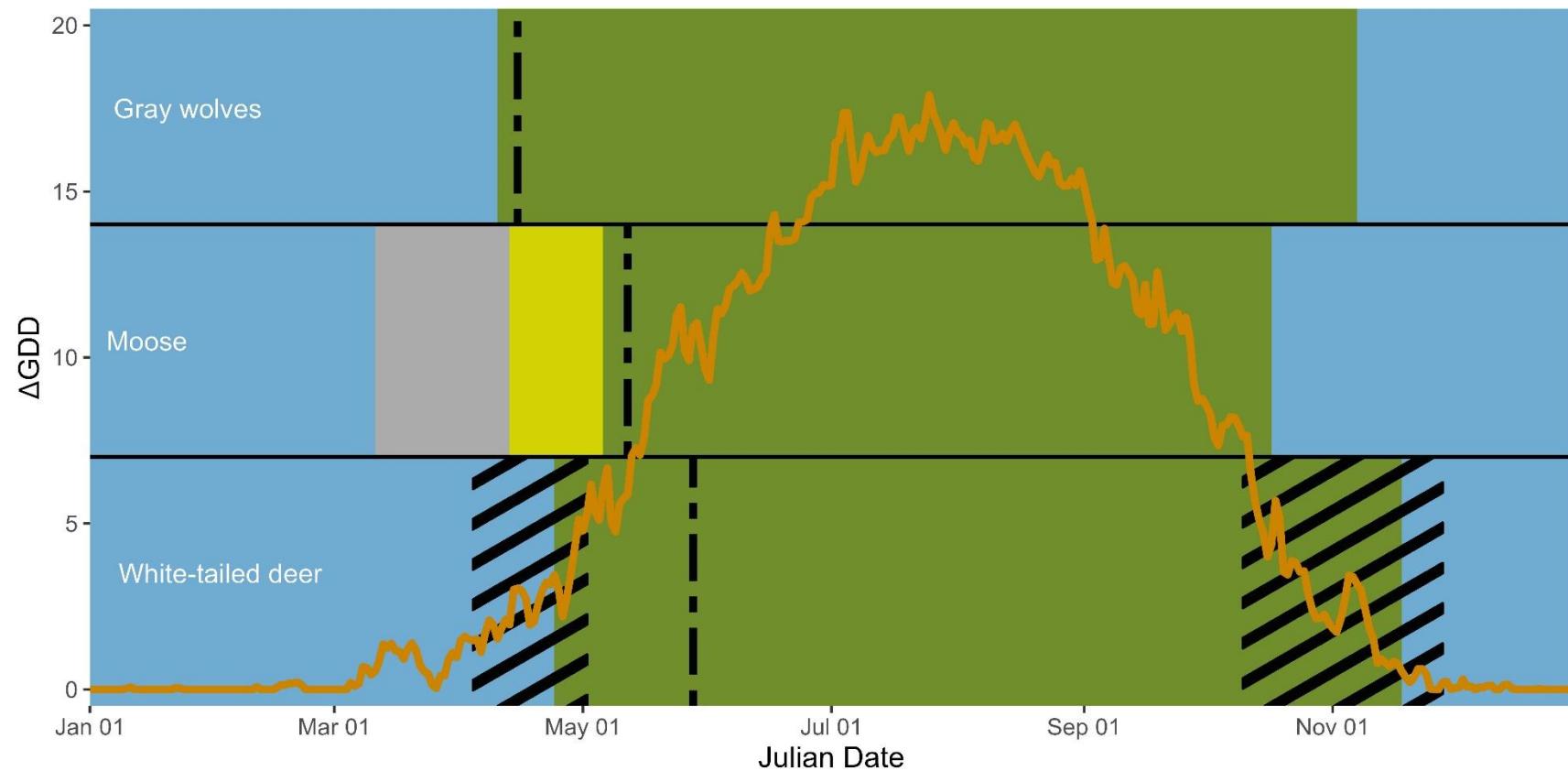


Figure 2.4. Timing of seasonal space use states for mainland gray wolves (*Canis lupus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. The orange line represents the average daily change in growing degree days (ΔGDD). Seasonal space use states are denoted by color where blue represents winter, green represents summer, gray represents spring shift, and yellow represents pre-parturition shift. Black dashed lines represent median annual parturition dates; black diagonal lines represent the spring and fall migration periods.

Island populations

We obtained data from 24 island gray wolves (32,044 locations) and 44 island moose (959,498 locations). One wolf dispersed to the mainland and was not analyzed. Wolves and moose did not form stable seasonal space use state clusters, and we were unable to test if wolves formed clusters after dens were established on the island due to insufficient data. Consequently, we analyzed wolf and moose resource selection year round with wRSFs using 27 wolf-years and 86 moose-years of data. Wolves did not select for any specific resource at the home range-level but selected for south-facing slopes and coniferous forests as well as against deciduous forests within their core ranges (Figure 2.3). Moose selected for south-facing slopes, shrublands, and coniferous forests as well as against wetlands and mixed forests at the home range-level. Within core ranges, moose selected for south-facing slopes and against deciduous forests.

Discussion

We found support for our hypothesis that gray wolf space use differs temporally when primary prey are migratory but not when primary prey are non-migratory. To our knowledge, we are the first to evaluate this space use pattern for a carnivore species with migratory versus non-migratory prey. Previous wolf studies suggested similar responses but did not compare between nearby areas with migratory or non-migratory prey (Walton et al. 2001; Anderson 2014; Roffler et al. 2018). Spotted hyenas (*Crocuta crocuta*) and grizzly bears (*Ursus arctos*) exhibited space use changes in the presence of migratory prey, but their responses were also not tested among non-migratory prey (Glenn and Miller 1980; Trinkel et al. 2004). Our results are further supported by the expectations of ecological seasonality and food web theory, which suggest predators should respond to seasonally changing prey availability or not respond if prey availability does not change (Basille et al. 2013; Furey et al. 2018; Peller et al. 2023). However,

application of our outcome to predators may not be universal. Mountain lions in Patagonia did not alter space use seasonally despite their primary prey being migratory (Gelin et al. 2017). This outcome may stem from migratory prey being sufficiently available year round to support their dietary needs (Gelin et al. 2017).

Seasonal changes in gray wolf space use were most likely driven by seasonal migrations of primary prey (i.e., mainland white-tailed deer) or the lack thereof (i.e., island moose). Deer, moose, and beaver are the primary prey of wolves in our study systems (Chenaux-Ibrahim 2015; Sovie et al. 2023), and despite beaver availability decreasing during winter due to seasonal freezing (Latham et al. 2013), we did not observe seasonal space use states in the absence of deer migration. Wolves whose primary prey were migratory caribou altered their space use seasonally (Walton et al. 2001; Basille et al. 2013) while those whose primary prey were non-migratory Sitka black-tailed deer (*O. hemionus sitkensis*) did not (Roffler et al. 2018). Further, mainland wolf space use in our study area changes synchronously with deer migration (Chapter 1).

Our island and mainland study systems were ecologically similar excepting their mammalian communities (CCRS et al. 2020; USGS 2020; NOAA 2022; Wehr et al. 2023). However, besides primary prey migration, there are several alternative explanations for the lack of seasonality among island gray wolves. Alternatives include spatial movement constraints, pack instability, ability to depredate moose, and weather conditions. Island populations were spatially constrained by water barriers (Licht et al. 2019; Orning et al. 2020) as were other wolves not exhibiting seasonal space use change (Roffler et al. 2018). However, island wolf population density during our study was lower than historical maxima (Romanski et al. 2020), and five monitored wolves did not use the entire island, which suggests wolves were not entirely constrained spatially. Further, island wolves and moose exhibited similar seasonal movement

strategies, as assessed using Migration Mapper (Merkle et al. 2022), to mainland wolves and moose suggesting they were not spatially constrained (Isle Royale National Park, *unpublished data*; Chapter 1).

We were unable to test the influence of pack instability, genetic rescue, and snow conditions on seasonal space use. Island wolves experienced interspecific strife immediately following introduction (Romanski et al. 2020). However, it is unlikely pack instability explains the lack of space use change because social carnivores rapidly overcome social tensions following reintroductions (Hayward et al. 2007), which was the case among introduced island wolves (Romanski et al. 2020). Ability of wolves to hunt moose has been correlated to their genetics (Hoy et al. 2023), but it is unlikely this relationship explains the lack of seasonal space use change because wolves introduced to IRNP rapidly began depredating moose (Romanski et al. 2020). Lack of snow data for the island precluded our ability to test its effects on seasonal space use. Though wolves may alter space use in response to snow depth and compaction (Fuller 1991; Paquet et al. 2010), it is unlikely snow conditions would result in an absence of seasonality rather than altered seasonal timing as observed among other species (Oliver et al. 2020; Rickbeil et al. 2020).

Our second hypothesis that parturition would alter space use of predators received mixed support. Mainland gray wolves switched seasonal space use states immediately before parturition, but island wolves did not. Mainland wolves, however, also maintained similar space use patterns for > 6 months following parturition. Wolves elsewhere altered their space use and resource selection multiple times during denning and rendezvous periods by decreasing movements and selecting flatter slopes (Ciucci and Mech 1992; Basille et al. 2013; Benson et al. 2015). In contrast to these studies, we did not use pre-defined seasons but instead used animal-

defined seasons with longer thresholds (i.e., seasonal transition thresholds [8 days] greater than the duration of moving windows [5 days]). We also accounted for pseudoreplication across individual animals in our resource selection functions which necessarily increased uncertainty in our population-level parameter estimation resulting in fewer identified changes in wolf resource selection (Alston et al. 2022a).

Ungulates, including moose and white-tailed deer, exhibit space use changes corresponding with parturition (Basille et al. 2013; Leech et al. 2017; Francis et al. 2021; Quinlan et al. 2022; Blum et al. 2023). Our mainland results corroborate these and other studies suggesting deer exhibit a single pre-parturition space use change (Petroelje et al. 2021; Darlington et al. 2022) and moose exhibit multiple spring space use changes (Basille et al. 2013; Severud et al. 2019a). However, we did not have sufficient data to assess resident and migratory deer space use separately, and mainland moose in our study exhibited these changes earlier than previously reported (Basille et al. 2013; Francis et al. 2021) while island moose exhibited no space use changes. A likely explanation is that prey space use is influenced by community dynamics similarly to predators. For example, the seasonal arrival of migratory insects can alter resident insect behavior when predators switch to consuming the more abundant migratory species (Satterfield et al. 2020). On the mainland, gray wolves increased their overlap with moose during summer when deer were less abundant due to migration (Chapter 1), which could result in a spatial moose response as suggested for moose co-occurring with migratory caribou (Basille et al. 2013). The absence of space use changes on the island could also be a consequence of the simpler predator-prey system as, unlike mainland wolves, island wolves do not compete with black bears (*Ursus americanus*), coyotes (*C. latrans*), and bobcats (*Lynx rufus*) for neonatal ungulates (Sih 1998; Kautz et al. 2019; Wehr et al. 2023) or because the high density of spatially

constrained island moose likely increases intraspecific resource competition relative to mainland moose (Messier 1994; Romanski et al. 2020).

Seasonal space use changes among our study populations were characterized by changes in resource selection. On the mainland, resource selection appeared to represent seasonal species-specific forage and cover needs. Gray wolves selected for wetlands, shrublands, and deciduous forests in summer, primary foraging locations of their principal prey (Donkor and Fryxell 1999; Tremblay et al. 2005; Chenaux-Ibrahim 2015; Street et al. 2016), and for south-facing slopes in winter which support better ungulate forage (Pearson et al. 1995; Zweifel-Schielly et al. 2009). Prey also selected for habitats with more forage and cover. Moose selected for flatter slopes nearer water in summer, needed for thermal refuge, escape terrain, and foraging (Stephens and Peterson 1984; McCann et al. 2016; Street et al. 2016), and for shrublands and near roads in winter, as observed elsewhere (Ball and Dahlgren 2002; Street et al. 2016). White-tailed deer selected for shrublands and deciduous forests in summer and steeper slopes in winter supporting foraging and mobility (Pearson et al. 1995; Tremblay et al. 2005; Zweifel-Schielly et al. 2009). These results support aspects of optimal foraging theory and leapfrog effect by indicating predators select habitats with the best seasonally available prey forage (MacArthur and Pianka 1966; Schoener 1974; Sih 1998).

Resource selection by island gray wolves and moose may also be explained by forage and cover seeking behaviors. Island wolves did not exhibit resource selection within their home ranges reflecting similar use of available space but did select for south-facing slopes and coniferous forests within core ranges, habitats with better moose forage (Pearson et al. 1995; Zweifel-Schielly et al. 2009). Browse selection by island moose differs from mainland moose due to historic overbrowsing (Krefting 1974). Our results suggest island moose selected

resources within these constraints by selecting for coniferous forests and against wetlands and deciduous forests instead of selecting for wetlands and shrublands as mainland moose did, which might otherwise be expected on the island (Stephens and Peterson 1984). Decreased forage availability may also increase moose selection for coniferous forests because they provide cover and ease of movement during winter (Balsom et al. 1996).

We observed intraspecific space use variation between populations of predators and prey inhabiting ecosystems with differing predator-prey communities but otherwise similar characteristics. Our results support species plasticity in adapting to site-specific community dynamics between trophic levels (Walton et al. 2001; Roffler et al. 2018; Roffler et al. 2021). Our insights into ecological seasonality were limited to space use dynamics; future studies could consider species-specific behaviors, such as mate-seeking or diet, to further improve temporal estimates of ecological seasons. When implementing models with improved behavioral data, we recommend use of cluster analyses when delineating ecological seasons as they provide less biased estimates of seasonal timing and improved insights into space use changes (Basille et al. 2013; Leech et al. 2017; Francis et al. 2021). Finally, we recommend using population-level wAKDE with wRSFs because of their improved ability to account for pseudoreplication across animals in estimating habitat use and movement characteristics (Alston et al. 2022a). Our results also demonstrate the importance of aligning seasonal data collection (e.g., scat collection for diet analysis, remote camera surveys for behavior analysis) with ecological seasons to better describe differences in resource use and other behaviors.

CHAPTER 3:

MOOSE AND WHITE-TAILED DEER MORTALITY PEAKS IN FALL AND LATE WINTER

Abstract

The Grand Portage Band of Lake Superior Chippewa manages for sustainable subsistence harvests of moose (moooz; *Alces alces*) and white-tailed deer (waawaashkeshi; *Odocoileus virginianus*). Large mammals, including moose and deer, exhibit seasonal behaviors such as altered space use and movement strategies. Predators (e.g., gray wolves [ma'iingan; *Canis lupus*]) and humans may adapt to seasonal prey space use resulting in seasonal mortality patterns. We assessed seasonal cause-specific mortality of adult moose (2010–2021) and deer (2016–2022) fitted with GPS collars on and around the Grand Portage Indian Reservation, Minnesota, USA (Gichi Onigaming; GPIR). We hypothesized survival would be influenced by species-specific space use patterns and weather. We estimated survival rates and mortality timing using time-to-event models. We recorded 42 moose mortalities (17 health-related, 8 predation, 4 subsistence harvest, 13 unknown) and 49 deer mortalities (26 predation, 13 harvest, 4 other, 6 unknown). Mean annual moose survival was 83.2% and peaked during late winter (about 25 April) and fall (about 8 October). Mean annual deer survival was 48.0% peaking during late winter (about 25 March) and during their fall migration period (about 11 November). Mortality timing coincided with transitions between space use states (i.e., periods of spatial stability) suggesting ungulates are at greater risk during these transitional periods, though movement strategy (i.e., resident vs. migratory) did not influence survival. Further, increased winter severity corresponded with decreased deer survival. We observed similar temporal peaks in mortality when harvest mortalities were censored suggesting our observed seasonal mortality peaks occur

naturally despite harvest comprising most fall deer mortality. Our results can inform population surveys and harvest regulations by identifying periods of mortality risk and population instability in Gichi Onigaming under Anishinaabe principles of seventh-generation conservation planning.

Introduction

Background

We conducted this study in and around Gichi Onigaming (the great carrying place) on the ancestral and present homelands of the Anishinaabe people. Also known as the Grand Portage Indian Reservation (GPIR), Minnesota, USA, Gichi Onigaming is the present home of the Grand Portage Band of Lake Superior Chippewa, a federally recognized sovereign nation within the United States. In 1854, the Lake Superior Chippewa signed a treaty ceding lands in northeastern Minnesota to the United States. Under the 1854 Treaty, members of the Grand Portage, Fond du Lac, and Bois Forte bands of Lake Superior Chippewa can exercise their usufructuary rights to hunt, fish, and gather throughout the 1854 Ceded Territory which spans northeastern Minnesota from Grand Portage to Moose Lake to Crane Lake (Thompson 2020; 1854 Treaty Authority 2023). These practices cannot be regulated by Minnesota state law, but may be governed by United States federal law, such as the Endangered Species Act (ESA) of 1973. Within Gichi Onigaming, resource harvest (e.g., wild fish and game, timber, and manoomin [wild rice; *Zizania palustris*]) is managed by the elected Tribal Council of the Grand Portage Band.

Our research emphasized three culturally important species to the Anishinaabe seventh-generation planning approach to environmental stewardship: mooz (moose; *Alces alces*), waawaashkeshi (white-tailed deer; *Odocoileus virginianus*), and ma'iingan (gray wolf; *Canis lupus*). Mooz populations in northeastern Minnesota are declining (Severud et al. 2022). These declines are concerning because mooz remain a primary subsistence species for the Anishinaabe

people. Waawaashkeshi are also an important subsistence species for the Anishinaabe people. Waawaashkeshi populations are growing in northeastern Minnesota, but an increased presence of waawaashkeshi may negatively influence mooz populations (Oliveira-Santos et al. 2021; Severud et al. 2023). Ma'iingan are integral to the Anishinaabe creation story, which establishes ma'iingan as kin to the Anishinaabe people (Gilbert et al. 2022). Gichi Onigaming is one of the only places in the conterminous United States where ma'iingan were never extirpated (Boitani 2003). Mooz and waawaashkeshi are primary prey of ma'iingan in Gichi Onigaming (Chenau-Ibrahim 2015).

Seasonal mortality

Seasonal mortality peaks are defined by reoccurring annual periods of greater mortality (Gurarie et al. 2020). Seasonal mortality is influenced by seasonal space use and species-specific movement strategies, which often change in response to shifting environmental conditions (Basille et al. 2013). Predator-prey interactions can vary seasonally in response to species-specific space use within local communities via mechanisms such as migratory coupling (Furey et al. 2018). Improved understanding of seasonal predator-prey interactions may alter interpretations of ecological concepts including apparent competition and prey switching (Holt 1977; Tschanz et al. 2007).

Prey often alter space and resource use seasonally to maximize energetic gain (Avgar et al. 2014). Wildebeest (*Connochaetes taurinus*) (Hopcraft et al. 2014) and caribou (*Rangifer tarandus*) (Couriot et al. 2023) exhibit large-scale space use changes via migration while roe deer (*Capreolus capreolus*) exhibit this pattern at smaller spatial extents by shifting their functional home ranges (Couriot et al. 2018). Resource selection by range-resident populations of sika deer (*Cervus nippon*) (Latham et al. 2015) and feral horses (*Equus caballus*)

(Schoenecker et al. 2023) also demonstrates seasonal changes in response to forage availability. However, space use change is often risky (Avgar et al. 2014; Forrester et al. 2015), and among partially migratory populations, migratory individuals generally incur greater mortality risk (Hebblewhite and Merrill 2007; Robinson et al. 2010).

Legal hunter harvest is a predominant source of anthropogenic large mammal mortality (Collins and Kays 2011; Hill et al. 2019). Wild boar (*Sus scrofa*) (Lagos et al. 2012), elk (Unsworth et al. 1993), and mule deer (*Odocoileus hemionus*) (Dellinger et al. 2018) mortality was greatest during legal hunting seasons. Hunting pressure may also influence natural mortality; Eurasian lynx (*Lynx lynx*) increased roe deer predation during hunting season as roe deer increased use of forests to avoid humans (Gehr et al. 2018).

Moose and white-tailed deer alter their space and resource use seasonally (Basille et al. 2013; Severud et al. 2019a; Darlington et al. 2022). Moose exhibit behavioral changes in spring associated with parturition and forage availability (Basille et al. 2013; Francis et al. 2021) and in winter by reducing movement rates and selecting for snow depths and habitats that appear to optimize energetic requirements and predation risk (Dussault et al. 2005; Cunningham et al. 2022). Deer alter their behavior during late winter switching from lower movement rates on south-facing slopes to higher movement rates in deciduous forests in response to forage availability and snow depth (Massee and Cote 2013; Darlington et al. 2022). Moose and deer mortality varies temporally, with greater natural mortality during winter than summer (Modafferi and Becker 1997; Musante et al. 2010; Vucetich et al. 2012; Dellinger et al. 2018).

Mortality studies generally use pre-defined or descriptive seasons, with few examining mortality in relation to seasonal space use or ecological seasons (Basille et al. 2013; Bastille-Rousseau et al. 2016). Space use states are temporally delineated periods defined by relatively

stable seasonal population-level space use (i.e., movements and resource selection) resulting from species-specific responses to changing biotic and abiotic conditions (e.g., available forage, reproductive activities, snowfall) (Chapter 2). We examined seasonal moose and white-tailed deer mortality in a predominantly subsistence harvest system within the context of seasonal space use states and movement strategies. Moose in our study area exhibit four space use states (summer, winter, spring, and pre-parturition) and three movement strategies (resident, migratory, or nomadic) (Chapter 1; Chapter 2). Deer exhibit two space use states (summer and winter) and two movement strategies (resident or migratory) (Chapter 1; Chapter 2).

We hypothesized moose and white-tailed deer survival would be influenced by movement strategies, space use states, and weather. We predicted moose and deer survival would be (1) similar among seasonal space use states because natural winter mortality and fall subsistence harvest would each contribute to their respective space use states, (2) lower among migratory individuals because of increased vulnerability during migration, (3) lower during winters and subsequent summers of greater winter severity as associated with cumulative malnutrition, and (4) higher during summers and subsequent winters with more growing degree-days (GDD) as associated with greater forage availability. Additionally, we predicted (5) the removal of hunter harvest mortalities from our models would result in the winter space use state being the only period of greater mortality risk.

Study Area

Our approximately 1,200 km² study area included GPIR (47.9614° N, 89.7594° W) and the surrounding 30 km inclusive of the migratory range of our study populations (Chapter 1). This area includes portions of the 1854 Ceded Territory in Minnesota west of GPIR as well as Ontario, Canada north of GPIR and is bordered by Lake Superior to the southeast (Figure 3.1).

Elevations are 183–674 m above sea level (USGS 2020). The area contains 17% deciduous forest, 11% coniferous forest, 44% mixed forest, 9% shrubland, 7% wetland, and \leq 5% each of other land covers (CCRS et al. 2020). Mean daily temperatures during 2009–2019 ranged from 23.3 ± 1.7 C° (mean \pm SD) in July to -17.8 ± 3.5 C° in January (NOAA 2022). Annual average rainfall was 281.9 ± 11.7 cm, and annual average snowfall was 351.6 ± 80.8 cm (NOAA 2022).

Hunter harvest regulations are governed by multiple jurisdictions. In Minnesota, tribal band members can acquire moose harvest permits within the 1854 Ceded Territory (1854 Treaty Authority 2023), but moose may not be harvested by non-band members (MNDNR 2023a). In Ontario, permits to harvest moose are available to Ontario residents (OMNRF 2023). White-tailed deer may be harvested by band members throughout the 1854 Ceded Territory (1854 Treaty Authority 2023), and non-band members who are residents of GPIR may obtain permits to harvest deer on GPIR. The public may obtain permits to harvest deer throughout the study area excluding GPIR (MNDNR 2023a; OMNRF 2023). Though legal in Ontario (OMNRF 2023), gray wolf harvest in Minnesota was legal only during 2012–2014 (Erb et al. 2018).

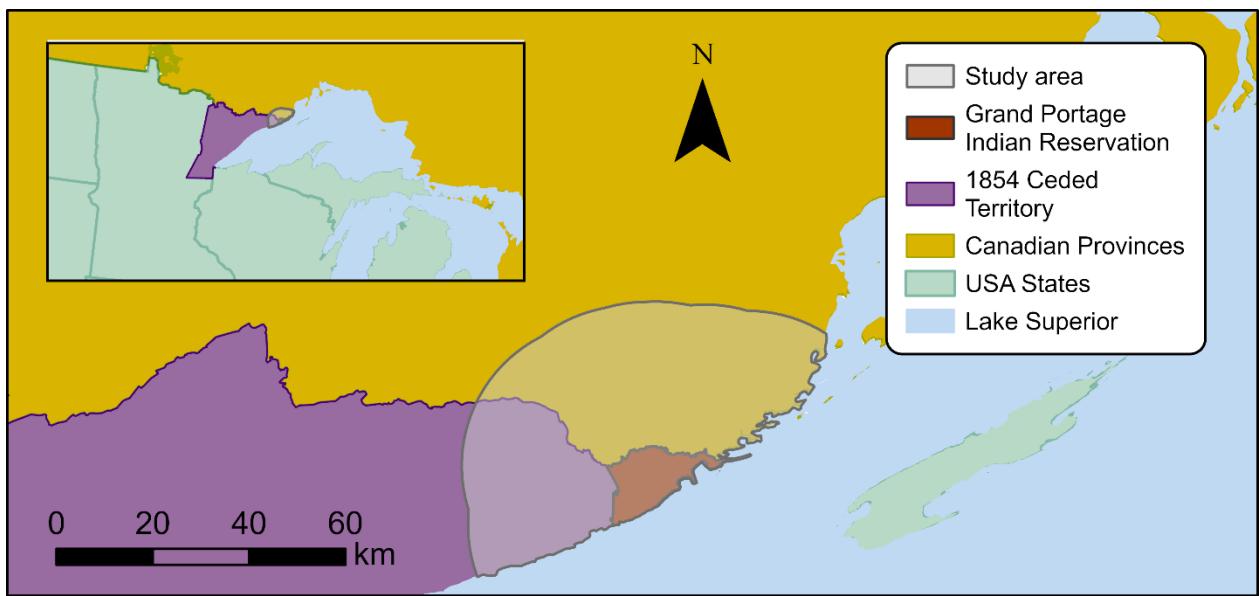


Figure 3.1. Study area on and near the Grand Portage Indian Reservation (GPIR), Minnesota, USA. Our study area included mainland areas near the coast of Lake Superior on GPIR, in the 1854 Ceded Territory within Minnesota, and in Ontario, Canada.

Methods

Data collection

We used data collected by the Grand Portage Band of Lake Superior Chippewa Department of Biology and Environment. We included moose captured using aerial darting during February 2010–March 2020 and white-tailed deer captured using clover traps during March 2016–April 2021 (VerCauteren et al. 1999; Barros et al. 2018; Oliveira-Santos et al. 2021). Moose and deer were monitored through 28 February 2021 and 28 February 2022, respectively. Sex and pregnancy were assessed at time of capture using physical characteristics and progesterone blood tests (Struck et al. 2023). Capture and handling protocols were approved by the Grand Portage Band of Lake Superior Chippewa Tribal Council, Michigan State University institutional animal care and use committee (IACUC) (PROTO202200266), and State University of New York College of Environmental Science and Forestry IACUC (210702).

Collars were programmed to send mortality alerts following 6 h of inactivity. Mortalities were assessed as soon as practical, typically \leq 4 days from receipt of the mortality alert. Date and cause of mortality were assessed using carcass remains and other evidence at mortality sites (Kautz et al. 2019; Kautz et al. 2020). Evidence of predation included predator tracks and scat, canine puncture wounds, hemorrhaging of punctured tissues, and caching (Petroelje et al. 2020). If a mortality was deemed a predation, it was assigned to a specific predator or otherwise considered an unidentified predation (Kautz et al. 2019; Kautz et al. 2020). Evidence of anthropogenic mortalities included proximity to roads, hemorrhaging of intact tissues, and bullet wounds; many anthropogenic mortalities were reported directly by hunters and vehicle drivers. Evidence of health-related mortalities included decreased movement rates before death, hair loss, and infected tissues (Wünschmann et al. 2015). When available, organ samples were submitted

to the University of Minnesota Veterinary Diagnostic Laboratory, St. Paul, Minnesota, USA for pathogen evaluation (Carstensen et al. 2018). We excluded mortalities occurring within 7 days of capture because animal behavior and mortality risk may be altered during this period (Northrup et al. 2014).

Seasonal space use states and movement strategies were previously determined for moose and white-tailed deer in and around GPIR using cluster analyses (Basille et al. 2013), and Brownian bridge movement models (Merkle et al. 2022), respectively (Chapter 1; Chapter 2). Moose space use states were spring (11 March–13 April), pre-parturition (14 April–6 May), summer (7 May–17 October), and winter (18 October–10 March) (Chapter 2). Deer space use states were summer (24 April–18 November) and winter (19 November–23 April) (Chapter 2). Though not previously identified as separate space use states, we also considered deer spring migration (4 April–2 May) and fall migration (10 October–28 November) as distinct periods because they describe seasonal deer movements for 67% of the population (Chapter 1). Using seasonal movements, we categorized individuals as resident (single year-round home range), migratory (seasonally shifting among 2–3 home ranges), nomadic (shifting among ≥ 4 home ranges), or unknown (movement strategy could not be assessed, typically due to mortality or collar failure soon after capture) (Chapter 1).

We used the National Oceanic and Atmospheric Administration (NOAA) Climate Data Online (CDO) tool to extract mean daily snow depth and temperature from weather stations within our study area (Cook County, Minnesota, USA) during 2010–2022 (NOAA 2022). We calculated cumulative winter severity index (CWSI) by summing 1 point for each day snow depth was > 38 cm and 1 point for each day mean ambient temperature was < -17.7 C° (DelGiudice et al. 2002; Kautz et al. 2020). We summed scores continuously beginning 19

November to coincide with the onset of the winter space use state for white-tailed deer (Chapter 2) and the median first day of CWSI accumulation during 2010–2022. We calculated GDD from mean daily temperatures with a latitudinal correction (van Wijk et al. 2012). We calculated GDD cumulatively beginning on 24 April to coincide with the onset of the summer space use state for deer (Chapter 2) and the end of CWSI accrual. We used the same CWSI and GDD values for moose and deer.

Data analysis

To test our hypothesis that space use state, movement strategy, and weather influenced seasonal mortality, we modeled weekly survival separately for moose and white-tailed deer using staggered entry extended Cox proportional hazards models in R (v4.2.1) (Therneau and Grambsch 2000; R Core Team 2023). Cox proportional hazards models fit a baseline hazard function using time-to-event and a covariate matrix (Lin and Wei 1989). To prepare our time-to-event data, we grouped monitoring data into individual-years from 1 March (the approximate mean capture date of moose and deer) to 28 February of the following year and assigned individuals monitored for multiple years unique individual-year identifiers. We reformatted monitoring data from daily to weekly steps and right-censored weeks in which an animal recorded 0 locations. We concluded monitoring if the animal died or was censored (individual alive on 28 February, collar failed, or collar intentionally removed). When an animal died, a mortality event was recorded and monitoring was concluded (Kautz et al. 2020; Therneau et al. 2023).

We included covariates for each of our first four predictions in our covariate matrix. We included (1) moose (winter, spring, pre-parturition, and summer) and white-tailed deer (winter and summer as well as spring migration and fall migration) space use states, (2) moose (resident, nomadic, migratory, or unknown) and deer (resident, migratory, or unknown) movement

strategies, (3) mean weekly CWSI, and (4) mean weekly GDD. We additionally included nuisance covariates for sex and pregnancy status of moose (male or female positive, negative, or unknown) and sex of deer (female or male) because of their potential influences on survival in harvested populations (Nelson and Mech 1986; Ballard et al. 1991). To asses our final prediction (5), we developed models including and excluding hunter harvest mortalities. In total, we developed two moose models and four deer models. For moose, one model included all mortalities and covariates, and the other excluded harvest mortalities. For deer, the first model included harvest mortalities and used only summer and winter as space use states. The second excluded harvest mortalities and used only summer and winter as space use states. The third included harvest mortalities and used spring migration, summer, fall migration, and winter as space use states. The fourth excluded harvest mortalities and used spring migration, summer, fall migration, and winter as space use states. Models including spring and fall migration as separate space use states were used to account for potential migration-specific risk. We fit all models using the *coxph* function in the *survival* R package (Andersen and Gill 1982; Therneau 2022; Therneau et al. 2023). We determined a covariate had significantly impacted survival if the associated *p*-value was < 0.05. We displayed results using the *survminer* R package (Kassambra et al. 2021).

We used multi-modal flexible parametric periodic hazard functions in the *cyclomort* R package to estimate the number of mortality peaks as well as the dates and durations of those peaks with 95% confidence intervals (Gurarie et al. 2020). The utility of these models is the temporal estimation of the hazard function, which describes periods of greater mortality risk (Gurarie et al. 2020). We used the same individual-year delineations from our Cox proportional hazards models in these multi-modal models and similarly included and excluded harvest

mortalities. We input individual-year mortality data for both species into each of six periodic hazard functions with 0–5 possible mortality peaks representing the number of possible transitions between space use states. We assessed model fit using Akaike's information criterion (AIC) (Gurarie et al. 2020; Ewing et al. 2023). We reported our results as mean (95% confidence interval [CI] = [lower 95% CI, upper 95% CI]).

Results

Moose

We monitored 109 adult moose over 11 years resulting in 283 moose-years (10,972 moose-weeks), and we recorded 42 mortalities. In moose-years, our sample included 51 males (18.0%), 88 pregnant females (31.1%), 22 non-pregnant females (7.8%), and 122 females of unknown pregnancy (43.1%). Our sample represented 149 nomadic (52.7%), 89 resident (31.4%), 24 migratory (8.5%), and 21 unknown movement strategy (7.4%) moose-years. Proximate causes of moose mortality included 17 health-related (40.5%; 5 brainworm parasite [*Parelaphostrongylus tenuis*], 5 winter tick [*Dermacentor albipictus*], 7 non-specific health issues), 8 gray wolf predation (19.0%), 4 subsistence hunter harvest (9.5%), and 13 unknown (31.0%).

Mean annual moose survival was 83.2% (95% CI = [78.7%, 88.0%]; Figure 3.2). Our Cox proportional hazards models indicated the spring and pre-parturition space use states contained the greatest risk, followed by the summer and then winter space use states. The multi-modal model corroborated this result indicating there were two mortality peaks (Table B.1): one in late winter, 25 April (95% CI = [9 April, 12 May]), for 54 days (95% CI = [29, 90]) during the spring and pre-parturition space use states, and one in fall during the transition between the summer and winter space use states, 8 October (95% CI = [17 September, 19 October]), for 25

days (95% CI = [11, 55]). Late winter mortalities ($n = 17$) were predominantly health-related (52.9%), gray wolf predation (17.6%), or unknown (29.4%) while fall mortalities were from five sources (Figure 3.3).

Resident, nomadic, and migratory movement strategies did not influence survival, but moose of unknown movement strategy had lower survival ($z = 5.11$, $p < 0.01$). No weather covariates were related to survival (Figure 3.3; Table B.2). Pregnant moose were less likely to die than males ($z = -2.43$, $p = 0.02$) but non-pregnant ($z = 0.48$, $p = 0.63$) and unknown pregnancy moose ($z = -0.58$, $p = 0.56$) exhibited similar survival rates to males (Figure B.1; Table B.3). When harvested moose were censored, estimates remained similar for Cox proportional hazards models (Table B.2) and multi-modal models (Figure 3.4). However, nomadic moose had greater survival than migratory moose and pregnant moose no longer exhibited greater survival than males when harvested moose were censored.

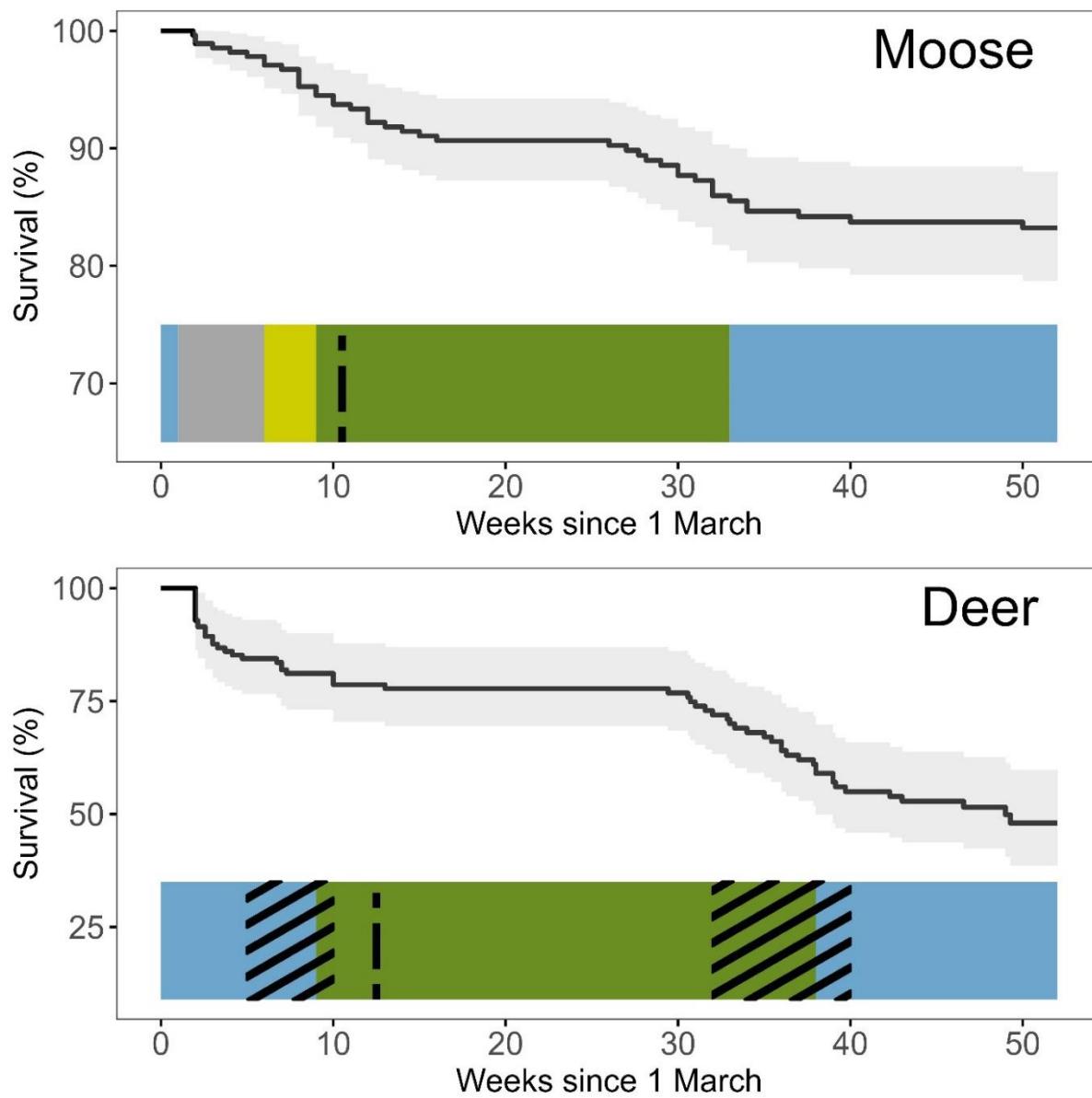


Figure 3.2. Moose (*Alces alces*; 2010–2021) and white-tailed deer (*Odocoileus virginianus*; 2016–2022) survival on and near the Grand Portage Indian Reservation, Minnesota, USA. Solid black lines indicate mean percent population survival with gray shading representing 95% confidence intervals. Colors represent space use states where gray is spring, yellow is pre-parturition, green is summer, and blue is winter. Black dashed lines represent median annual parturition dates, and black diagonal lines represent spring and fall migration periods. Models include harvest mortalities.

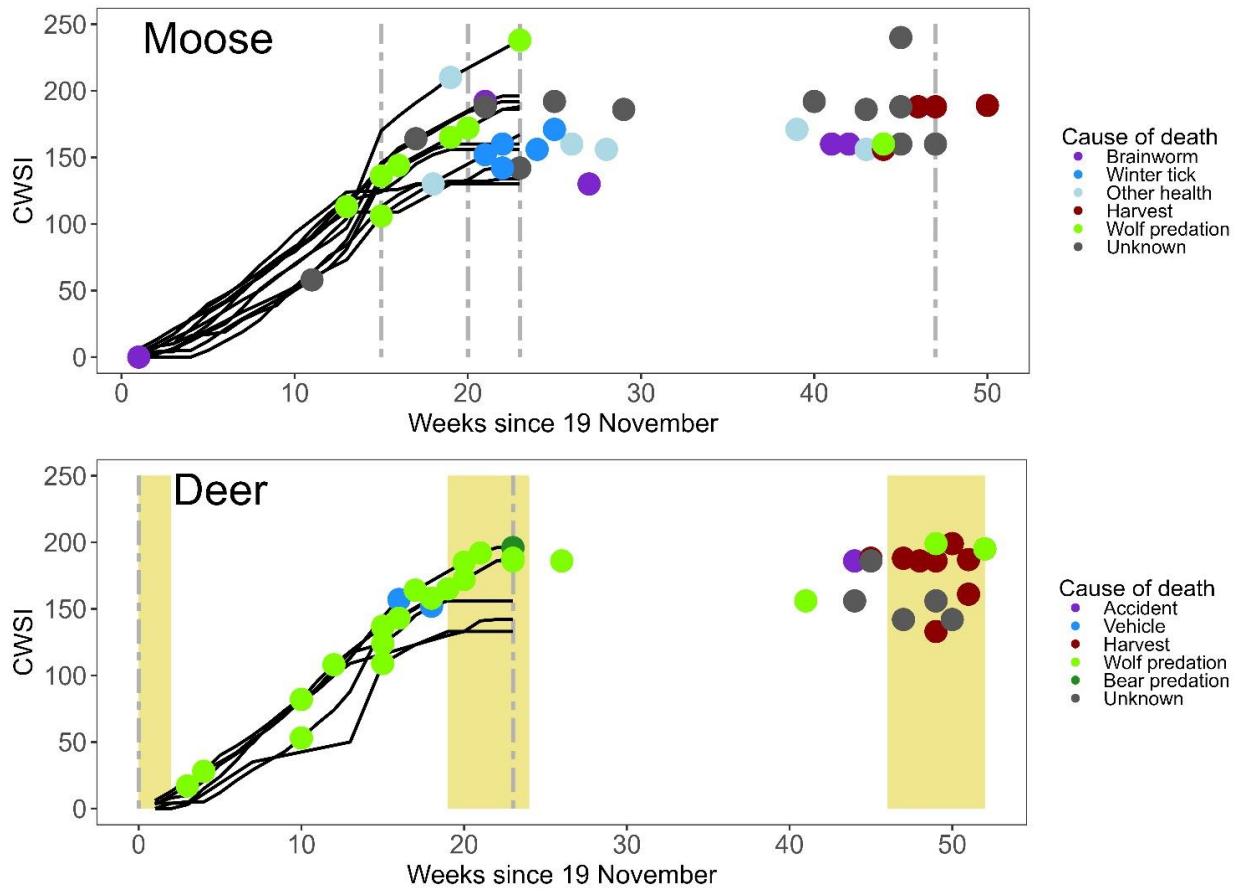


Figure 3.3. Timing of moose (*Alces alces*; 2010–2021) and white-tailed deer (*Odocoileus virginianus*; 2016–2022) mortalities on and near the Grand Portage Indian Reservation, Minnesota, USA relative to cumulative winter severity index (CWSI). Black lines represent each year's CWSI values during 19 November–24 April (Weeks 0–23). Gray dashed lines delineate space use states, yellow highlighting indicates deer migration periods, and colored circles delineate mortality sources.

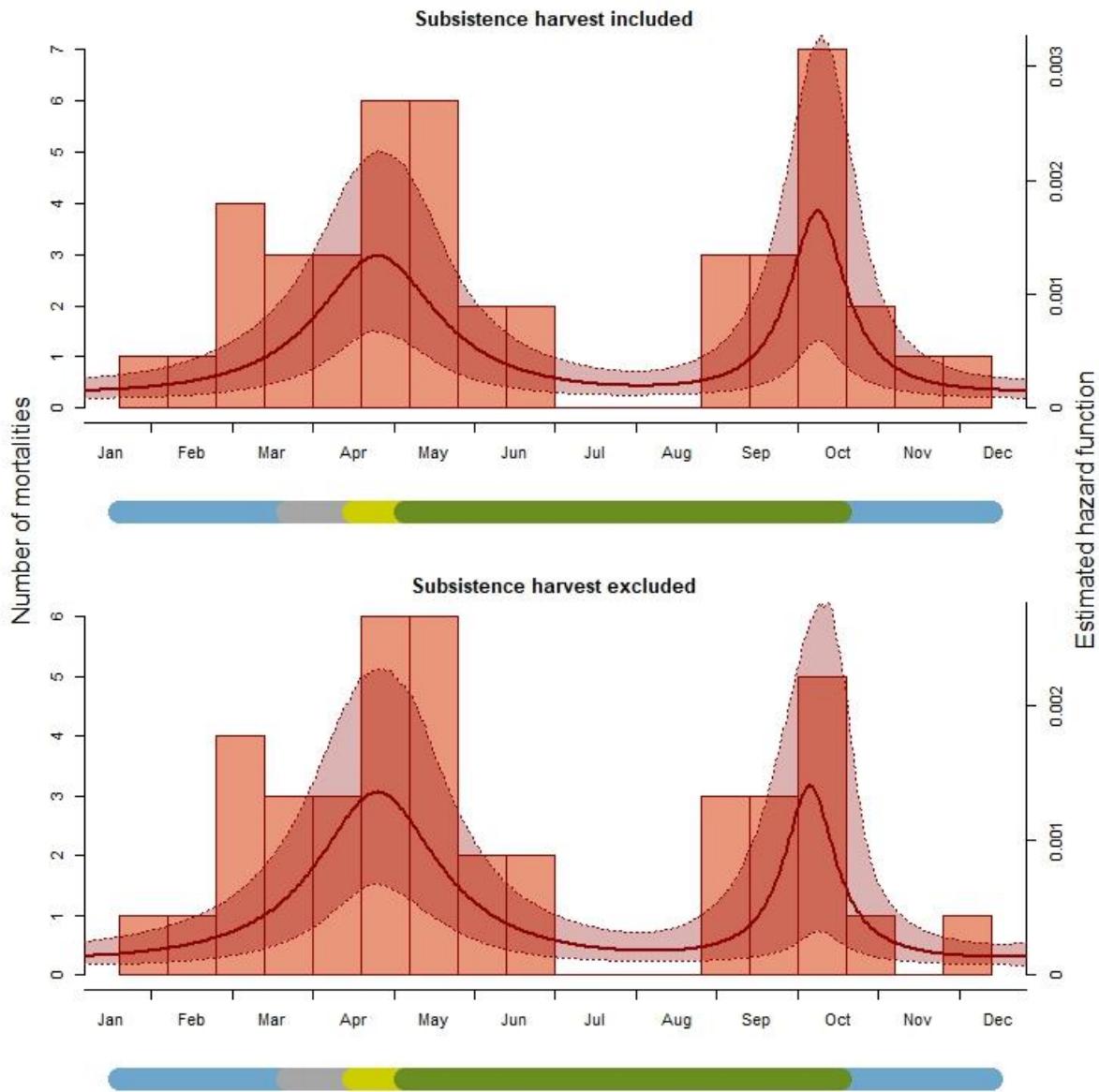


Figure 3.4. Periodic hazard function describing seasonal moose (*Alces alces*) mortality on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. The upper panel represents mortality with subsistence harvest included and the lower panel excludes subsistence harvest. Histograms represent the number of mortalities in a given time period; solid lines represent the estimated hazard function with shading indicating 95% confidence intervals. Colored bars beneath months represent space use states where gray is spring, yellow is pre-parturition, green is summer, and blue is winter.

White-tailed deer

We monitored 75 adult white-tailed deer (2 dispersed outside the study area and were removed from our analyses) for six years resulting in 124 deer-years (3,745 deer-weeks) and 49 mortalities. In deer-years, our sample included 34 males (27.4%) and 90 females (72.6%). Our sample included 69 migratory (55.6%), 30 resident (24.2%), and 25 unknown movement strategy (20.2%) deer-years. Deer mortalities included 25 gray wolf predation (51.0%), 13 hunter harvest (26.5%), 3 vehicle collision (6.1%), 1 black bear (*Ursus americanus*) predation (2.0%), 1 accident (2.0%; fell from cliff), and 6 unknown (12.2%).

Mean annual white-tailed deer survival was 48.0% (95% CI = [38.6%, 59.8%]; Figure 3.2). Our Cox proportional hazards 2- and 4-season models had covariate estimates that did not result in competing interpretations (Table B.4), and space use state did not influence survival in either model. Our multi-modal model indicated deer mortality was best described by two peaks (Table B.1). There was a late winter mortality peak, 25 March (95% CI = [11 March, 8 April]), for 41 days (95% CI = [23, 69]) and a fall mortality peak, 11 November (95% CI = [5 November, 17 November]) for 19 days (95% CI = [10, 35]). Both mortality peaks occurred during transitions between space use states and migration periods (i.e., winter, spring migration, summer, and fall migration) resulting in statistically similar distributions of mortality across space use states in our Cox models. Gray wolf predation accounted for most late winter mortality ($n = 13$, 76.5%) while harvest accounted for most fall mortality ($n = 11$, 78.6%; Figure 3.3).

Resident and migratory movement strategies also did not influence survival in our Cox proportional hazards model, but unknown movement strategy white-tailed deer had lower survival ($z = 4.77$, $p < 0.01$) as did all deer when CWSI was greater ($z = 2.52$, $p = 0.01$; Figure 3.3). Sex and GDD did not influence mortality risk in this model (Figure B.1). When harvest

mortalities were censored, the 2- and 4-season models produced similar coefficients and interpretations (Table B.5). The exception was that mortality was greater during the winter space use state in the 4-season model without harvest ($z = 2.10$, $p = 0.04$). Matching this exception, the timing, 7 November (95% CI = [October 11, December 3]), and duration 47 days (95% CI = [16, 103]) of the fall mortality peak in our multi-model model without harvest were altered (Figure 3.5).

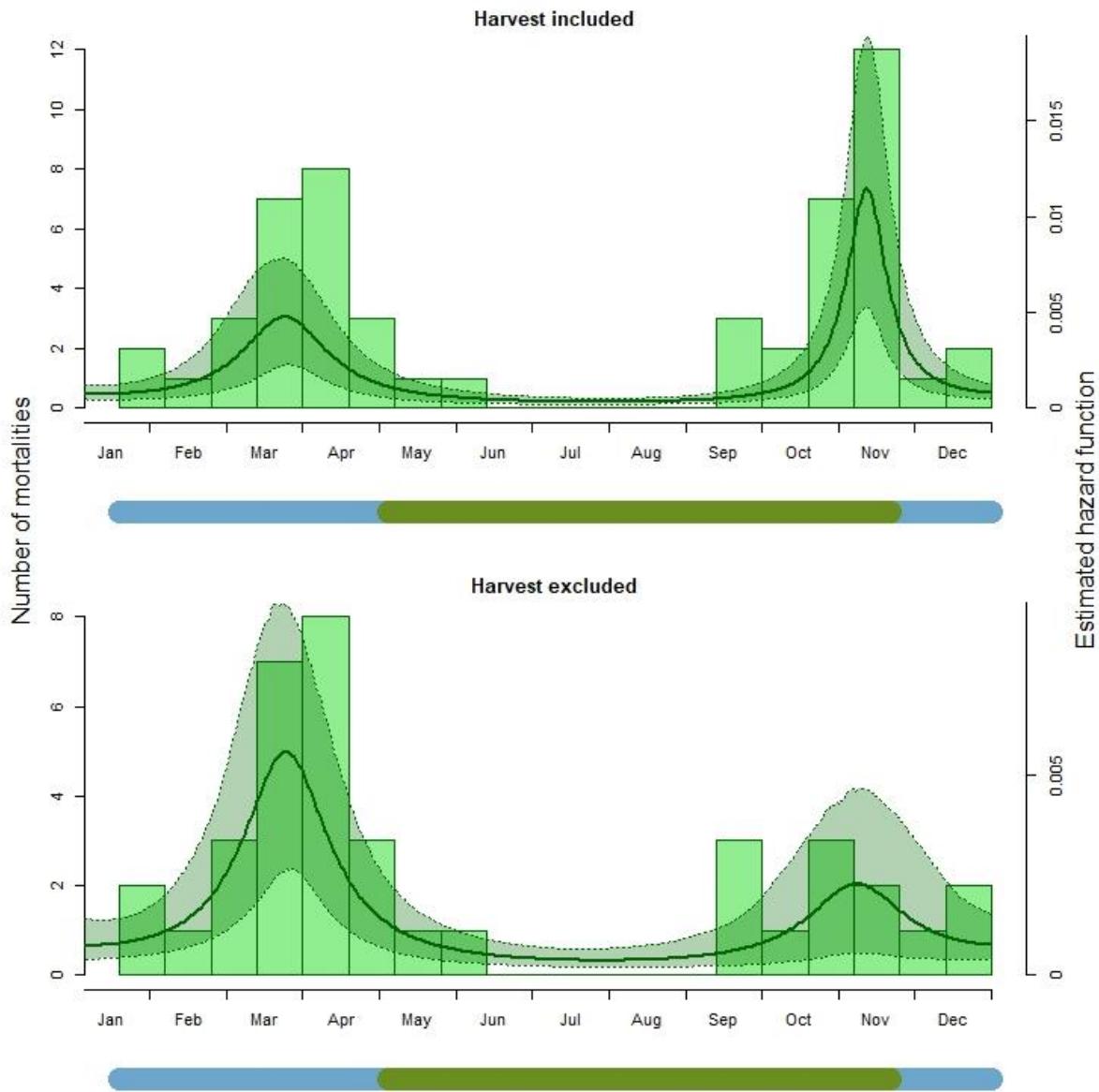


Figure 3.5. Periodic hazard function describing seasonal mortality of white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2022. The upper panel models mortality with harvest included and the lower panel excludes harvest. Histograms represent number of mortalities in a given time period; solid lines represent the estimated hazard function with shading indicating 95% confidence intervals. Colored bars beneath months represent space use states where green is summer and blue is winter.

Discussion

We found mortality risk of moose and white-tailed deer was greatest during transitional periods between space use states, which partially supported our first prediction. Moose mortality risk peaked in April during the spring–pre-parturition–summer space use state transitions and October during the summer–winter space use state transition. Deer mortality peaked in March immediately before spring migration movements and November during the fall migration period. Moose and deer mortality elsewhere was also greatest in late winter and during fall hunting seasons (Lenarz et al. 2009; Musante et al. 2010; Dellinger et al. 2018; Kautz et al. 2020). Moose and deer in our study area exhibited similar ecological seasons (defined by space use states in this study) to other populations (Basille et al. 2013; Francis et al. 2021; Petroelje et al. 2021; Chapter 2), but our observation of seasonal mortality occurring during transitions between ecological seasons may be the first. Caribou mortality in the Northwest Territories, Canada peaked in late April and mid-July (Gurarie et al. 2020; Kelly 2020), likely transition periods between ecological seasons (i.e., spring dispersal, pre-calving, calving, and late summer) as identified among caribou in Quebec, Canada (Basille et al. 2013). Hen harrier (*Circus cyaneus*) mortality in Britain was greatest during post-fledging, dispersal, and winter settlement periods unassessed as ecological seasons but likely transitional considering hen harriers alter their space use and social interactions during these periods (Ewing et al. 2023).

Opposing our second prediction, movement strategy largely did not influence mortality. Migratory and resident moose exhibited similar survival as did migratory and resident white-tailed deer. Migration is often risky due to decreased vigilance and lessened familiarity with new areas (Hebblewhite and Merrill 2007; Hopcraft et al. 2014; Forrester et al. 2015; Gehr et al. 2020). In partially migratory elk populations, migratory individuals generally incur greater risk

than residents (Hebblewhite and Merrill 2009; Robinson et al. 2010) as do migratory deer in our study system (Chapter 1). In contrast, we found mortality was equally likely among movement strategies. A potential explanation for this difference is the scale of migratory movements in our study system. Winter and summer ranges of migratory moose are from 1–20 km apart and from 3–33 km apart for deer (Chapter 1). Comparatively, elk migration distances are typically greater, and predation pressure may vary more between their seasonal ranges (Kauffman et al. 2020; Hebblewhite et al. 2021). Moose and deer with unknown movement strategies experienced greater mortality in our analyses, but this was likely an artefact of moose and deer with unknown movement strategies dying before their movement strategy could be adequately assessed (Chapter 1).

Our third prediction regarding winter severity received mixed support. Moose experienced a late winter mortality peak due primarily to gray wolf predation and health-related causes. Moose are likely more susceptible to the cumulative effects of seasonal malnutrition and parasites (i.e., winter ticks [Wolf et al. 2021]) during late winter putting them at greater risk of predation and health-related mortality (Musante et al. 2010). However, increased winter severity did not predict decreased moose survival in our study; this may be because moose can use greater snow depths to reduce wolf predation risk (Fuller 1991; Dussault et al. 2005). Comparatively, white-tailed deer in our study experienced greater mortality in more severe winters and in summers following more severe winters. This result matches prior work indicating winter severity during the current and preceding year can cause late-winter survival bottlenecks and reduce survival (Mech et al. 1987; Kautz et al. 2020). We acknowledge, however, that the metric we used to assess winter severity (CWSI [DelGiudice et al. 2002]) may not sufficiently explain winter weather variability and its influence on moose and deer. Threshold levels of snow

depth considered by CWSI (38 cm) may be too low to influence moose survival. Further, CWSI weights all snow depths above the threshold equally and does not consider snow quality (i.e., density or top layer crustiness), which likely influence moose, deer, and wolf mobility.

Though our fourth prediction that increased GDD would increase survival was not supported, it is possible the moose mortality peak in late summer reflected a second period of moose susceptibility to parasites, seasonal malnutrition, and predation. Supporting this possibility, moose in Minnesota experienced heat stress in summer and selected for thermal cover (Street et al. 2016; Carstensen et al. 2018). A further analysis of moose mortality using thermal metabolic threshold as a heat stress indicator reported decreased survival under warmer conditions (Lenarz et al. 2009). Increased GDD also did not improve white-tailed deer survival during summer or through the subsequent winter, which contrasts mule deer (Hobbs 1989). These results suggest summer forage availability likely does not influence survival in this system.

Our models produced generally similar results when harvest mortalities were removed, which counters our fifth prediction and suggests fall mortality peaks could represent periods of greater natural mortality similarly to late winter mortality peaks. A difference between the multimodal models with and without harvest was the increased width of the fall white-tailed deer mortality peak when harvest was excluded. A potential explanation for this difference is that hunting seasons typically occur in similar timeframes each year. Our estimated fall deer mortality peak with harvest (11 November) coincided with the midpoints of annual rifle deer hunting seasons in Ontario (e.g., 7 October–15 December in 2023 [OMNRF 2023]) and Minnesota (e.g., 4–18 November in 2023 [MNDNR 2023a]), periods during which Grand Portage Band members also exhibit peak effort and harvest (Grand Portage Band of Lake

Superior Chippewa, *unpublished data*). That this fall deer mortality peak remained present when harvest mortalities were censored, despite harvest being the primary cause of mortality during this period, was unexpected. The presence of a second natural mortality peak may support evidence that migratory deer experience greater gray wolf predation risk during the fall migration period (Chapter 1) similar to other ungulates (Kojola et al. 2004; Hebblewhite and Merrill 2007). Indeed, the six non-harvest migratory deer mortalities of known cause that occurred during fall were directly or indirectly attributed to wolves.

Management implications

Spatial (e.g., designated inland white-tailed deer hunting zones) or temporal (e.g., later seasons) alterations to hunting regulations on GPIR could increase harvest of migratory deer to reduce potential for deer–moose disease transmission. A leading cause of adult moose mortality in northeastern Minnesota is brainworm parasite (Carstensen et al. 2018), and deer movements during migration are directly related to brainworm transmission on GPIR (Oliveira-Santos et al. 2021). In our study, 27% of harvested deer were residents while 73% were migratory; these proportions are similar to population-level estimates of migration rates (67% of deer are migratory, 33% are not [Chapter 1]). Concentrating harvest efforts inland would increase harvest of migratory deer, and delaying hunting seasons (e.g., after 8 November, the date after which > 50% of migratory deer have reached their winter range [Chapter 1]) would increase the proportion of migratory deer available for harvest on GPIR. As mortalities peaked during transitions between space use states or ecological seasons, we suggest management actions (e.g., hunting seasons, supplemental food) during these periods could be used with increased efficacy. We further recommend population surveys occur outside periods of greatest mortality or

transitional space use. For moose and deer in our study area, early- to mid-winter (about 15 December–15 February) was most stable.

BIBLIOGRAPHY

- 1854 Treaty Authority (2023) Treaty harvest. 1854 Treaty Authority.
<https://www.1854treatyauthority.org/treaty-harvest/treaty-harvest.html>. Accessed 11 November 2023
- Adams LG, Farnell R, Oakley MP, Jung TS, Larocque LL, Lortie GM, Mclelland J, Reid ME, Roffler GH, Russell DE (2019) Evaluation of maternal penning to improve calf survival in the Chisana caribou herd. *Wildlife Monographs* 204:5–46
- Ahlén I, Baagøe HJ, Bach L (2009) Behavior of Scandinavian bats during migration and foraging at sea. *Journal of Mammalogy* 90:1318–1323
- Alston JM, Fleming CH, Kays R, Streicher JP, Downs CT, Ramesh T, Calabrese JM (2022a) Mitigating pseudoreplication and bias in resource selection functions with autocorrelation-informed weighting. *Methods in Ecology and Evolution* 14:643–654
- Alston JM, Fleming CH, Noonan MJ, Tucker MA, Silva I, Folta C, Akre TS, Ali AH, Belant JL, Beyer D et al. (2022b) Clarifying space use concepts in ecology: range vs. occurrence distributions. *bioRxiv* 2022:509951
- Andersen PK, Gill RD (1982) Cox's regression model for counting processes: a large sample study. *Annals of Statistics* 10:1100–1120
- Anderson MS (2014) The role of human altered landscapes and predators in the spatial overlap between moose, wolves, and endangered caribou. Thesis, University of Alberta, Edmonton, Alberta, Canada
- Avgar T, Street G, Fryxell JM (2014) On the adaptive benefits of mammal migration. *Canadian Journal of Zoology* 92:481–490
- Ball JP, Dahlgren J (2002) Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by a migrating moose (*Alces alces*) population in winter: relation to habitat composition and road barriers. *Scandinavian Journal of Forest Research* 17:427–435
- Ballard WB, Ayres LA, Krausman PR, Reed DJ, Fancy SG (1997) Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs* 135:3–47
- Ballard WB, Whitman JS, Reed DJ (1991) Population dynamics of moose in south-central Alaska. *Wildlife Monographs* 114:3–49
- Balsom S, Ballard WB, Whitlaw HA (1996) Mature coniferous forest as critical moose habitat. *Alces* 32:131–140
- Barnowe-Meyer KK, White PJ, Davis TL, Byers JA (2009) Predator-specific mortality of pronghorn on Yellowstone's northern range. *Western North American Naturalist* 69:186–194

- Barros DS, Evans AL, Arnemo JM, Stenbacka F, Ericsson G (2018) Effective thiafentanil immobilization and physiological responses of free-ranging moose (*Alces alces*) in northern Sweden. *Veterinary Anaesthesia and Analgesia* 45:502–509
- Basille M, Fortin D, Dussault C, Ouellet JP, Courtois R (2013) Ecologically based definition of seasons clarifies predator–prey interactions. *Ecography* 36:220–229
- Bastille-Rousseau G, Rayl ND, Ellington EH, Schaefer JA, Peers MJL, Mumma MA, Mahoney SP, Murray DL (2016) Temporal variation in habitat use, co-occurrence, and risk among generalist predators and a shared prey. *Canadian Journal of Zoology* 94:191–198
- Benson JF, Mills KJ, Patterson BR (2015) Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. *Biological Conservation* 182:223–232
- Berger J (2007) Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* 3:620–623
- Bergerud A, Ferguson R, Butler H (1990) Spring migration and dispersion of woodland caribou at calving. *Animal Behaviour* 39:360–368
- Blum ME, Stewart KM, Shoemaker KT, Cox M, Wakeling BF, Dilts TE, Bennett JR, Bleich VC (2023) Changes in selection of resources with reproductive state in a montane ungulate. *Movement Ecology* 11:20
- Boitani L (2003) Wolf conservation and recovery. In: Mech LD, Boitani L (eds) *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois, USA. pp 317–340
- Boom MP, Lameris TK, Schreven KHT, Buitendijk NH, Moonen S, de Vries PP, Zaynagutdinova E, Nolet BA, van der Jeugd HP, Eichhorn G (2023) Year-round activity levels reveal diurnal foraging constraints in the annual cycle of migratory and non-migratory barnacle geese. *Oecologia* 202:287–298
- Bräger S, Harraway J, Manly B (2003) Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). *Marine Biology* 143:233–244
- Brandell EE, Fountain-Jones NM, Gilbertson MLJ, Cross PC, Hudson PJ, Smith DW, Stahler DR, Packer C, Craft ME (2021) Group density, disease, and season shape territory size and overlap of social carnivores. *Journal of Animal Ecology* 90:87–101
- Brinkman TJ, Jenks JA, DePerno CS, Haroldson BS, Osborn RG (2004) Survival of white-tailed deer in an intensively farmed region of Minnesota. *Wildlife Society Bulletin* 32:726–731
- Broekhuis F, Elliot NB, Keiwua K, Koinet K, Macdonald DW, Mogensen N, Thuo D, Gopalaswamy AM (2021) Resource pulses influence the spatio-temporal dynamics of a large carnivore population. *Ecography* 44:358–369

- Brönmark C, Skov C, Brodersen J, Nilsson PA, Hansson LA (2008) Seasonal migration determined by a trade-off between predator avoidance and growth. *PLoS One* 3:e1957
- Buehler DM, Piersma T (2008) Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical Transactions of the Royal Society B* 363:247–266
- Calenge C (2006) The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519
- Cardillo M, Warren DL (2016) Analysing patterns of spatial and niche overlap among species at multiple resolutions. *Global Ecology and Biogeography* 25:951–963
- Carmone Jr. FJ, Kara A, Maxwell S (1999) HINoV: a new model to improve market segment definition by identifying noisy variables. *Journal of Marketing Research* 36:501–509
- Carstensen M, Hildebrand EC, Plattner D, Dexter M, St-Louis V, Jennelle C, Wright RG (2018) Determining cause-specific mortality of adult moose in northeast Minnesota, February 2013–July 2017. Technical Report, Minnesota Department of Natural Resources, St. Paul, Minnesota, USA
- CCRS, CCMEO, NRCan, CONABIO, CONAFOR, INEGI, USGS (2020) 2015 land cover of North America at 30 meters. Dataset, Canada Centre for Remote Sensing, Ottawa, Ontario, Canada
- Chenaux-Ibrahim Y (2015) Seasonal diet composition of gray wolves (*Canis lupus*) in northeastern Minnesota determined by scat analysis. Thesis, University of Minnesota, Minneapolis, Minnesota, USA
- Ciucci P, Mech LD (1992) Selection of wolf dens in relation to winter territories in northeastern Minnesota. *Journal of Mammalogy* 73:899–905
- Clare JDJ, Zuckerberg B, Liu N, Stenglein JL, Van Deelen TR, Pauli JN, Townsend PA (2023) A phenology of fear: investigating scale and seasonality in predator-prey games between wolves and white-tailed deer. *Ecology*:e4019
- Collins C, Kays R (2011) Causes of mortality in North American populations of large and medium-sized mammals. *Animal Conservation* 14:474–483
- Corkeron PJ, Connor RC (1999) Why do baleen whales migrate? *Marine Mammal Science* 15:1228–1245
- Couriot OH, Cameron MD, Joly K, Adamczewski J, Campbell MW, Davison T, Gunn A, Kelly AP, Leblond M, Williams J et al. (2023) Continental synchrony and local responses: climatic effects on spatiotemporal patterns of calving in a social ungulate. *Ecosphere* 14:e4399

- Couriot OH, Hewison AJM, Saïd S, Cagnacci F, Chamaillé-Jammes S, Linnell JDC, Mysterud A, Peters W, Urbano F, Heurich M (2018) Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia* 187:47–60
- Cunningham CX, Liston GE, Reinking AK, Boelman NT, Brinkman TJ, Joly K, Hebblewhite M, Boutin S, Czetwertynski S, Sielecki LE (2022) Human and animal movements combine with snow to increase moose-vehicle collisions in winter. *Environmental Research Letters* 17:125007
- Darlington S, Ladle A, Burton AC, Volpe JP, Fisher JT (2022) Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. *Scientific Reports* 12:1072
- de Amorim RC, Hennig C (2015) Recovering the number of clusters in data sets with noise features using feature rescaling factors. *Information Sciences* 324:126–145
- Deacy W, Leacock W, Armstrong JB, Stanford JA (2016) Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. *Ecology* 97:1091–1098
- DelGiudice GD, Riggs MR, Joly P, Pan W (2002) Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* 66:698–717
- Dellinger J, Shores C, Marsh M, Heithaus M, Ripple W, Wirsing A (2018) Impacts of recolonizing gray wolves (*Canis lupus*) on survival and mortality in two sympatric ungulates. *Canadian Journal of Zoology* 96:760–768
- Dinno A (2015) Nonparametric pairwise multiple comparisons in independent groups using Dunn's test. *Stata Journal* 15:292–300
- Donkor NT, Fryxell JM (1999) Impact of beaver foraging on structure of lowland boreal forests of Algonquin Provincial Park, Ontario. *Forest Ecology and Management* 118:83–92
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitao PJ (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46
- Dussault C, Ouellet JP, Courtois R, Huot J, Breton L, Jolicoeur H (2005) Linking moose habitat selection to limiting factors. *Ecography* 28:619–628
- Erb J, Humpal C, Sampson B (2018) Distribution and abundance of wolves in Minnesota, 2017–18. Technial Report, Minnesota Department of Natural Resources, Minneapolis, Minnesota, USA

- Ewing SR, Thomas CE, Butcher N, Denman B, Douglas DJT, Anderson DIK, Anderson GQA, Bray J, Downing S, Dugan R (2023) Illegal killing associated with gamebird management accounts for up to three-quarters of annual mortality in hen harriers *Circus cyaneus*. Biological Conservation 283:110072
- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282–288
- Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586
- Fleming CH, Calabrese JM (2022a) ctmm: continuous-time movement modeling. R package version 1.1.0
- Fleming CH, Calabrese JM (2022b) Variograms and model selection. <https://cran.r-project.org/web/packages/ctmm/vignettes/variogram.html>. Accessed 11 May 2023
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. Ecology 96:1182–1188
- Forrester TD, Casady DS, Wittmer HU (2015) Home sweet home: fitness consequences of site familiarity in female black-tailed deer. Behavioral Ecology and Sociobiology 69:603–612
- Fox J (2015) Applied regression analysis and generalized linear models. Sage Publications, Thousand Oaks, California, USA
- Frades I, Matthiesen R (2010) Overview on techniques in cluster analysis. In: Matthiesen R (ed) Bioinformatics methods in clinical research. Humana Press, New York, New York, USA. pp 81–107
- Frame PF, Meier TJ (2007) Field-assessed injury to wolves captured in rubber-padded traps. Journal of Wildlife Management 71:2074–2076
- Francis AL, Procter C, Kuzyk G, Fisher JT (2021) Female moose prioritize forage over mortality risk in harvested landscapes. Journal of Wildlife Management 85:156–168
- Fryxell J, Sinclair A (1988) Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241
- Fuller TK (1989) Denning behavior of wolves in north-central Minnesota. American Midland Naturalist 121:184–188
- Fuller TK (1991) Effect of snow depth on wolf activity and prey selection in north central Minnesota. Canadian Journal of Zoology 69:283–287

- Furey NB, Armstrong JB, Beauchamp DA, Hinch SG (2018) Migratory coupling between predators and prey. *Nature Ecology & Evolution* 2:1846–1853
- Furey NB, Hinch SG, Bass AL, Middleton CT, Minke-Martin V, Lotto AG (2016) Predator swamping reduces predation risk during nocturnal migration of juvenile salmon in a high-mortality landscape. *Journal of Animal Ecology* 85:948–959
- Gable TD, Windels SK, Bruggink JG, Barber-Meyer SM (2018) Weekly summer diet of gray wolves (*Canis lupus*) in northeastern Minnesota. *American Midland Naturalist* 179:15–27
- Gehr B, Bonnot NC, Heurich M, Cagnacci F, Ciuti S, Hewison AM, Gaillard JM, Ranc N, Premier J, Vogt K (2020) Stay home, stay safe – site familiarity reduces predation risk in a large herbivore in two contrasting study sites. *Journal of Animal Ecology* 89:1329–1339
- Gehr B, Hofer EJ, Pewsner M, Ryser A, Vimercati E, Vogt K, Keller LF (2018) Hunting-mediated predator facilitation and superadditive mortality in a European ungulate. *Ecology and Evolution* 8:109–119
- Gelin ML, Branch LC, Thornton DH, Novaro AJ, Gould MJ, Caragiulo A (2017) Response of pumas (*Puma concolor*) to migration of their primary prey in Patagonia. *PLoS One* 12:e0188877
- Gilbert JH, David P, Price MW, Oren J (2022) Ojibwe perspectives toward proper wolf stewardship and Wisconsin's February 2021 wolf hunting season. *Frontiers in Ecology and Evolution* 10:782840
- Glenn LP, Miller LH (1980) Seasonal movements of an Alaska Peninsula brown bear population. *International Conference on Bear Research and Management* 4:307–312
- Grand Portage Band of Lake Superior Chippewa (2023) Tribal Land & Resources. <https://www.grandportageband.com/tribal-land-resources/>. Accessed 7 April 2023
- Grigg JL (2007) Gradients of predation risk affect distribution and migration of a large herbivore. Thesis, Montana State University, Bozeman, Montana, USA
- Guillemette M (2001) Foraging before spring migration and before breeding in common eiders: does hyperphagia occur? *Condor* 103:633–638
- Gurarie E, Cagnacci F, Peters W, Fleming CH, Calabrese JM, Mueller T, Fagan WF (2017) A framework for modelling range shifts and migrations: asking when, whither, whether and will it return. *Journal of Animal Ecology* 86:943–959
- Gurarie E, Cheraghi F (2017) marcher: migration and range change estimation in R. R package version 0.0-2

Gurarie E, Ovaskainen O (2013) Towards a general formalization of encounter rates in ecology. *Theoretical Ecology* 6:189–202

Gurarie E, Thompson PR, Kelly AP, Larter NC, Fagan WF, Joly K (2020) For everything there is a season: analysing periodic mortality patterns with the cyclomort R package. *Methods in Ecology and Evolution* 11:129–138

Hauge TM, Keith LB (1981) Dynamics of moose populations in northeastern Alberta. *Journal of Wildlife Management* 45:573–597

Hayes RD, Farnell R, Ward RMP, Carey J, Dehn M, Kuzyk GW, Baer AM, Gardner CL, O'Donoghue M (2003) Experimental reduction of wolves in the Yukon: ungulate responses and management implications. *Wildlife Monographs* 152:1–35

Hayward MW, Adendorff J, O'Brien J, Sholto-Douglas A, Bissett C, Moolman LC, Bean P, Fogarty A, Howarth D, Slater R (2007) Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *Open Conservation Biology Journal* 1:1–11

Hebblewhite M (2006) Linking predation risk and forage to ungulate population dynamics. Dissertation, University of Alberta, Edmonton, Alberta, Canada

Hebblewhite M, Martin H, Williams S, Coulombe G, Hessami M, Gano B, Merrill E, Trottier M, Normandeau J, Flowers M et al. (2021) Ya Ha Tinda elk project: long-term monitoring of the partially migratory Ya Ha Tinda elk population, predators, and foraging resources. Technical Report, University of Montana, Missoula, Montana, USA

Hebblewhite M, Merrill EH (2007) Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia* 152:377–387

Hebblewhite M, Merrill EH (2009) Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 90:3445–3454

Hebblewhite M, Merrill EH (2011) Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. *Oikos* 120:1860–1870

Hebblewhite M, Merrill EH, McDonald TL (2005) Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111:101–111

Hennig C (2007) Cluster-wise assessment of cluster stability. *Computational Statistics & Data Analysis* 52:258–271

Hennig C (2020) fpc: flexible procedures for clustering. R package version 2.2-9

- Hill JE, DeVault TL, Belant JL (2019) Cause-specific mortality of the world's terrestrial vertebrates. *Global Ecology and Biogeography* 28:680–689
- Hobbs NT (1989) Linking energy balance to survival in mule deer: development and test of a simulation model. *Wildlife Monographs* 101:3–39
- Holt RD (1977) Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229
- Hopcraft JGC, Morales JM, Beyer H, Borner M, Mwangomo E, Sinclair A, Olff H, Haydon DT (2014) Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs* 84:355–372
- Horne JS, Garton EO, Krone SM, Lewis JS (2007) Analyzing animal movements using Brownian bridges. *Ecology* 88:2354–2363
- Hoy SR, Hedrick PW, Peterson RO, Vucetich LM, Brzeski KE, Vucetich JA (2023) The far-reaching effects of genetic process in a keystone predator species, grey wolves. *Science Advances* 9:eadc8724
- Hoy SR, Peterson RO, Vucetich JA (2022) Ecological studies of wolves on Isle Royale: annual report 2021-2022. Technical Report, Michigan Technological University, Houghton, Michigan, USA
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71
- Kassambra A (2023) ggpubr: 'ggplot2' based publication ready plots. R package version 0.6.0
- Kassambra A, Kosinski M, Biecek P (2021) survminer: drawing survival curves using 'ggplot2'. R package version 0.4.9
- Kassambra A, Mundt F (2020) factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7
- Kauffman MJ, Copeland HE, Cole E, Cuzzocreo M, Dewey S, Fattebert J, Gagnon J, Gelzer E, Graves TA, Hersey K et al. (2020) Ungulate migrations of the western United States, volume 1. Technical Report, United States Geological Survey, Laramie, Wyoming, USA
- Kautz TM, Belant JL, Beyer Jr. DE, Strickland BK, Duquette JF (2020) Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: evidence for a late-winter survival bottleneck. *Ecology and Evolution* 10:1666–1677
- Kautz TM, Belant JL, Beyer Jr. DE, Strickland BK, Petroelje TR, Sollmann R (2019) Predator densities and white-tailed deer fawn survival. *Journal of Wildlife Management* 83:1261–1270

- Kelly A (2020) Seasonal patterns of mortality for boreal caribou (*Rangifer tarandus caribou*) in an intact environment. Thesis, University of Alberta, Edmonton, Alberta, Canada
- Kittle AM, Anderson M, Avgar T, Baker JA, Brown GS, Hagens J, Iwachewski E, Moffatt S, Mosser A, Patterson BR (2017) Landscape-level wolf space use is correlated with prey abundance, ease of mobility, and the distribution of prey habitat. *Ecosphere* 8:e01783
- Kittle AM, Bukombe JK, Sinclair AR, Mduma SA, Fryxell JM (2016) Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. *Movement Ecology* 4:1–18
- Kojola I, Huitu O, Toppinen K, Heikura K, Heikkilä S, Ronkainen S (2004) Predation on European wild forest reindeer (*Rangifer tarandus*) by wolves (*Canis lupus*) in Finland. *Journal of Zoology* 263:229–235
- Krefling LW (1974) The ecology of the Isle Royale moose with special reference to the habitat. University of Minnesota, Minneapolis, Minnesota, USA
- Lack D (1954) Cyclic mortality. *Journal of Wildlife Management* 18:25–37
- Lagos L, Picos J, Valero E (2012) Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. *European Journal of Wildlife Research* 58:661–668
- Latham ADM, Herries D, Latham MC (2015) Seasonal patterns of resource selection by introduced sika deer (*Cervus nippon*) in Kaweka Forest Park Recreational Hunting Area, New Zealand. *New Zealand Journal of Ecology* 39:291–302
- Latham ADM, Latham MC, Knopff KH, Hebblewhite M, Boutin S (2013) Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography* 36:1276–1290
- Leech H, Jelinski DE, DeGroot L, Kuzyk G (2017) The temporal niche and seasonal differences in predation risk to translocated and resident woodland caribou (*Rangifer tarandus caribou*). *Canadian Journal of Zoology* 95:809–820
- Lenarz MS, Nelson ME, Schrage MW, Edwards AJ (2009) Temperature mediated moose survival in northeastern Minnesota. *Journal of Wildlife Management* 73:503–510
- Licht DS, Moen RA, Brown DP, Romanski MC, Gitzen RA (2019) The Canada lynx (*Lynx canadensis*) of Isle Royale: over-harvest, climate change, and the extirpation of an island population. *Canadian Field-Naturalist* 129:139–151
- Lin DY, Wei LJ (1989) The robust inference for the Cox proportional hazards model. *Journal of the American Statistical Association* 84:1074–1078

MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. *American Naturalist* 100:603–609

Macdonald DW (1984) Carnivore social behaviour—does it need patches? (reply). *Nature* 307:390

Madsen T, Shine R (1996) Seasonal migration of predators and prey--a study of pythons and rats in tropical Australia. *Ecology* 77:149–156

Masse A, Cote SD (2013) Spatiotemporal variations in resources affect activity and movement patterns of white-tailed deer (*Odocoileus virginianus*) at high density. *Canadian Journal of Zoology* 91:252–263

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP (2009) Habitat selection at multiple scales. *Ecoscience* 16:238–247

McCann NP, Moen RA, Windels SK, Harris TR (2016) Bed sites as thermal refuges for a cold-adapted ungulate in summer. *Wildlife Biology* 22:228–237

Mech LD (1977) Wolf-pack buffer zones as prey reservoirs. *Science* 198:320–321

Mech LD, Barber-Meyer SM (2020) Sixty years of white-tailed deer (*Odocoileus virginianus*) yarding in a gray wolf (*Canis lupus*)–deer system. *Canadian Field-Naturalist* 133:343–351

Mech LD, Boitani L (2003) Wolf social ecology. In: Mech LD, Boitani L (eds) *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, Illinois, USA. pp 1-34

Mech LD, McRoberts RE, Peterson RO, Page RE (1987) Relationship of deer and moose populations to previous winters' snow. *Journal of Animal Ecology* 56:615–627

Melzheimer J, Streif S, Wasiolka B, Fischer M, Thalwitzer S, Heinrich SK, Weigold A, Hofer H, Wachter B (2018) Queuing, takeovers, and becoming a fat cat: long-term data reveal two distinct male spatial tactics at different life-history stages in Namibian cheetahs. *Ecosphere* 9:e02308

Merkle JA, Gage J, Sawyer H, Lowrey B, Kauffman MJ (2022) Migration Mapper: identifying movement corridors and seasonal ranges for large mammal conservation. *Methods in Ecology and Evolution* 13:2397–2403

Messier F (1994) Ungulate population models with predation: a case study with the North American moose. *Ecology* 75:478–488

Michelot C, Leclerc M, Taillon J, Dussault C, Hénault Richard J, Côté SD (2023) Evidence of migratory coupling between grey wolves and migratory caribou. *Oikos* 2023:e10150

- Middleton O, Svensson H, Scharlemann JP, Faurby S, Sandom C (2021) CarniDIET 1.0: a database of terrestrial carnivorous mammal diets. *Global Ecology and Biogeography* 30:1175–1182
- Mitchell WA, Lima SL (2002) Predator-prey shell games: large-scale movement and its implications for decision-making by prey. *Oikos* 99:249–259
- MNDNR (2023a) Minnesota hunting & trapping regulations. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA
- MNDNR (2023b) Minnesota normal annual snowfall: 1981-2010.
https://www.dnr.state.mn.us/climate/summaries_and_publications/normals_snow_1981_2010.html. Accessed 15 August 2023
- Modafferi RD, Becker EF (1997) Survival of radiocollared adult moose in lower Susitna River Valley, southcentral Alaska. *Journal of Wildlife Management* 61:540–549
- Moorhouse-Gann RJ, Kean EF, Parry G, Valladares S, Chadwick EA (2020) Dietary complexity and hidden costs of prey switching in a generalist top predator. *Ecology and Evolution* 10:6395–6408
- Musante AR, Pekins PJ, Scarpitti DL (2010) Characteristics and dynamics of a regional moose *Alces alces* population in the northeastern United States. *Wildlife Biology* 16:185–204
- Musiani M, Leonard JA, Cluff HD, Gates CC, Mariani S, Paquet PC, Vila C, Wayne RK (2007) Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat colour and association with migratory caribou. *Molecular Ecology* 16:4149–4170
- National Park Service (2022) Minong: a Traditional Cultural Property.
<https://www.nps.gov/ISRO/learn/historyculture/american-indian.htm>. Accessed 4 May 2023
- Nelson ME, Mech LD (1981) Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs* 77:3–53
- Nelson ME, Mech LD (1986) Mortality of white-tailed deer in northeastern Minnesota. *Journal of Wildlife Management* 50:691–698
- Nelson ME, Mech LD (1991) Wolf predation risk associated with white-tailed deer movements. *Canadian Journal of Zoology* 69:2696–2699
- Newsome TM, Boitani L, Chapron G, Ciucci P, Dickman CR, Dellinger JA, López-Bao JV, Peterson RO, Shores CR, Wirsing AJ (2016) Food habits of the world's grey wolves. *Mammal Review* 46:255–269

Nielson MR, Sawyer H, McDonald TL (2013) BBMM: Brownian bridge movement model. R package version 3.0

NOAA (2000) NOAA medium resolution shoreline. Dataset, National Oceanic and Atmospheric Administration, Washington, D.C., United States

NOAA (2022) Climate Data Online (CDO). Dataset, National Climatic Data Center, Asheville, North Carolina, USA

Northrup JM, Anderson Jr. CR, Wittemyer G (2014) Effects of helicopter capture and handling on movement behavior of mule deer. *Journal of Wildlife Management* 78:731–738

Nuñez TA, Hurley MA, Graves TA, Ortega AC, Sawyer H, Fattebert J, Merkle JA, Kauffman MJ (2022) A statistical framework for modelling migration corridors. *Methods in Ecology and Evolution* 13:2635–2648

O'Brien O, Allen S, Krützen M, Connor R (2020) Alliance-specific habitat selection by male Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. *Animal Behaviour* 164:39–49

Oliveira-Santos LGR, Moore SA, Severud WJ, Forester JD, Isaac EJ, Chenaux-Ibrahim Y, Garwood T, Escobar LE, Wolf TM (2021) Spatial compartmentalization: a nonlethal predator mechanism to reduce parasite transmission between prey species. *Science Advances* 7:eabj5944

Oliver RY, Mahoney PJ, Gurarie E, Krikun N, Weeks BC, Hebblewhite M, Liston G, Boelman N (2020) Behavioral responses to spring snow conditions contribute to long-term shift in migration phenology in American robins. *Environmental Research Letters* 15:045003

OMNRF (2022) Ontario Road Network (ORN) segment with address. Dataset, Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada

OMNRF (2023) 2023 hunting regulations summary. Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario, Canada

Orning EK, Romanski MC, Moore SA, Chenaux-Ibrahim Y, Hart J, Belant JL (2020) Emigration and first-year movements of initial wolf translocations to Isle Royale. *Northeastern Naturalist* 27:701–708

Paquet PC, Alexander S, Donelon S, Callaghan C (2010) Influence of anthropogenically modified snow conditions on wolf predatory behaviour. In: Musiani M, Boitani L, Paquet PC (eds) *The world of wolves: new perspectives on ecology, behaviour, and management*. University of Calgary Press, Calgary, Alberta, Canada. pp 157-174

Pearson SM, Turner MG, Wallace LL, Romme WH (1995) Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecological Applications* 5:744–755

Pebesma E (2018) Simple features for R: standardized support for spatial vector data. *R Journal* 10:439–446

Peller T, Guichard F, Altermatt F (2023) The significance of partial migration for food web and ecosystem dynamics. *Ecology Letters* 26:3–22

Petroelje TR, Belant JL, Beyer Jr. DE, Svoboda NJ (2019) Subsidies from anthropogenic resources alter diet, activity, and ranging behavior of an apex predator (*Canis lupus*). *Scientific Reports* 9:13438

Petroelje TR, Belant JL, Beyer Jr. DE, Svoboda NJ (2020) Identification of carnivore kill sites is improved by verified accelerometer data. *Animal biotelemetry* 8:18

Petroelje TR, Kautz TM, Beyer Jr. DE, Belant JL (2021) Interference competition between wolves and coyotes during variable prey abundance. *Ecology and Evolution* 11:1413–1431

Phillips R, Berg WE, Siniff D (1973) Moose movement patterns and range use in northwestern Minnesota. *Journal of Wildlife Management* 37:266–278

Potvin C, Roff DA (1993) Distribution-free and robust statistical methods: viable alternatives to parametric statistics. *Ecology* 74:1617–1628

Quenette PY (1990) Functions of vigilance behaviour in mammals: a review. *Acta oecologica* 11:801–818

Quinlan BA, Rosenberger JP, Kalb DM, Abernathy HN, Thorne ED, Ford WM, Cherry MJ (2022) Drivers of habitat quality for a reintroduced elk herd. *Scientific Reports* 12:20960

R Core Team (2023) R: a language and environment for statistical computing. Software, R Foundation for Statistical Computing, Vienna, Austria

Reneerkens J, Morrison RIG, Ramenofsky M, Piersma T, Wingfield JC (2002) Baseline and stress-induced levels of corticosterone during different life cycle substages in a shorebird on the high arctic breeding grounds. *Physiological and Biochemical Zoology* 75:200–208

Rickbeil GJM, Coops NC, Berman EE, McClelland CJR, Bolton DK, Stenhouse GB (2020) Changing spring snow cover dynamics and early season forage availability affect the behavior of a large carnivore. *Global Change Biology* 26:6266–6275

Robinson BG, Hebblewhite M, Merrill EH (2010) Are migrant and resident elk (*Cervus elaphus*) exposed to similar forage and predation risk on their sympatric winter range? *Oecologia* 164:265–275

Roffler GH, Allen JM, Massey A, Levi T (2021) Metabarcoding of fecal DNA shows dietary diversification in wolves substitutes for ungulates in an island archipelago. *Ecosphere* 12:e03297

Roffler GH, Gregovich DP (2018) Wolf space use during denning season on Prince of Wales Island, Alaska. *Wildlife Biology* 2018:wlb.00468

Roffler GH, Gregovich DP, Larson KR (2018) Resource selection by coastal wolves reveals the seasonal importance of seral forest and suitable prey habitat. *Forest Ecology and Management* 409:190–201

Romanski MC, Orning EK, Kellner KF, Beyer Jr. DE, Brzeski KE, Hart J, Lonsway Jr. DH, McLaren AAD, Moore SA, Patterson BR et al. (2020) Wolves and the Isle Royale environment: restoring an island ecosystem, 2018–2020. Technical Report, National Park Service, Isle Royale National Park, Michigan, USA

Ruprecht JS, Hersey KR, Hafen K, Monteith KL, DeCesare NJ, Kauffman MJ, MacNulty DR (2016) Reproduction in moose at their southern range limit. *Journal of Mammalogy* 97:1355–1365

Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV, Woolmer G (2002) The human footprint and the last of the wild. *BioScience* 52:891–904

Satterfield DA, Sillett TS, Chapman JW, Altizer S, Marra PP (2020) Seasonal insect migrations: massive, influential, and overlooked. *Frontiers in Ecology and the Environment* 18:335–344

Sawyer H, LeBeau CW, McDonald TL, Xu W, Middleton AD (2019) All routes are not created equal: an ungulate's choice of migration route can influence its survival. *Journal of Applied Ecology* 56:1860–1869

Schoenecker KA, Esmaeili S, King SRB (2023) Seasonal resource selection and movement ecology of free-ranging horses in the western United States. *Journal of Wildlife Management* 87:e22341

Schoener TW (1974) The compression hypothesis and temporal resource partitioning. *Proceedings of the National Academy of Sciences* 71:4169–4172

Schooler SL, Finnegan SP, Fowler NL, Kellner KF, Lutto AL, Parchizadeh J, van den Bosch M, Zubiria Perez A, Masinde LM, Mwampeta SB et al. (2022) Factors influencing lion movements and habitat use in the western Serengeti ecosystem, Tanzania. *Scientific Reports* 12:18890

Servheen C (1983) Grizzly bear food habits, movements, and habitat selection in the Mission Mountains, Montana. *Journal of Wildlife Management* 47:1026–1035

Severud WJ, Berg SS, Ernst CA, DelGiudice GD, Moore SA, Windels SK, Moen RA, Isaac EJ, Wolf TM (2022) Statistical population reconstruction of moose (*Alces alces*) in northeastern Minnesota using integrated population models. *PLoS One* 17:e0270615

- Severud WJ, DelGiudice GD, Obermoller TR (2019a) Association of moose parturition and post-parturition habitat with calf survival. *Journal of Wildlife Management* 83:175–183
- Severud WJ, DelGiudice GD, Obermoller TR, Enright TA, Wright RG, Forester JD (2015) Using GPS collars to determine parturition and cause-specific mortality of moose calves. *Wildlife Society Bulletin* 39:616–625
- Severud WJ, Kautz TM, Belant JL, Moore SA (2023) Mineral licks as a potential nidus for parasite transmission. *Food Webs* 36:e00299
- Severud WJ, Obermoller TR, DelGiudice GD, Fieberg JR (2019b) Survival and cause-specific mortality of moose calves in northeastern Minnesota. *Journal of Wildlife Management* 83:1131–1142
- Signer J, Fieberg J, Avgar T (2019) Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution* 9:880–890
- Sih A (1998) Game theory and predator–prey response races. In: Dugatkin L, Reeve H (eds) Game theory and animal behavior. Oxford University Press, Oxford, United Kingdom. pp 221–238
- Sims DW, Southall EJ, Richardson AJ, Reid PC, Metcalfe JD (2003) Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series* 248:187–196
- Sinclair EH, Zeppelin TK (2002) Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammalogy* 83:973–990
- Smereka CA, Frame PF, Edwards MA, Frame DD, Slater OM, Derocher AE (2020) Seasonal habitat selection of cougars *Puma concolor* by sex and reproductive state in west-central Alberta, Canada. *Wildlife Biology* 2020:wlb.00735
- Sovie AR, Romanski MC, Orning EK, Marneweck DG, Nichols R, Moore SA, Belant JL (2023) Temporal variation in translocated Isle Royale wolf diet. *Ecology and Evolution* 13:e9873
- Stephens PW, Peterson RO (1984) Wolf-avoidance strategies of moose. *Ecography* 7:239–244
- Street GM, Fieberg J, Rodgers AR, Carstensen M, Moen R, Moore SA, Windels SK, Forester JD (2016) Habitat functional response mitigates reduced foraging opportunity: implications for animal fitness and space use. *Landscape Ecology* 31:1939–1953
- Struck M, Severud WJ, Chenaux-Ibrahim YM, Isaac EJ, Brown JL, Moore SA, Wolf TM (2023) Refining the moose serum progesterone threshold to diagnose pregnancy. *Conservation Physiology* 11:coad003

Suraci JP, Smith JA, Chamaillé-Jammes S, Gaynor KM, Jones M, Luttbeg B, Ritchie EG, Sheriff MJ, Sih A (2022) Beyond spatial overlap: harnessing new technologies to resolve the complexities of predator–prey interactions. *Oikos* 2022:e09004

Theon E (2022) padr: quickly get datetime data ready for analysis. R package version 0.6.2

Therneau TM (2022) A package for survival analysis in R. R package version 3.3-1

Therneau TM, Crowson C, Atkinson E (2023) Using time dependent covariates and time dependent coefficients in the Cox model. <https://stat.ethz.ch/R-manual/R-patched/library/survival/doc/timedep.pdf>. Accessed 6 June 2023

Therneau TM, Grambsch PM (2000) Modeling survival data: extending the Cox model. Springer, New York, New York, USA

Thompson DP (2020) The right to hunt and fish therein: understanding Chippewa treaty rights in Minnesota's 1854 Ceded Territory. 1854 Treaty Authority, Duluth, Minnesota, USA

Tischler KB, Severud WJ, Peterson RO, Vucetich JA, Bump JK (2022) Aquatic areas provide high nitrogen forage for moose (*Alces alces*) in Isle Royale National Park, Michigan, USA. *Alces* 58:75–90

Tremblay JP, Thibault I, Dussault C, Huot J, Côté SD (2005) Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. *Canadian Journal of Zoology* 83:1087–1096

Trinkel M, Fleischmann PH, Steindorfer AF, Kastberger G (2004) Spotted hyenas (*Crocuta crocuta*) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. *Journal of Zoology* 264:125–133

Tschanz B, Bersier LF, Bacher S (2007) Functional responses: a question of alternative prey and predator density. *Ecology* 88:1300–1308

Unsworth JW, Kuck L, Scott MD, Garton EO (1993) Elk mortality in the Clearwater drainage of northcentral Idaho. *Journal of Wildlife Management* 57:495–502

USCB (2021) TIGER data products. Dataset, U.S. Department of Commerce, Suitland, Maryland, USA

USGS (2020) 1 arc-second digital elevation models (DEMs) - USGS National Map 3DEP downloadable data collection. Dataset, United States Geological Survey, Reston, Virginia, USA

Van de Vuurst P, Moore SA, Isaac EJ, Chenaux-Ibrahim Y, Wolf TM, Escobar LE (2022) Reconstructing landscapes of ungulate parturition and predation using vegetation phenology. *Current Zoology* 68:275–283

- van Wijk RE, Kölzsch A, Kruckenberg H, Ebbingse BS, Müskens GJDM, Nolet BA (2012) Individually tracked geese follow peaks of temperature acceleration during spring migration. *Oikos* 121:655–664
- VerCauteren KC, Beringer J, Hygnstrom SE (1999) Use of netted cage traps for capturing white-tailed deer. In: Proulx G (ed) Mammal trapping. U.S. Department of Agriculture Animal and Plant Health Inspection Service, Fort Collins, Colorado, USA. pp 155–164
- Vijayan S, Lee J, Balaban-Feld J, Mitchell W, Kotler B, Rosenzweig ML, Lotan T, Abramsky Z (2019) Time to revisit? A predator's previous successes and failures in prey capture determine its return time to patches. *Oecologia* 190:387–397
- Vindenes Y, Langvatn R, Mysterud A (2023) Shifting seasonality of annual growth through ontogeny for red deer at northern latitudes. *Ecosphere* 14:e4639
- Vucetich JA, Huntzinger BA, Peterson RO, Vucetich LM, Hammill JH, Beyer Jr. DE (2012) Intra-seasonal variation in wolf *Canis lupus* kill rates. *Wildlife Biology* 18:235–245
- Walesiak M, Dudek A (2021) Searching for optimal clustering procedure for a data set. R package version 0.49-2
- Walton LR, Cluff HD, Paquet PC, Ramsay MA (2001) Movement patterns of barren-ground wolves in the central Canadian Arctic. *Journal of Mammalogy* 82:867–876
- Wehr NH, Boone HM, Wehr SR, Belant JL (2023) Island characteristics and species traits predict mammal diversity across islands of the great lakes of North America. *Biodiversity and Conservation* 32:3465–3480
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- White KS, Barten NL, Crouse S, Crouse J (2014) Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology* 95:225–237
- White P, Proffitt KM, Mech LD, Evans SB, Cunningham JA, Hamlin KL (2010) Migration of northern Yellowstone elk: implications of spatial structuring. *Journal of Mammalogy* 91:827–837
- Whiting S, Long J, Coyne M (2007) Migration routes and foraging behaviour of olive ridley turtles *Lepidochelys olivacea* in northern Australia. *Endangered Species Research* 3:1–9
- Wolf TM, Chenaux-Ibrahim YM, Isaac EJ, Wünschmann A, Moore SA (2021) Neonate health and calf mortality in a declining population of North American moose (*Alces alces americanus*). *Journal of Wildlife Diseases* 57:40–50

Wünschmann A, Armien AG, Butler E, Schrage M, Stromberg B, Bender JB, Firshman AM, Carstensen M (2015) Necropsy findings in 62 opportunistically collected free-ranging moose (*Alces alces*) from Minnesota, USA (2003–13). *Journal of Wildlife Diseases* 51:157–165

Xavier JC, Velez N, Trathan PN, Cherel Y, De Broyer C, Cánovas F, Seco J, Ratcliffe N, Tarling GA (2018) Seasonal prey switching in non-breeding gentoo penguins related to a wintertime environmental anomaly around South Georgia. *Polar Biology* 41:2323–2335

Zweifel-Schielly B, Kreuzer M, Ewald KC, Suter W (2009) Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. *Ecography* 32:103–113

APPENDIX A:
CHAPTER 1 SUPPLEMENTARY MATERIALS

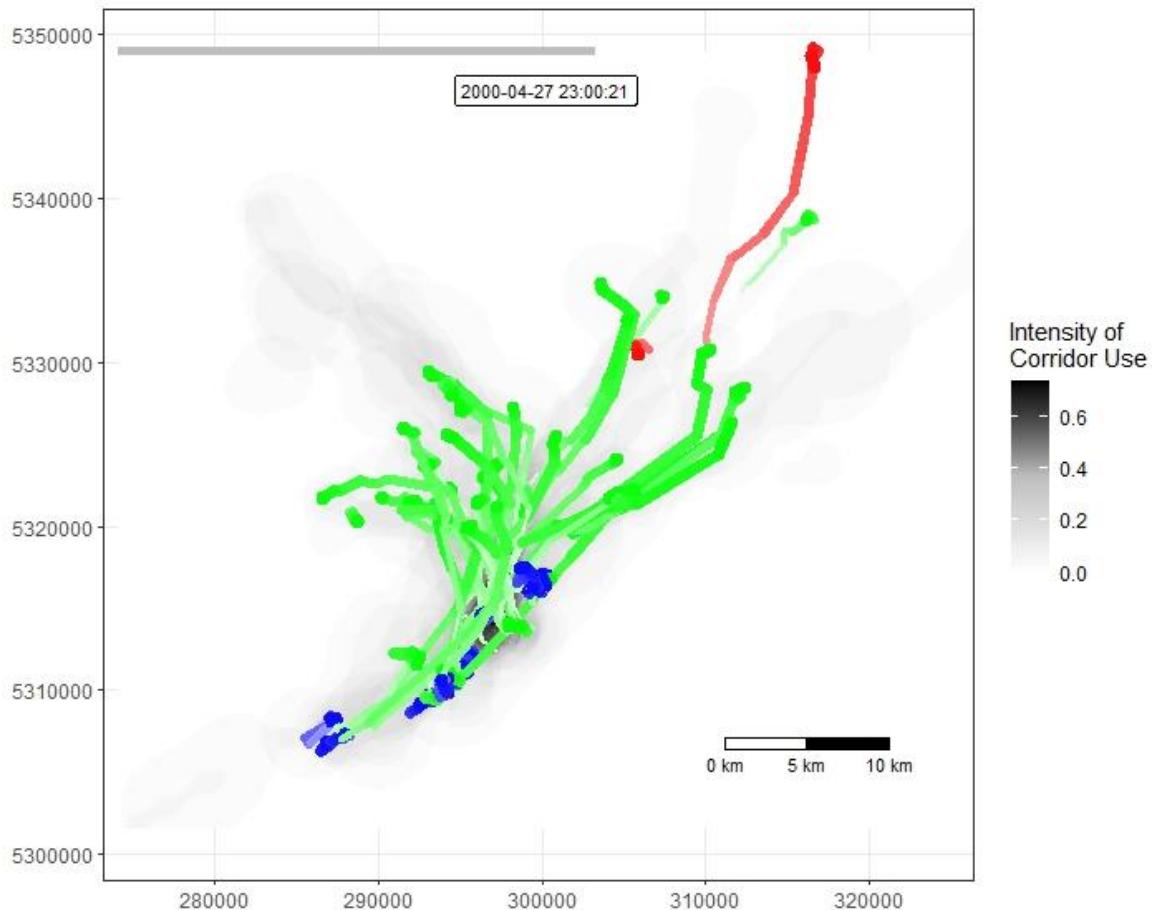


Figure A.1. Screenshot from video of white-tailed deer (*Odocoileus virginianus*) spring migration on the Grand Portage Indian Reservation, Minnesota, USA, 2016–2021. Green dots represent migratory deer, blue dots represent resident deer, and red dots represent deer that dispersed or whose movement strategies could not be assessed. Black shading represents the combined spring and fall migration corridor. The year in chronology was altered to merge movements across years.

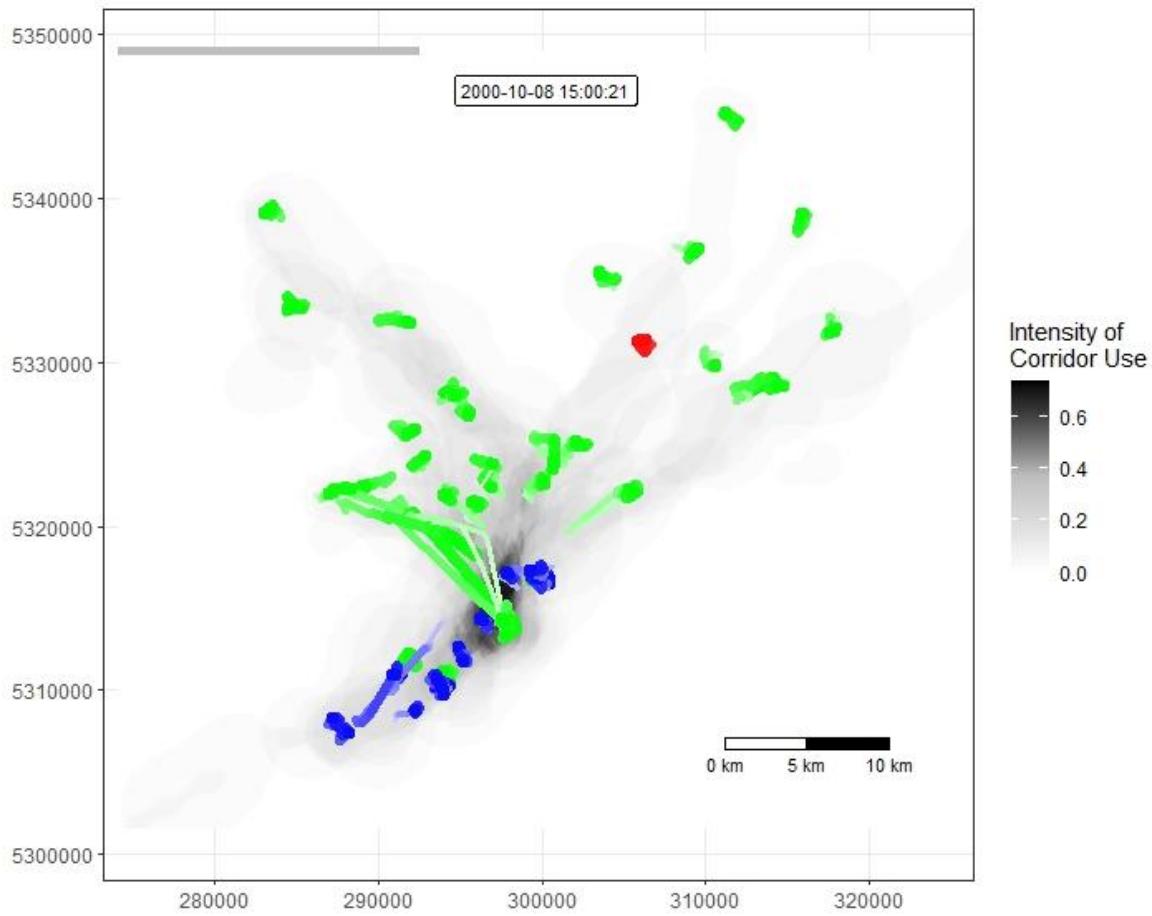


Figure A.2. Screenshot from video of white-tailed deer (*Odocoileus virginianus*) fall migration on the Grand Portage Indian Reservation, Minnesota, USA, 2016–2021. Green dots represent migratory deer, blue dots represent resident deer, and red dots represent deer that dispersed or whose movement strategies could not be assessed. Black shading represents the combined spring and fall migration corridor. The year in chronology was altered to merge movements across years.

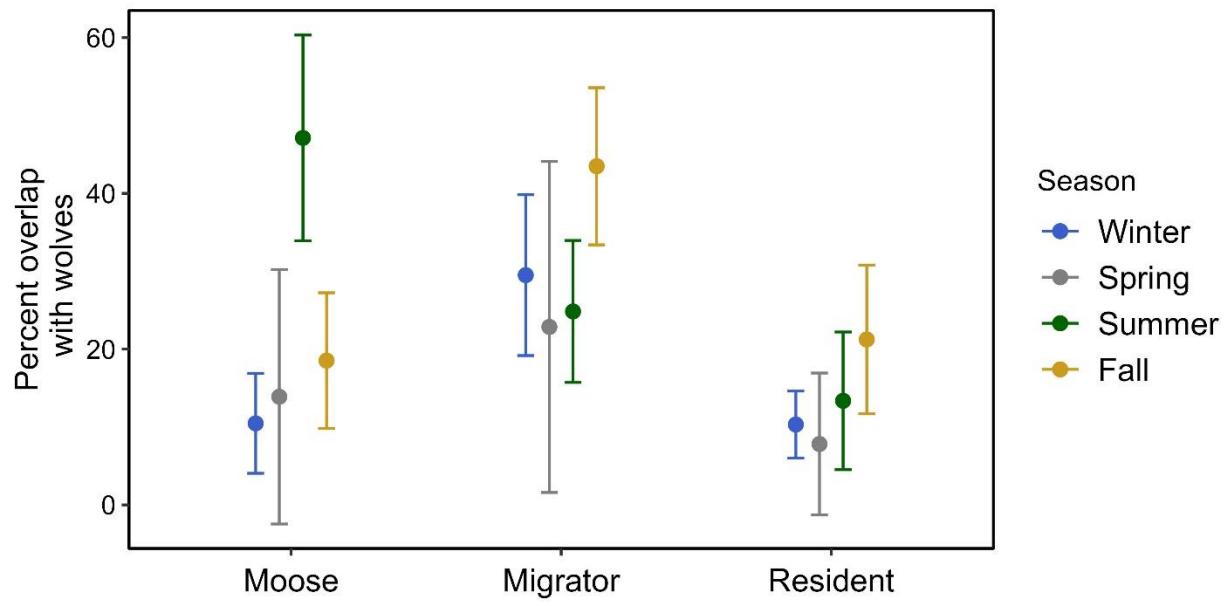


Figure A.3. Seasonal percent overlap of gray wolves (*Canis lupus*) with prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Percent overlap was calculated using 50% wolf UD s and 50% occurrence distributions of moose (*Alces alces*), migratory white-tailed deer (*Odocoileus virginianus*), and resident deer. Points represent means with 95% CI. Spring and fall represent the deer migration period.

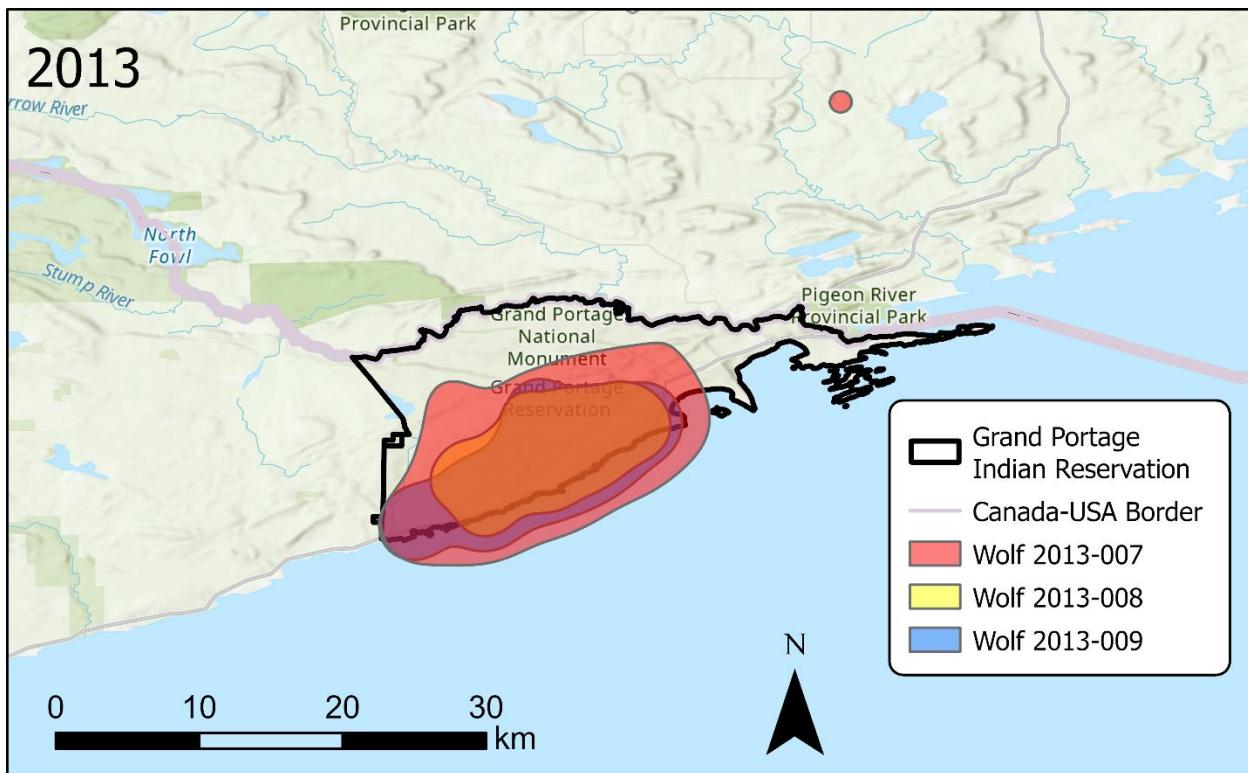


Figure A.4. Maps of annual gray wolf (*Canis lupus*) home ranges on the Grand Portage Indian Reservation, Minnesota, USA, 2013–2021. Home ranges were estimated using 95% kernel density estimators in R package *adehabitatHR* (Calenge 2006). Basemaps include World Hillshade and World Topographic Map from ArcGIS Pro (v3.0.3, Esri, Redlands, California, USA).

Figure A.4 (cont'd)

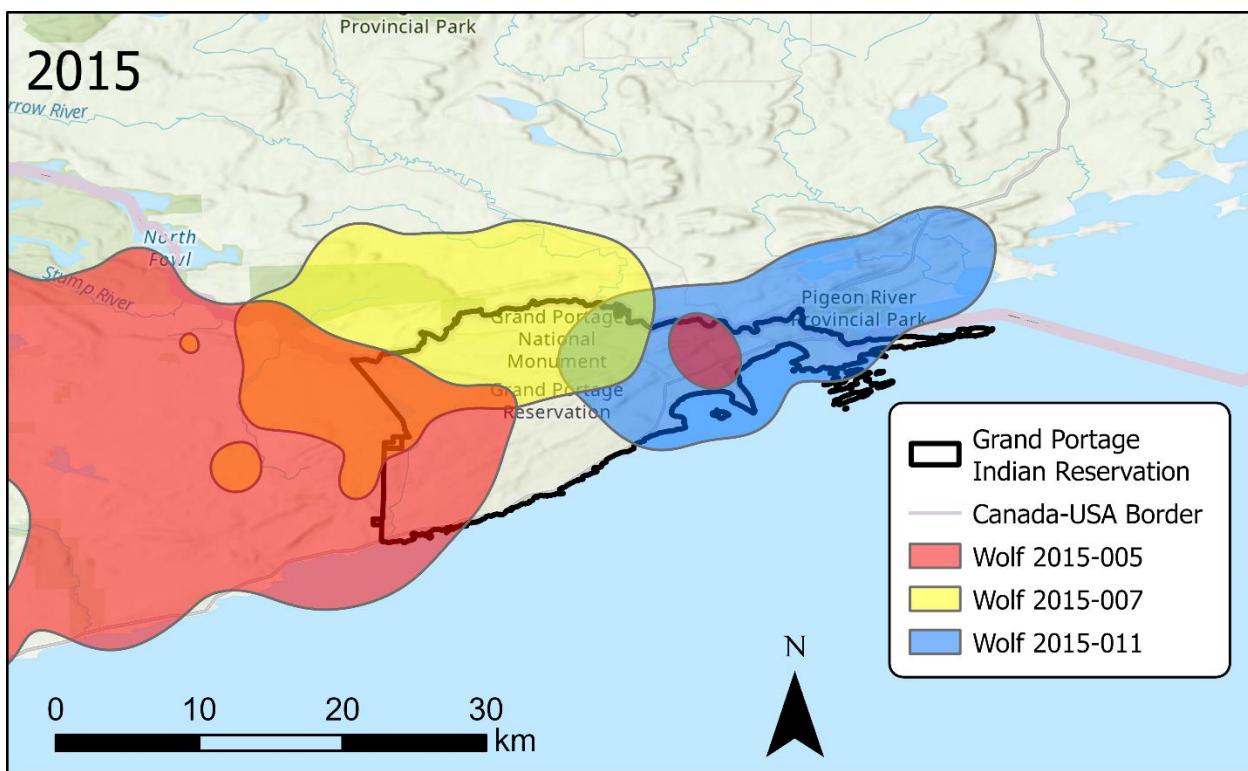
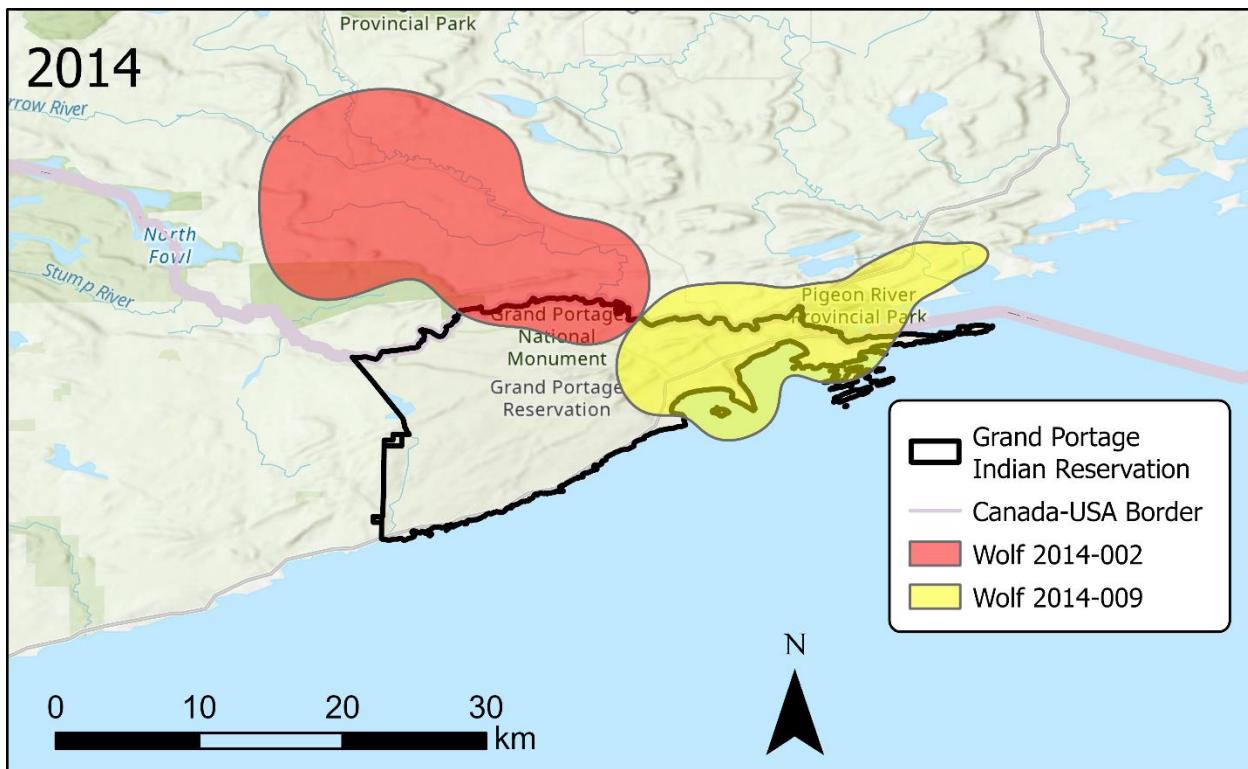


Figure A.4 (cont'd)

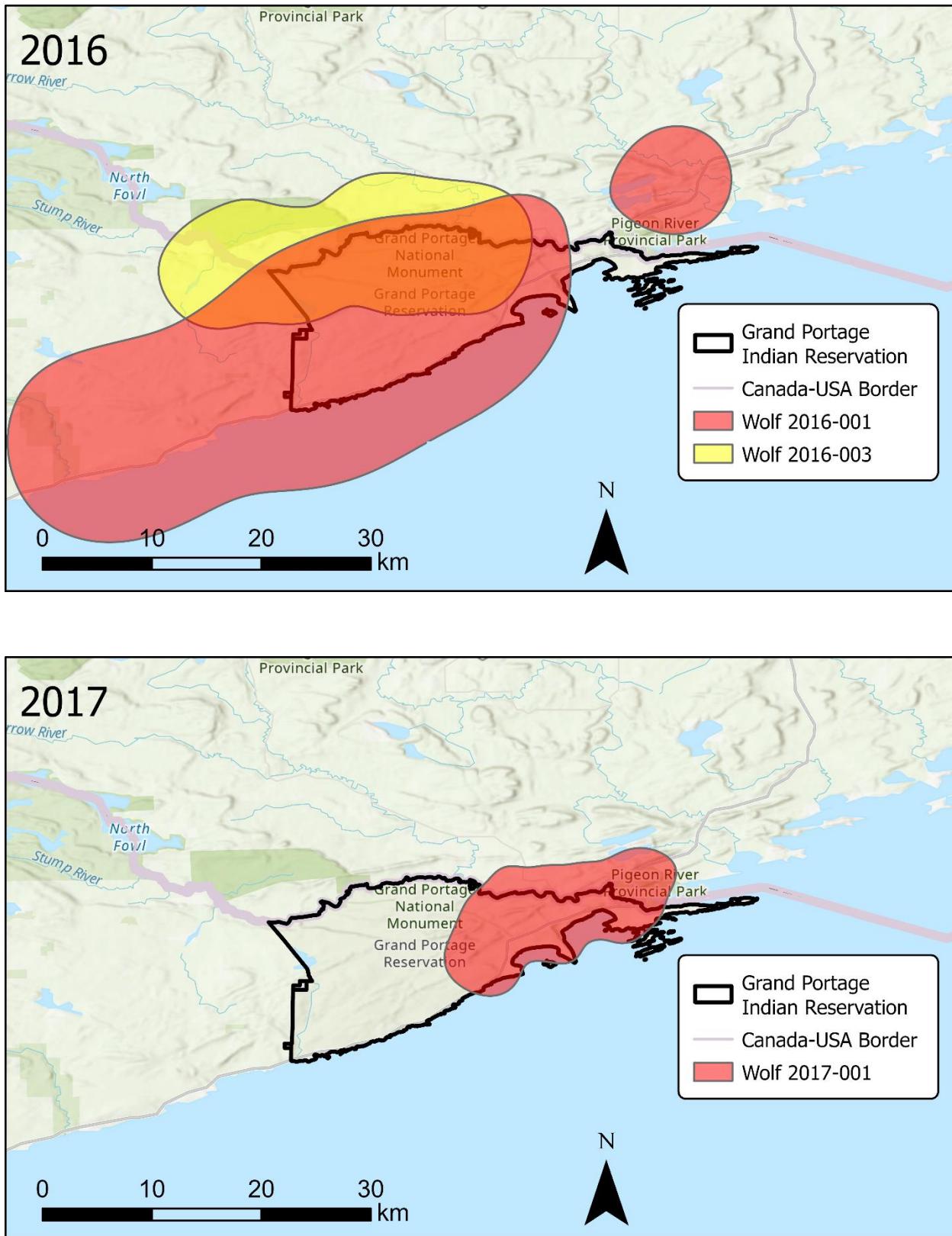


Figure A.4 (cont'd)

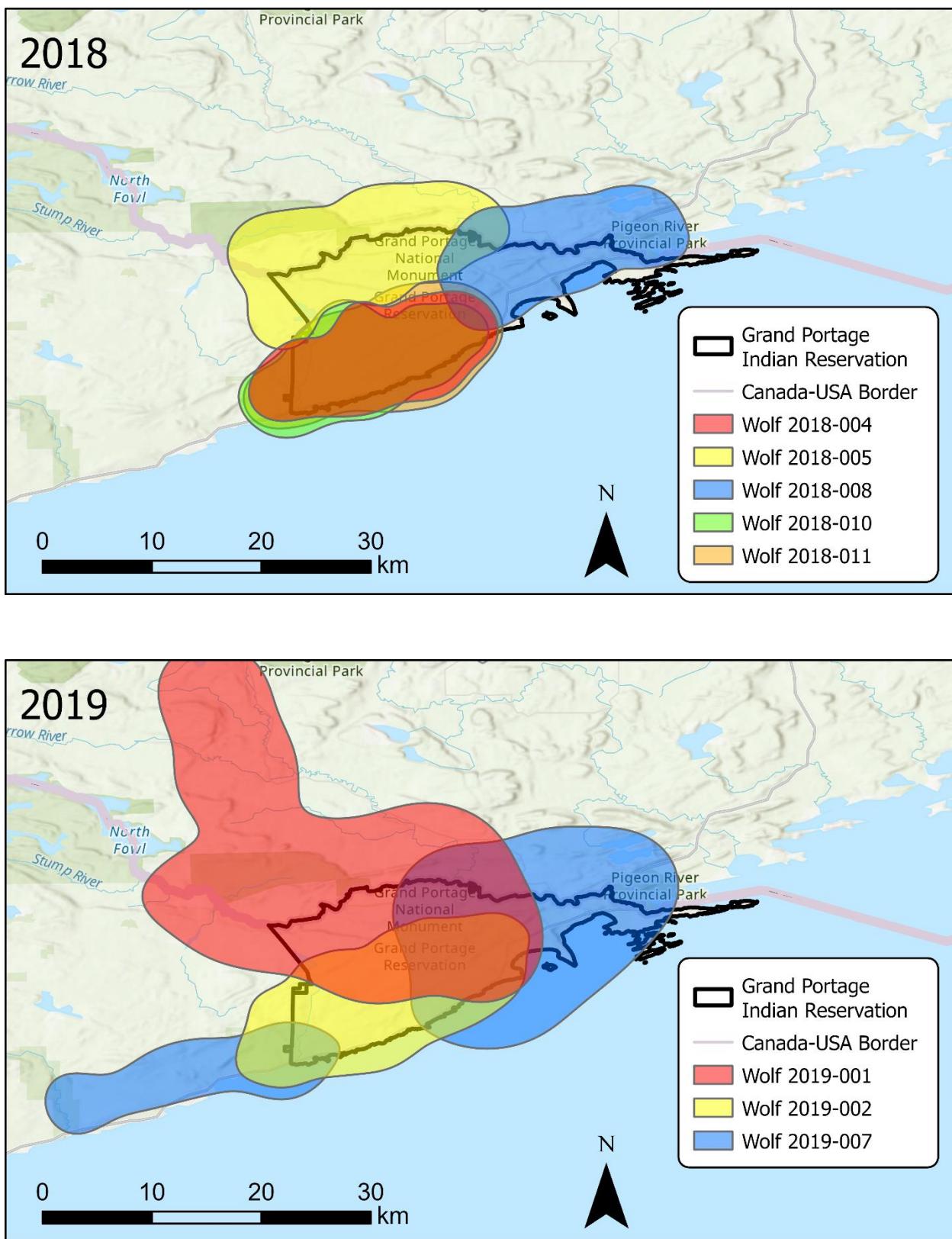


Figure A.4 (cont'd)

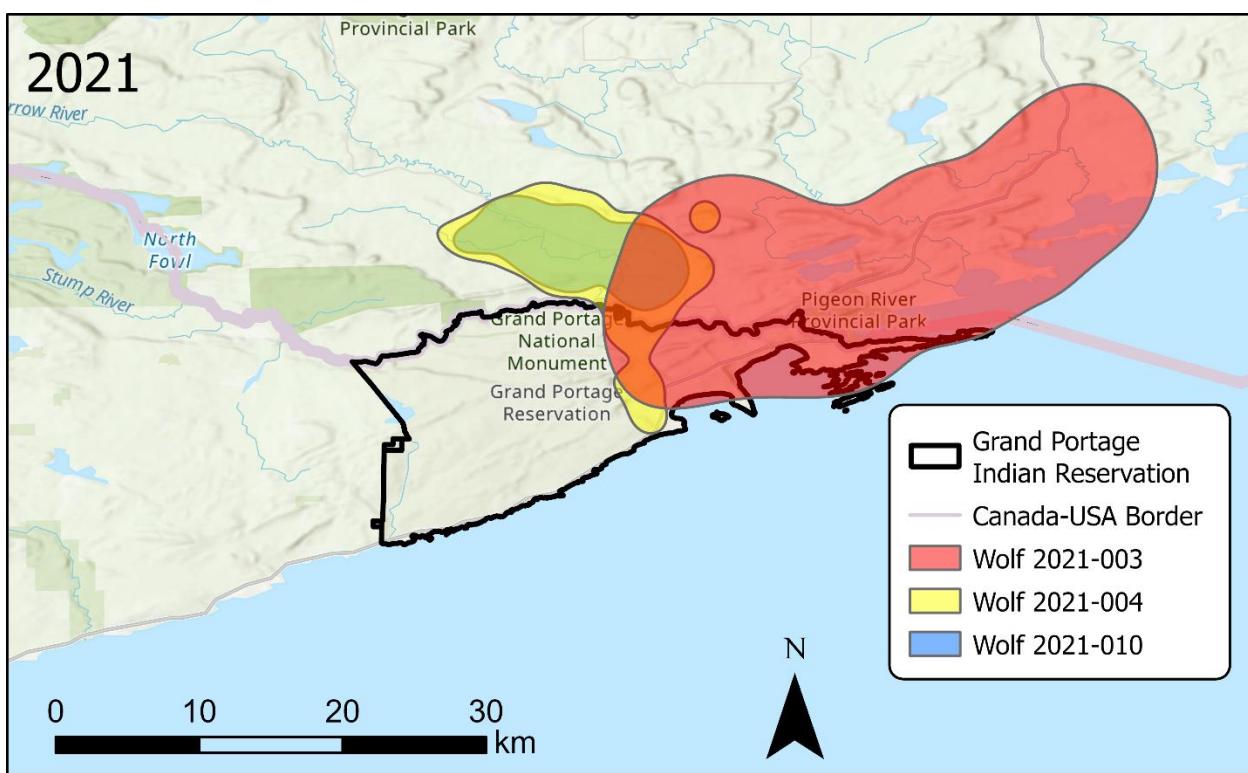
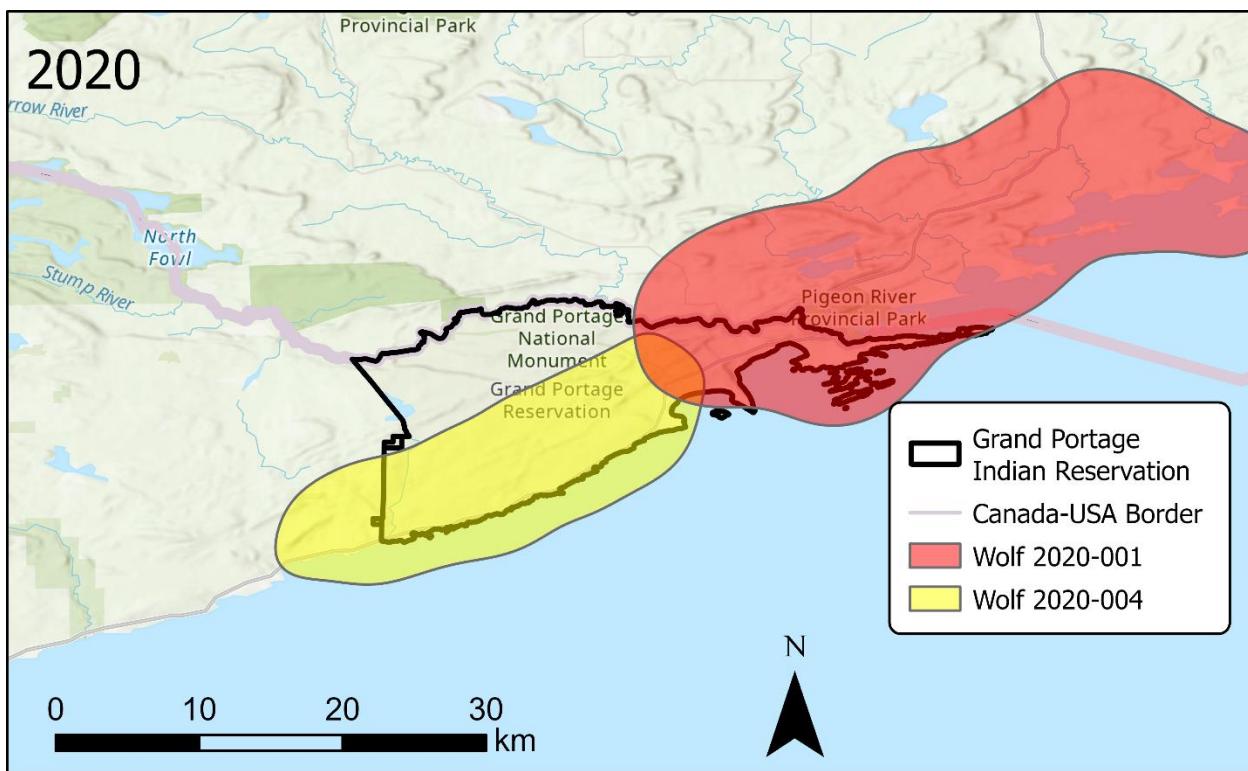


Table A.1. Kruskal-Wallis tests for differences in percent overlap of gray wolves (*Canis lupus*) and prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021.

Comparisons of percent overlap of individual-level wolf 50% UD with population-level 50% occurrence distributions of moose (*Alces alces*), the white-tailed deer (*Odocoileus virginianus*) migration corridor, the composite deer population, migratory deer only, or resident deer only are presented. A significant test ($p < 0.05$) indicates percent overlap of wolves with the indicated population changed seasonally. Dunn tests identify seasons during which overlap differed.

Population	χ^2	p-value	Dunn test
Moose	21.08	< 0.01	Table S3
Deer migration corridor	6.65	0.08	N/A
Composite deer	7.09	0.07	N/A
Migratory deer	7.23	0.07	N/A
Resident deer	1.35	0.72	N/A

Table A.2. Mann-Whitney tests for differences in percent overlap of gray wolves (*Canis lupus*) with prey on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Population comparisons represent percent overlap of individual-level wolf 50% UD (n) with population-level 50% occurrence distributions of moose- (*Alces alces*) seasons (N) and resident-, migratory-, and composite- white-tailed deer (*Odocoileus virginianus*) seasons (N). A significant test ($p < 0.05$) indicates percent overlap of wolves with specified populations differed during the specified season; the population with greater overlap is designated in the final column.

n (wolves)	Population 1 (N)	Population 2 (N)	Season	W	p-value	Greater overlap
33	Composite deer (45)	Moose (214)	Winter	774	< 0.01	Composite deer
11	Composite deer (104)	Moose (268)	Spring	69	0.62	N/A
25	Composite deer (96)	Moose (256)	Summer	213	0.05	Moose
32	Composite deer (73)	Moose (213)	Fall	751	< 0.01	Composite deer
33	Resident deer (13)	Migratory deer (32)	Winter	744	0.01	Migratory deer
11	Resident deer (35)	Migratory deer (69)	Spring	76	0.32	N/A
25	Resident deer (29)	Migratory deer (67)	Summer	425	0.03	Migratory deer
32	Resident deer (18)	Migratory deer (55)	Fall	736	< 0.01	Migratory deer

Table A.3. Dunn tests for differences in percent overlap of gray wolves (*Canis lupus*) with moose (*Alces alces*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Seasonal comparisons represent percent overlap of individual-level wolf 50% and 95% UDs (n) with population-level 50% and 95% occurrence distributions of moose (N). A significant test ($p < 0.05$) indicates percent overlap of wolves with moose differed between seasons; the season with greater overlap is designated in the final column.

Wolves		Moose		Distribution	Z	p-value	Greater overlap
n (Season 1)	n (Season 2)	Season 1 (N)	Season 2 (N)				
32	11	Fall migration (213)	Spring migration (268)	50%	1.16	0.49	N/A
32	25	Fall migration (213)	Summer (256)	50%	-2.71	0.03	Summer
11	25	Spring migration (268)	Summer (256)	50%	-3.12	0.01	Summer
32	33	Fall migration (213)	Winter (214)	50%	1.75	0.24	N/A
11	33	Spring migration (268)	Winter (214)	50%	0.08	0.93	N/A
25	33	Summer (256)	Winter (214)	50%	4.36	< 0.01	Summer
32	11	Fall migration (213)	Spring migration (268)	95%	1.32	0.37	N/A
32	25	Fall migration (213)	Summer (256)	95%	-2.29	0.09	N/A
11	25	Spring migration (268)	Summer (256)	95%	-2.96	0.02	Summer
32	33	Fall migration (213)	Winter (214)	95%	2.09	0.11	N/A
11	33	Spring migration (268)	Winter (214)	95%	0.17	0.87	N/A
25	33	Summer (256)	Winter (214)	95%	4.26	< 0.01	Summer

Table A.4. Dunn tests for differences in percent overlap of gray wolves (*Canis lupus*) with white-tailed deer (*Odocoileus virginianus*) on and near the Grand Portage Indian Reservation, Minnesota, USA, 2012–2021. Seasonal comparisons represent percent overlap of individual-level wolf 95% UD (n) with population-level 95% occurrence distributions of composite deer-seasons (N) or migratory deer-seasons (N). A significant test ($p < 0.05$) indicates percent overlap of wolves with the specified population differed between seasons; the season with greater overlap is designated in the final column.

Wolves		Deer		Population	Z	p-value	Greater overlap
n (Season 1)	n (Season 2)	Season 1 (N)	Season 2 (N)				
32	11	Fall migration (73)	Spring migration (104)	Composite	2.80	0.03	Fall migration
32	25	Fall migration (73)	Summer (96)	Composite	2.05	0.16	N/A
11	25	Spring migration (104)	Summer (96)	Composite	-1.19	0.70	N/A
32	33	Fall migration (73)	Winter (45)	Composite	3.08	0.01	Fall migration
11	33	Spring migration (104)	Winter (45)	Composite	-0.62	0.54	N/A
25	33	Summer (96)	Winter (45)	Composite	0.82	0.83	N/A
32	11	Fall migration (55)	Spring migration (69)	Migratory	2.77	0.03	Fall migration
32	25	Fall migration (55)	Summer (67)	Migratory	2.51	0.05	Fall migration
11	25	Spring migration (69)	Summer (67)	Migratory	-0.83	1.00	N/A
32	33	Fall migration (55)	Winter (32)	Migratory	3.28	0.01	Fall migration
11	33	Spring migration (69)	Winter (32)	Migratory	-0.45	0.66	N/A
25	33	Summer (67)	Winter (32)	Migratory	0.54	1.00	N/A

APPENDIX B:
CHAPTER 3 SUPPLEMENTARY MATERIALS

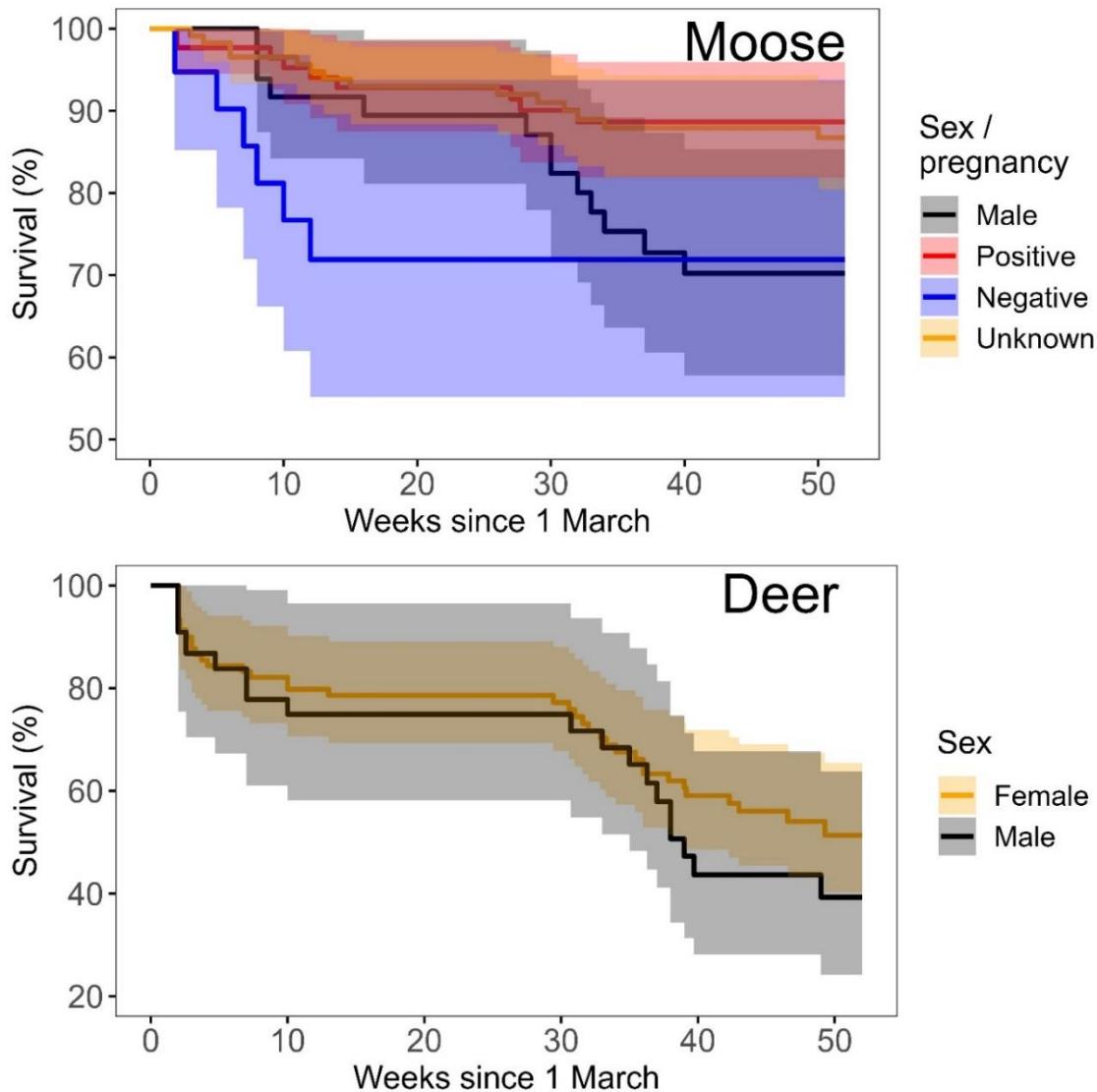


Figure B.1. Moose (*Alces alces*; 2010–2021) and white-tailed deer (*Odocoileus virginianus*; 2016–2022) survival on and near the Grand Portage Indian Reservation, Minnesota, USA.

Moose are categorized by sex and pregnancy status, and deer populations are categorized by sex.

Solid lines indicate mean percent survival with colored buffers representing 95% confidence intervals. Models include harvest mortalities.

Table B.1. Akaike information criterion (AIC) scores assessing model fits of moose (*Alces alces*; 2010–2021) and white-tailed deer (*Odocoileus virginianus*; 2016–2022) mortality peaks on and near the Grand Portage Indian Reservation, Minnesota, USA. Mortality peaks are the number of possible peaks in each model; ΔAIC is the difference between the best fitting model and the reported model. Models were fit with harvest mortalities included and excluded. Model AIC scores could not be assessed for models with ≥ 3 mortality peaks because confidence intervals were infinite.

Mortality peaks	Moose				Deer			
	With harvest		Without harvest		With harvest		Without harvest	
	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC	AIC	ΔAIC
0	242.42	17.33	227.82	16.26	157.22	50.53	128.71	20.62
1	243.49	18.4	223.88	12.32	149.17	42.48	114.56	6.47
2	225.09	0.00	211.56	0.00	106.69	0.00	108.09	0.00
≥ 3	-	-	-	-	-	-	-	-

Table B.2. Model coefficients for staggered entry extended Cox proportional hazards models of moose (*Alces alces*) survival on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. The first model included subsistence harvest while the second model censored subsistence harvested moose. A significant ($p < 0.05$) test indicates the covariate predicted mortality with positive z-values representing decreased survival.

Covariate	Subsistence harvest included				Subsistence harvest excluded			
	β	se	z	p	β	se	z	p
Pregnant: No ^a	0.24	0.50	0.48	0.63	0.58	0.53	1.11	0.27
Pregnant: Yes ^a	-1.08	0.45	-2.43	0.02	0.25	0.51	0.49	0.63
Pregnant: Unknown ^a	-0.26	0.44	-0.58	0.56	-0.72	0.49	-1.48	0.14
Movement: Nomadic ^b	-0.79	0.54	-1.47	0.14	-1.16	0.56	-2.08	0.04
Movement: Resident ^b	-0.37	0.57	-0.65	0.52	-0.63	0.58	-1.09	0.28
Movement: Unknown ^b	2.98	0.58	5.11	< 0.01	2.89	0.59	4.89	< 0.01
Space use state: Pre-parturition ^c	-2.14	1.14	-1.88	0.06	-2.11	1.14	-1.85	0.06
Space use state: Summer ^c	-6.20	1.51	-4.11	< 0.01	-6.14	1.51	-4.06	< 0.01
Space use state: Winter ^c	-10.76	1.89	-5.69	< 0.01	-10.63	1.93	-5.50	< 0.01
GDD	-0.32	0.23	-1.36	0.17	-0.32	0.23	-1.36	0.17
CWSI	-0.16	0.33	-0.48	0.63	-0.38	0.38	-0.99	0.32

^aReference category for pregnancy was males; ^breference category for movement status was migratory; ^creference category for space use state was spring.

Table B.3. Moose (*Alces alces*) survival estimates on and near the Grand Portage Indian Reservation, Minnesota, USA, 2010–2021. Mean survival with lower and upper 95% confidence intervals is reported by sex and pregnancy status (female positive, negative, or unknown or male). Space use states include spring (11 March–13 April), pre-parturition (14 April–6 May), summer (7 May–17 October), and winter (18 October–10 March). Survival estimates represent rates from 1 March to the end of the indicated week approximated by space use state.

Space use state	Weeks since 1 March	Positive			Negative			Unknown			Male		
		Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper	Mean	Lower	Upper
Spring	6	0.98	0.95	1.00	0.90	0.78	1.00	0.97	0.93	1.00	1.00	1.00	1.00
Pre-parturition	9	0.97	0.93	1.00	0.81	0.66	1.00	0.97	0.93	1.00	0.92	0.84	1.00
Summer	33	0.89	0.82	0.96	0.72	0.55	0.94	0.89	0.83	0.95	0.78	0.66	0.91
Winter	52	0.89	0.82	0.96	0.72	0.55	0.94	0.87	0.80	0.94	0.70	0.58	0.85

Table B.4. Model coefficients for staggered entry extended Cox proportional hazards models of white-tailed deer (*Odocoileus virginianus*) survival on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2022. Two- and four-season models are presented with spring and fall migrations considered separate space use states in the four-season model. Space use states were summer (24 April–18 November) and winter (19 November–23 April), with spring migration (4 April–2 May) and fall migration (10 October–28 November) periods. A significant ($p < 0.05$) test indicates the covariate predicted mortality with positive z-values representing decreased survival. These models include harvest mortalities.

Covariate	Two-season model				Four-season model			
	β	se	z	p	β	se	z	p
Sex: Male ^a	0.44	0.32	1.39	0.16	0.44	0.32	1.37	0.17
Movement: Resident ^b	0.34	0.38	0.90	0.37	0.35	0.38	0.91	0.36
Movement: Unknown ^b	1.76	0.37	4.77	< 0.01	1.77	0.67	4.83	< 0.01
Space use state: Spring migration ^c	-	-	-	-	0.7	0.72	0.09	0.93
Space use state: Fall migration ^c	-	-	-	-	0.77	0.89	0.87	0.39
Space use state: Winter ^c	-0.34	1.27	-0.27	0.79	1.58	1.02	1.54	0.12
GDD	0.33	0.50	0.67	0.50	0.12	0.33	0.37	0.71
CWSI	0.83	0.33	2.52	0.01	1.19	0.35	3.40	< 0.01

^aReference category for sex was females; ^breference category for movement status was migratory; ^creference category for space use state was summer.

Table B.5. Model coefficients for staggered entry extended Cox proportional hazards models of white-tailed deer (*Odocoileus virginianus*) survival on and near the Grand Portage Indian Reservation, Minnesota, USA, 2016–2022. Two- and four-season models are presented with spring and fall migrations considered separate space use states in the four-season model. Space use states were summer (24 April–18 November) and winter (19 November–23 April), with spring migration (4 April–2 May) and fall migration (10 October–28 November) periods. A significant ($p < 0.05$) test indicates the covariate predicted mortality with positive z-values representing decreased survival. These models exclude harvest mortalities.

Covariate	Two-season model				Four-season model			
	β	se	z	p	β	se	z	p
Sex: Male ^a	0.20	0.41	0.48	0.63	0.17	0.41	0.42	0.68
Movement: Resident ^b	0.19	0.49	0.39	0.70	0.20	0.49	0.42	0.68
Movement: Unknown ^b	1.76	0.40	4.44	< 0.01	1.78	0.39	4.54	< 0.01
Space use state: Spring migration ^c	-	-	-	-	0.56	0.79	0.71	0.49
Space use state: Fall migration ^c	-	-	-	-	1.48	1.00	1.47	0.14
Space use state: Winter ^c	0.82	1.47	0.56	0.58	2.46	1.17	2.10	0.04
GDD	-0.04	0.57	-0.08	0.94	-0.01	0.32	-0.04	0.97
CWSI	0.76	0.40	1.92	0.05	1.00	0.41	2.44	0.01

^aReference category for sex was females; ^breference category for movement status was migratory; ^creference category space use state was summer.