UNIVERSITY OF CALGARY

Factors Influencing Seasonal Migrations of Pronghorn Across the Northern Sagebrush Steppe

by

Andrew F. Jakes

A DISSERTATION
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

GRADUATE PROGRAM IN ENVIRONMENTAL DESIGN
CALGARY, ALBERTA
SEPTEMBER, 2015

ABSTRACT

Pronghorn (*Antilocapra americana*) undertake seasonal migrations and long-distance movements to satisfy annual life history requirements. To investigate these phenomena, 185 females were collared across the Northern Sagebrush Steppe (NSS) to classify migration and long-distance movement states and to analyze movement metrics. Based on 170 animal years, 55% of individuals undertook seasonal migrations. I also identified long-distance fawning-associated and driven movements during the study period. Thirty-six individuals used stopover sites during seasonal migration, principally during spring. During spring, migration was slow, sinuous and lengthy to exploit quality forage. During fall, fawning-associated and driven movements, movements were faster, more linear and shorter than spring. Both fall and spring stopover sites exhibited similar metrics, likely to profit from high quality forage areas. Next, I modelled multi-scalar migratory pathway selection in response to anthropogenic factors and environmental gradients. I found that pronghorn responded to road, well and hydrology variables at specific densities at finer scales. Generally, migratory pronghorn selected grasslands, intermediate slopes and south-facing aspects compared to other landcover types and topographic conditions. Pronghorn highly avoided increased well and road densities compared to lower densities of these features. Seasonal variation showed that during fall, pronghorn used large hydrologic systems while in spring pronghorn selected high quality forage areas. Pronghorn selected stopover sites with higher forage productivity values and lower densities of well attributes versus migratory pathways during both seasons. Relative to cultivated habitats, pronghorn avoided stopover sites in grassland or shrubland habitats versus migratory pathways. At finer scales, pronghorn slightly avoided anthropogenic features across the landscape, but at broader scales, pronghorn strongly selected against roads, natural resource wells and well drilling. I used a scale-integrated mapping approach to evaluate if such spatial predictions performed as well or better than single order scales to predict migration pathways. Finally, using scale-integrated spatial predictions, I assessed connectivity across the NSS to identify seasonal pronghorn connectivity networks. I concluded that multi-scale migration followed hierarchically nested theory where finer scale decisions are conditional on broader scales that can be assessed sequentially. I suggest that the pronghorn is a broad-scale focal species useful for designing conservation networks across the NSS.

KEY WORDS: Pronghorn, *Antilocapra americana*, migration, long-distance movement, logistic regression, multi-scalar connectivity, Northern Sagebrush Steppe, anthropogenic factors influencing migration

ACKNOWLEDGMENTS

Funding for this project was provided by: Alberta Conservation Association (ACA), Montana Fish, Wildlife & Parks (FWP), U.S. Bureau of Land Management (BLM), World Wildlife Fund (WWF), University of Calgary - Faculty of Environmental Design, University of Calgary - Faculty of Graduate Studies, Saskatchewan Ministry of Environment (SK MOE), MITACS Inc. - Accelerate Program, Alberta Sport Recreation Parks and Wildlife Foundation, and Montana Chapter of The Wildlife Society & Counter Assault Inc. In-kind support was provided by Montana Chapter of The Nature Conservancy (TNC), The Miistakis Institute, FWP, ACA, BLM and WWF.

I have found that, unlike anything I have ever experienced, a PhD dissertation is both a personal and professional awakening. I have a number of individuals that I would like to thank, with deepest and most genuine sincerity for their expertise, guidance, humor, dedication and staunch support towards me and towards conservation in general. I thank my committee members, Drs. Cormack Gates, Mark Hebblewhite and Darren Bender for candid and enjoyable discussions and comments on pronghorn and movement ecology; your dedication, organization and edits at the front and back end of my project provided invaluable contributions to my ecological inferences. I thank Dr. Nick DeCesare for his analytical assistance, humor and friendship; without your support, I may still be working away! I thank Paul Jones for his sound and stable support and dedication; your efforts helped me more than I can detail. I thank Dr. Kyran Kunkel for his field and personal support; your encouragement and tenacity never wavered. I thank my field intern Samantha Howlett from University of Gloucestershire; your enthusiasm and hard work made the long summer hours in Malta and Glasgow a joy! Finally, I thank my pilot Dixon Hitch; besides having the coolest name of anyone I have ever met, thanks for being rock solid and listening to static with me for countless hours. Numerous other professional and personal collaborators were integral in my work. They say it takes a village to raise a child; perhaps here, it takes a dedicated wildlife management and conservation community to finalize an international project! In no particular order, I thank Mark & Barb Sullivan, Kelvin & Leila Johnson, Justin Gude, Scott Story, Adam Messer, Jeff Herbert, Ken McDonald, Scott Thompson, Lydia Bailey, Adam Peterson,

Bob Cochran and the entire Region 6 staff with FWP; John Carlson, Pat Gunderson, Craig Miller, Rich Adams, Mark Albers and Fritz Prellwitz with BLM; Dennis Jorgensen, Erin Poor, Colby Loucks, Sarah Olimb and Steve Forrest with WWF; Doug Manzer and Mike Grue with ACA; Brian Martin, Shawn Cleveland, Amy Pearson and Alison James with TNC; Greg Chernoff with Miistakis Institute; pilots Clyde Robinson and Chad Cyrus; fellow graduate students Byron Weckworth, Mike Suitor, Tyler Muhly, Rachelle Haddock, Karl Zimmer, Joe St. Peter, Michael Kohl, Wibke Peters and Marisa Lipsey at University of Calgary and University of Montana, respectively; photographer Michael Foresberg; Jen Taillefer and Crystal Hickey with University of Calgary; Paul Luckas and Joshua Goldberg with University of Montana; Dale Eslinger and Al Violette with Alberta Sustainable Resource and Development; John Pogorzelic, Chuck Lees and Ed Beveridge with SK MOE; Dean Smith with Prairie Farm Rehabilitation Administration; Carmen Luma and Randy Matchett with U.S. Fish & Wildlife Service; Quicksilver Air Inc.; the people of Ft. Belknap and Ft. Peck reservations and the communities and people of the high-line region of Montana, in particular those in Malta.

Most significantly, I thank my family for their understanding and relentless support of this endeavor. My parents and siblings mean so much to me; words on a page cannot express my love and support for them. To my mother – every day I say thank you and smile because of the optimistic traits you have instilled in me. You have been steadfast when life felt like a roller-coaster. I am stronger because of you and you will always be an angel on my shoulder. To my son Greysen – you have never known me as anything else but a “pronghorn expert,” as you like to say. Every day, I went through this experience, I got up because of you; every day, I worked a little bit harder, because of you; and every day became a little brighter, because of you. You have made me a more patient and resourceful man. I am the most fortunate parent in the world because I get to be your dad. I promise that your resilience, caring and sweet personality will allow you to achieve wonders. And I promise I will be with you for every step of your journey as you have been there for every step of this journey of mine. You are a lover of wildlife and wild places and I hope to always share and strengthen those ties you have to the land. It is our place of solace and deep, eternal joy. To my lovely fiancée Catherine – you have brought me hope and happiness, loyalty and laughs, emotion and excitement and the confidence of being a better man because of this journey that you have taken with me. You have gone through this every step of the way and I thank you for being there more than anyone else. This is just the beginning for us and I truly believe that it's "all gravy" from here on out! Finally, to my father – you keep me strong, you keep me focused, and you have continued to keep me doing the right thing. We find out what our true nature is as humans and perhaps more so, as energy. I am proud of my past, what I have accomplished here and am confident and excited for what lies ahead.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACRONYMS

ACA – Alberta Conservation Association

AIC – Akaike's information criteria

AIC_c – Akaike's information criteria corrected for small sample size

ΔAIC – Measure of each model under consideration relative to the best model

BLM – U.S. Bureau of Land Management

FWP – Montana Fish, Wildlife & Parks

GIS – Geographic information system

GLMM – Generalized linear mixed model

GPS – Global positioning system

ISSF – Scale-integrated step selection function

LDM – Long-distance movement

MCP – Minimum Convex Polygon

MODIS – Moderate resolution imaging spectrometer

NDVI – Normalized difference vegetation index

NGO – Non-profit organization

NSD – Net-squared displacement

NSS – Northern Sagebrush Steppe

NSSI – Northern Sagebrush Steppe Initiative

ROW – Right of way

RSF – Resource selection function

SD – Standard deviation

SDM – Short-distance movement

SK MOE – Saskatchewan Ministry of Environment

SSF – Step selection function

TNC – Montana Chapter of The Nature Conservancy

WWF – World Wildlife Fund

CHAPTER 1: INTRODUCTION

BACKGROUND

Approximately 8% or 9 million km^2 of the world's land surface is temperate grasslands (White et al. 2000). Grasslands are home to a disproportionally large human population thanks to the ecological amenities, food and economic stability they provide (Chape et al. 2003). Only 4.6% of temperate grasslands are currently protected by country or international laws, regulations and agreements and as a result are one of the most imperiled ecosystems (Hannah et al. 1995, Forrest et al. 2004, Henwood 2006). Grassland communities face continued direct and indirect ecological threats from anthropogenic development disrupting natural ecological processes and diminishing wildlife populations (Thirgood 2004, Hobbs et al. 2008). Conversion of native landscapes to agricultural croplands must be considered one of the greatest ecological threats to grasslands due to direct habitat loss (Chape et al. 2003, Forrest 2004). Compounding this direct loss, historically domestic livestock were commonly stocked at densities exceeding natural system capacity, and as a result, overgrazing and degradation to remaining native habitat occurred (Noss et al. 1995). Infrastructure such as roads, power lines, canals and fences to support agricultural and ranching practices exist in grasslands in high densities. This infrastructure fragments the landscape, decreases patch sizes, facilitates invasive species, alters hydrology, and either partially impedes or completely blocks animal movement (Trombulak and Frissell 2000, Fahrig, 2003, Harrington and Conover 2006). In addition, the continuous demand for energy from oil and natural gas resource extraction across grasslands increases habitat loss, further fragments the landscape and provides additional access to humans to previously expansive native grassland areas (Copeland 2009).

Large ungulates serve an integral role in the structure and functions of grassland ecosystems due to their large spatial requirements, foraging needs and behaviors, and role in predator-prey dynamics (Sinclair 2003). Even more so, migratory ungulates galvanize ecological processes across large grassland areas through nutrient dispersal, stimulation of plant growth and predation opportunities (Thirgood 2004, Mueller et al. 2008, Harris et al. 2009). Migration by large herbivores is generally understood as a seasonal roundtrip movement between discrete areas not used at other times of the year (Baker 1978, Berger 2004). Ungulate migration is an adaptive strategy that is derived from complex interactions between control factors both endogenous (genetic imprinting, behavioral traits, demography) and exogenous (ecological requirements and environmental cues) (Dingle and Drake 2007, Bowlin et al. 2010). Ungulate migrations occur worldwide and have been shown to be in response, largely, to precipitation and resulting forage productivity in Africa (Wilmshurst et al. 1999), Asia (Singh et al. 2010) and North America (Hebblewhite et al. 2008). Naturally, resources utilized by ungulates may be heterogeneously distributed throughout a region (Owen-Smith 2004). In contrast, landscapes dominated by human development (i.e. agricultural landscapes) have more patchily distributed resources (Brennan and Kuvelsky 2005, Polasky et al. 2005, Samways et al. 2010). As a result, across the globe various ungulate migrations are threatened by increasing human activities in grasslands, including wildebeest (*Connochaetes taurinus*), saiga (*Saiga tatarica*), and Mongolian gazelle (*Procapra gutturosa*) (Thirgood et al. 2004, Berger et al. 2008, Mueller et al. 2008). Ungulate resource and movement selection occurs at varying scales and, following hierarchical theory, is conditional to selections made at broader scales (Rettie and Messier 2000, Chekiewicz and Boyce 2009, DeCesare et al. 2012). Landscape connectivity between large resource patches within an anthropogenic influenced matrix is believed to be an important component for sustaining healthy wildlife populations (Beier and Noss 1998). In conservation landscape planning, connectivity refers to the extent to which a species or population can move among landscape elements in a mosaic of habitat types (Hilty et al. 2006). Fragmentation refers to the unnatural parceling of habitat into patches, possibly leading to patch isolation (Hobbs et al. 2008). The landscape connectivity measures physical relationships among habitat patches and describes the degree to which landscapes provide movement of genetic material, organisms or population flows (Hilty et al. 2006, Taylor et al. 2006). Because migrations are a repeated movement phenomenon, ungulate migration can be a useful in regional planning efforts as a means for identifying and maintaining landscape connectivity throughout a system (Beier et al. 2008).

The pronghorn (*Antilocapra americana*) is North America's only extant endemic ungulate, with a range within prairie, shrubland-steppe and desert habitats from Northern Mexico to Southern Canada (White et al. 2007). Pronghorn co-evolved with fleet predators on the open landscapes of North America and consequently have extremely keen eyesight and are the second-fast land animal in the world (O'Gara and Janis 2004). Though once thought to compete with American bison in sheer numbers at approximately 30 million individuals, present predictions total the number close to 1.2 million individuals across its range, which has contracted considerably (Yoakum 2004). Pronghorn seem to be more active foragers near sunrise and sunset (Schwartz et al. 1977) but energetic requirements stemming from their size and their vigilant behavior keep them foraging throughout most of the day (Hofmann 1989). Compared to other North American ruminants, their smaller rumens do not allow them to efficiently process low quality high fiber foods (Schwartz et al. 1977). Among all ungulates, pronghorn have an extremely high hypsodonty index and a relatively narrow muzzle, which indicates they are concentrate feeders (Van Soest 1994). However, Hofmann (1989) classifies pronghorn as intermediate or mixed feeders, which is somewhat of an oddity based on their body size and narrow muzzle. It is important to note that because of these morphophysiological adaptations, pronghorn are one of the most overlapped intermediate/mixed feeder with concentrate feeders along the ruminant specialization continuum presented in Hofmann (1989). Pronghorn seasonally switch forage types and their dietary position along the ruminant specialization continuum allows them to take advantage of food sources that provide the highest nutritional quality and digestibility to maximize dietary crude protein intake and minimize fiber content (Schwartz et al. 1977, Schwartz et al. 1981).

At the end of the summer season across the Northern Hemisphere's temperate grasslands, environmental conditions begin to deteriorate and forage senescence occurs. During this time, pronghorn may initiate exploratory movements to seek improved forage conditions or from social interactions during the rut (Kitchen 1974, Hoskinson and Tester 1980, Byers 1997). In fall, pronghorn select forbs and browse in addition to cultivated forbs and grasses that may still be developing. Pronghorn may then engage in fall migrations to target winter ranges that support maintenance requirements and minimize energy expenditure. In winter, nutrient-rich vegetation is scarce and pronghorn typically survive on evergreen browse, mainly sagebrush species that protrudes through snow and provides some nutritional value (Schwartz and Nagy 1976). In the spring, pronghorn select developing grasses which provide the highest crude protein content (Schwartz and Nagy 1976). From mid-May through early June, pronghorn show high fidelity to fawning areas where they typically give birth to twins in areas where succulent forbs are selected (Wiseman et al. 2006). As hiders, fawns select areas where small movements are required and forage is vertically structured to promote camouflage (Barrett 1984, Wiseman et al. 2006). During the summer, forage quantity is peaked and pronghorn forage on diverse vegetation, including forbs, legumes and perennial crops.

Across pronghorn range, a segment of a population may engage in seasonal migrations, defined as partial migration (Dingle and Drake 2007). Pronghorn utilize migration and other long-distance movements to maximize access to high nutrition vegetation, improve physical condition for increased reproductive success, and respond to changing environmental conditions (Fryxell and Sinclair 1988, Bolger et al. 2007). Anthropogenic development across pronghorn range is relatively recent (last 200 years). Tilling native landscapes for agricultural production is a major factor influencing pronghorn distribution and habitat use and can result in direct habitat loss (O’Gara and McCabe 2004). Linear features such as roads and fences fragment the landscape, altering pronghorn distribution and movements (Gavin and Komers 2006, Harrington and Conover 2006, Siedler et al. 2014). Energy development from oil and natural gas production and supporting infrastructure has also been shown to influence pronghorn distribution and habitat use (Beckmann et al. 2012). Long-distance movements, including migrations, may be a particularly important adaptation for pronghorn at the periphery of their range because these movements offer escape from extreme environmental conditions and stochastic events. Therefore, managing for their continuation at the edge of pronghorn range is imperative to sustain populations, especially in the face of accelerated alterations.

The Homestead Act of 1862 in the United States and parallel legislation that soon followed in Canada (The Dominion Lands Act 1872) encouraged rural settlement, tillage and development of grasslands for crop production across the northern reaches of the

North American Great Plains, an area referred to here as the Northern Sagebrush Steppe (NSS) (Figure 2.1). Agricultural settlement across the NSS brought rapid and significant alterations to the land, including extensive cultivation, urban development, livestock grazing, fences, and transportation systems (Smith and Hoppe 2000, Forest et al. 2004, Riley et al. 2007). Today, approximately 24% of the combined area of mixed-grass and shortgrass prairie remains intact in the Canadian Prairie Provinces, with the largest proportion in Alberta (~40%) (Alberta Environment 2007). Although the rate of new tillage has recently slowed in the NSS, Northern Montana still experienced a 5-10% increase in tillage from 1982-1997 (Forrest et. al 2004). Additionally, fossil fuel extraction has developed rapidly in the NSS since the mid-1970s and is a major driver of economic activity and landscape change in the area (Saskatchewan Environment 2005, Alberta Environment 2007). As a consequence of ongoing development, the NSS continues to transform into diminishing increasingly isolated patches of remnant native prairie within a matrix of annual and perennial croplands.

Worldwide and including the NSS, grassland systems have received the highest impacts from human activities, and therefore management of these systems is urgent for large herbivore conservation (Hannah et al. 1995, Harris et al. 2009). The effects from anthropogenic pressures on pronghorn migrations are not well understood. However increased anthropogenic activities across the NSS may heighten difficulties placed on pronghorn and could constrain migration leading to disconnections within the most northern population and between others. Based on ecological requirements, I expect various environmental and anthropogenic features will influence pronghorn migration pathway selection at different magnitudes and at different scales. I expect that migration pathway selection is hierarchically nested; meaning pronghorn selection at finer scales is conditional on migration pathway selection that occurred previously at broader scales (Rettie and Messier 2000, Thullier and Meyer 2006, DeCesare et al. 2012).

The need to provide solutions to balance pronghorn movement requirements within an ever-growing human dominant landscape is apparent. In my research I investigated the influence of environmental gradients and anthropogenic factors on seasonal migrations by pronghorn to provide the basis for designing a connectivity network for use at the northern periphery of pronghorn range to benefit wildlife and humans mutually.

PURPOSE

Metrics for long-distance movements and migratory components for pronghorn are lacking in the literature on this species. Additionally, multi-scalar migratory pathway selection in response to environmental and anthropogenic influences for pronghorn and its utility in developing connectivity networks deserve attention. The purpose of my work was to develop a multi-scalar hierarchically nested modeling approach to predict pronghorn migration pathways for use in designing a connectivity network at the northern edge of pronghorn range, thus providing a foundation for a species diversity regional network by promoting hierarchically nested scales of movement selection for conservation.

OBJECTIVES

The objectives of my dissertation research were to:

1) Assimilate regional data into spatiotemporal layers
2) Classify and determine metrics for various movement behaviors and states across individuals
3) Predict multi-scalar seasonal pronghorn migration pathways across the NSS and integrate scales into one spatial prediction for conservation planning
4) Create pronghorn connectivity network maps across the NSS
5) Provide objective methods for defining and analyzing hierarchically nested migratory pathway selection

APPROACH

To address my research objectives, I sequentially approached field and analytical work. First, I collaborated with key entities (federal, state/provincial agencies, NGOs) to acquire and compile spatiotemporal data layers across the NSS that may influence pronghorn migration (Appendix 1.1). A number of partnerships were established and, as a result, important layers were created for subsequent analysis. Concurrently, multi-year field work capturing and tracking pronghorn movements afforded me critical insights into pronghorn behavior and ecology while providing an introduction to the culture and environmental attributes of the system.

I collected daily relocation global positioning system (GPS) data from collaborating agencies and organizations working on pronghorn spatial ecology to build multiple geodatabases covering pronghorn movements across the three NSS jurisdictions. Chapter 2 is a descriptive chapter to identify and categorize pronghorn movements and metrics. Databases were first used to categorize individuals as either migrators or residents based on results using net-squared displacement (Chapter 2). Long-distance movements such as fawning-associated movements and driven movements were also identified from these methods. In addition, I identified stopover sites within migratory pathways using additional methodology (Chapter 2). I calculated mean movement periods for each category across the population. For each seasonal long-distance movement and stopover site category, I calculated movement metrics and ran a between-class analysis to group movement types based on similar metrics (Chapter 2).

I then added explanatory variables to each case and corresponding control point to model migratory pathway selection at third-order and second-order scales. I randomly withdrew 20% of individuals from each season to validate global models. First, I used incrementally increasing search radii on anthropogenic and hydrologic features to target the feature density that pronghorn most respond to at third-order scales for subsequent modeling (Chapter 3). I used step selection functions to predict probability of pronghorn migration at the third-order scale, using a multi-step approach. I then used mixed-effect modeling to predict pronghorn migration at the second-order scale. Resulting maps for each scale were condensed into one scale-integrated step selection function (ISSF) map output (Chapter 3). Using both training and testing data, I validated multi-scalar maps against ISSF map outputs using Spearman rank correlations. In addition, I used mixed-effect modeling approaches to predict stopover site selection from migratory pathways during both fall and spring migrations. I used Akaike’s Information Criterion to compare models with and without anthropogenic features (wells and roads) included to determine their influence to pronghorn migratory pathway selection at third and second-order scales.

I used resulting seasonal migratory ISSF map outputs as cost surface layers to model pronghorn connectivity across the system (Chapter 4). I used a suite of objective approaches to model connectivity. I used pronghorn annual seasonal range size to identify grassland habitat patches in the NSS and then distributed 1000 random points within habitat patches to act as beginning and end terminals required in connectivity modeling. This allowed for the identification of corridors both between and within habitat patches. I used the "Linkage Mapper" set of tools to construct least-cost pathways for both seasons across the NSS and refined previous methods to validate results using pronghorn relocations (Driezen et al. 2007, McRae and Kavanagh 2011) (Chapter 4). Next, I truncated validated least-cost pathways to identify a reasonable corridor width based on the highest proportion of pronghorn relocations within the minimum area. Finally, I prioritized corridors using "Pinchpoint Mapper" tools both between and within habitat patches (McRae 2012*a*) (Chapter 4). The resulting seasonal maps provide a pronghorn connectivity network across the NSS.

Based on conditional results attained starting at Chapter 2 through Chapter 4 and from previous literature, I provide management implications for pronghorn in the Northern Sagebrush Steppe (Chapter 5).

CHAPTER 2: CLASSIFYING THE MIGRATORY BEHAVIOR OF PRONGHORN ON THEIR NORTHERN RANGE

INTRODUCTION

Migration is an adaptive strategy common across taxa derived from complex interactions between exogenous (ecological requirements and environmental cues) and endogenous (genetic imprinting, behavioral traits, demography) control factors that animals undertake to improve fitness across spatiotemporal gradients (Webster et a. 2002, Alerstam et al. 2003, Dingle and Drake 2007, Bowlin et al. 2010). Migration can generally be defined as a seasonal round-trip movement between discrete areas not used at other times of the year by the individual (Baker 1978, Berger 2004) and generally consists of two major components, the migratory pathway and stopover sites along this pathway (Calvert et al. 2009, Sawyer and Kauffman 2011).

Most ungulate populations are partially migratory, where some individuals migrate while others remain residents (Dingle and Drake 2007). Individuals may or may not migrate based on spatiotemporal heterogeneity in forage quality, environmental conditions, density-dependent influences, predation, insect harassment and parasitism, and anthropogenic influences (Fryxell and Sinclair 1988, Berger 2004, Bolger et al. 2007, Hebblewhite and Merrill 2007, Hebblewhite et al. 2008, Sawyer et al. 2009, Mysterud et al. 2011, Avgar et al. 2014). A growing body of literature has also identified genetic factors, social learning and spatial recognition as migration drivers of individuals in ungulate populations (Sweanor and Sandegren 1988, Fischhoff et al. 2007, White et al. 2007, Barnowe-Meyer et al. 2013, Naidoo et al. 2014). In addition, the ability to switch between migratory strategies by individuals is believed to be based on fluctuations in population densities and demographic rates, age or body condition, balancing risk-reward paradigms or in response to spatiotemporal distributions of resources (Lack 1968, Perez-Tris and Telleria 2002, Hebblewhite et al. 2006, Hebblewhite and Merrill 2011, Gaillard 2013). In general, the theory that migratory strategies by individuals may be plastic has brought increased attention to switching strategies and is an important phenomenon to further understand (Chapman et al. 2011).

At the end of the summer season in the Northern Hemisphere's temperate grasslands, ungulates have accumulated nutrition and energy reserves for the impending rut and winter seasons. As environmental conditions begin to deteriorate and forage senescence occurs in the fall and early winter, ungulates may initiate exploratory movements to seek improved forage conditions (Pennycuick 1975, Hoskinson and Tester 1980). Ungulates may then engage in fall migration to target winter foraging areas and to endure winter at these locals to improve survival prospects. Ungulates will use stopovers sites along migration pathways if high quality forage is encountered (Sawyer and Kauffman 2011). During fall migrations, ungulates may or may not exhibit high fidelity to specific winter ranges; i.e. they may migrate only as far as required to arrive at suitable locations (Bruns 1977, Nelson 1995, Sawyer et al. 2009). Although winter range selection has a learned behavioral element, selection is flexible and adaptable as availability and conditions change annually. Once on initial winter ranges, ungulates may undertake "driven" movements between winter ranges as a response to local storms and snow accumulation. These movements are different from predictable seasonal migration; they are a response to extreme local conditions and are a risky mechanism used by individuals to escape harsh conditions and improve chances of survival (Martinka 1966, Barrett 1982, Ortega and Franklin 1995, Fieberg et al. 2008). These movements may be exceedingly fast and linear, with duration and magnitude as great as necessary to evade local conditions. Individuals that selected either resident or migratory strategies may use driven movements to improve survival. Spring migrations are return movements to fawning/calving locations and summer areas that ungulates may show high fidelity towards (Main and Coblentz 1996, Welch et al. 2000). Spring migrations take advantage of improving forage quality, which is best found in young forbs and grasses, for two main purposes. The first is to meet nutritional requirements and to restore depleted tissue reserves lost during winter. The second is to energetically prepare for fawning/calving (i.e. support fetal growth in-utero, support mammary function, parturition, post-parturition care) (Parker et al. 2009, Tollefson et al. 2010). Ungulate migrations occur worldwide and have been shown to be in response, largely, to precipitation and resulting forage productivity in Africa (Wilmshurst et al. 1999), Asia (Singh et al. 2010) and North America (Hebblewhite et al. 2008). Across the Northern

Hemisphere’s temperate grasslands, forage quality increases following increasing latitudinal and altitudinal gradients over time during the spring (Hebblewhite et al. 2008, Sawyer et al. 2009). During spring, ungulates may attempt to temporally match migration duration and timing with increasing forage quality, in other words, to follow the “green wave” (Mysterud 2013). One tactic is to use stopover sites to take advantage of high quality patches of forage in addition to matching migration with improving forage quality across the landscape (Sawyer and Kauffman 2011, Seidler et al. 2014). The direction and magnitude of spring migration are determined by where ungulates are at the end of winter in relation to fawning/calving sites and summer range.

The ability of landscapes to support ungulate migrations is declining worldwide, presumably due to habitat alteration by humans and climate change (Berger 2004, Thirgood et al. 2004, Bolger et al. 2007, Harris et al. 2009). Advancements in data collection and analytical approaches provide opportunities to offset these declines. The use of GPS technology has allowed the use of intra-daily location data to classify and parameterize movement metrics in wild ungulates. Inter-seasonal movements can now be distinguished using movement metrics such as movement rate, turning angle, sinuosity, distance between relocations and net squared displacement (Vander Wal and Rodgers 2009, Bunnefeld et al. 2011). Additionally, methods encompassing movement metrics have been developed to identify stopover sites considered critical components of ungulate migration (Van Moorter et al. 2010, Sawyer and Kauffman 2011, Thurfjell et al. 2014). Further understanding the phases of migration and metrics of such movements is necessary for informing the design of spatial models and interpreting their outcomes.

In this chapter, I analyzed fall and spring movement patterns of adult female pronghorn (*Antilocapra americana*) radio-collared in Alberta (AB), Saskatchewan (SK), and Montana (MT), an area referred to as the Northern Sagebrush Steppe (hereafter NSS) (Figure 2.1). The pronghorn is an indigenous ungulate to North America and is the only species extant in its taxonomic family (O’Gara and Janis 2004). It is a highly vagile species, known for fleetness and acute eyesight, and ranges across the prairies, intermountain valleys and sagebrush steppes of Western North America. Pronghorn populations are often partially migratory (Berger 2004, White el al. 2007, Kolar et al. 2011) and as with other ungulates, migratory individuals may use stopover sites (Sawyer et al. 2009, Sawyer and Kauffman 2011, Poor et al. 2012). I tested two specific concepts about pronghorn seasonal movement patterns. During fall migration I expected exploratory movements and movements forced by changes to local conditions. I predicted that winter range destinations would vary, and fall migrations would demonstrate higher movement rates, exhibit less tortuosity and be shorter in duration and magnitude than spring migration. At the onset of fall migration, female pronghorn are in good body condition (Jacques et al. 2009, Kolar et al. 2011), and consequently, there should be fewer stopovers during fall than during spring migration. Pronghorn exhibit high fidelity to fawning areas (Wiseman et al. 2006, White et al. 2007); therefore, spring migration represents a return to specific locations from geographically variable winter ranges. Recovery of body condition and high nutritional demands during late gestation should require pronghorn to follow gradients in plant phenology and to select high quality forging patches during spring migration. Accordingly, I predicted that spring migrations would be slower, exhibit high tortuosity, and ultimately be longer in duration and magnitude than fall migrations. Furthermore, I anticipated that pronghorn should use stopover sites more frequently during spring migration to match temporal latitudinal gradients of forage quality. Results of this study can be used to predict migratory patterns of pronghorn and contribute to conservation planning for the species in the NSS, and that the methods employed can be replicated to analyze movement patterns of other migratory species.

METHODS

Study Area

I studied pronghorn migratory movements across the NSS, the northern limit of the species' range. The study area encompassed 315,876 km^2 and includes the prairie regions of AB, SK and Northern MT. The landscape is relatively flat with open plains and rolling hills as a result of glacial recession and deposits. Rivers and other waterways have exposed badlands and created deep coulees throughout the region (Mitchell 1980). Annual temperatures across the region fluctuate dramatically. For example, temperatures in the city of Swift Current, SK, range from highs of 38.9°C to lows of -44.4°C. The region is considered semi-arid, receiving an annual average of 392 mm of precipitation, with approximately 70% as rainfall (Environment Canada 2010). The region is a patchwork of native habitat, pastures, and irrigated and dryland agricultural fields. Native grassland species include Needle and thread grass (*Stipa comata*), June grass (*Koeleria cristata*), Western wheatgrass (*Agropyron smithii*) and blue grama (*Bouteloua gracilis*). Evergreen shrubs include silver sagebrush (*Artemisia cana*), big sagebrush (*Artemisia tridentata*), pasture sagewort (*Artemisia frigid*) and horizontal juniper (*Juniperus horizontalis*). Forbs and other native vegetation include American silverberry (*Elaeagnus commutate*), Western snowberry (*Symphoricarpos occidentalis*), prickly wild rose (*Rosa acicularis*), and prickly pear cactus (*Opuntia polyacantha*). Major cultivated crops include alfalfa, lentils, peas, canola, wheat, mustard, and hay (Coupland, 1961, Mitchell 1980).

Land administration and development varies across the NSS. The majority of the region is privately owned. The remaining lands are owned by U.S. Bureau of Land Management (BLM), U.S. Fish & Wildlife Service (FWS), Montana Department of Natural Resources and Conservation (DNRC), Crown Lands (either federally or provincially managed) and tribal lands. A mix of land use occurs across the region. Cattle production is intensely practiced in Alberta and Montana, while farming is generally more frequent in Saskatchewan. Oil and natural gas wells dot the landscape in high frequencies in Alberta and growing numbers in Montana and Saskatchewan. Relative to other regions in the U.S. and Southern Canada, there are low densities of paved roads; however, the resurgence of natural gas and oil production has led to increased service road building. Human population is relatively sparse with highest densities in Lethbridge and Medicine Hat, AB, Regina and Swift Current, SK, and Havre and Glasgow, MT.

Capture and Data Collection

Pronghorn were captured during the winter across the NSS from 2003-2010 via net gun fired from a helicopter (Barrett et al. 1982). Pronghorn were captured proportionally in cultivated habitat, mixed habitat (cultivated and native habitat at broad scales) and native habitat annually from 2003-2006 (Jones et al. 2005). In general, pronghorn captured in cultivated habitat migrated less than those captured in mixed or native habitats (Jones et al. 2015). Pronghorn captured from 2007-2010 were captured in open native landscapes along the Milk River breaks in Montana where higher densities of individuals are typically located (Sheriff 2006). Consequently, the range of landscape types were sampled during the study. Only female pronghorn were captured, as female drive population dynamics (Eberhardt 2002). GPS telemetry collars (Lotek GPS 3300 and ARGOS 7000SA models; Lotek Wireless, Newmarket, Ontario, Canada) were deployed across the region, following Jones et al. (2015). A total of 185 individuals were captured with relocations taken every two (*n*=64) or four (*n*=121) hours with 173 collars retrieved (94% success rate). Attention was placed on standardizing capture procedures to ensure sufficient numbers of collars on individuals with similar makeup of sex and age class so to not reduce inferences attained from data. I noted that in other pronghorn studies, no significant differences in timing and distance of spring and fall migration were noted between sexes or age classes (Kolar et al. 2011). In addition, female pronghorn may make exploratory movements at the end of summer due to social interactions with rutting males (Kitchen 1974, Byers 2007). However, the rut occurs primarily during the last three weeks of September and mating behaviors should not influence the ensuing fall migration of either sex (Clancey et al. 2012, Byers 1997). Because pronghorn mortality occurred (*n*=54) and some individuals had multi-year data (*n*=13), there was a total of 170 unique animal years analyzed. Mortality primarily occurred from winter exposure/starvation, predation, vehicle/train collisions and capture myopathy. The Alberta Conservation Association obtained wildlife capture and handling permits #11861, #16707 and #20394 from Alberta Sustainable Resource Development approved by The Alberta Wildlife Animal Care Committee, while WWF obtained wildlife capture and handling permit #11-2007 from the Montana Fish, Wildlife & Parks approved by the Institutional Animal Care and Use Committee (IACUC), and wildlife capture and handling permit # 09FW040 from the Saskatchewan Ministry of Environment approved by the University of Saskatchewan Committee on Animal Care and Supply. Data from each individual's first two days was discarded to account for post-capture related movements. GPS collars had a 98% fix-success rate and so I did not consider fix success to be a likely source of bias in subsequent analysis (Friar et al. 2010).

Classifying Pronghorn Movements

I refined the Bunnefeld et al. (2011) method to quantify movement parameters such as start/stop dates, duration and displacement distances so as to objectively classify an individual's seasonal migration and explore other potential long-distance movements per individual (Appendix 2.1). In brief, this method classifies different movement behaviors on the basis of annual patterns in net squared displacement (NSD). NSD is a single parameter that measures the Euclidean distance between a starting location and each subsequent location along a movement pathway. Similar to others (Mysterud et al. 2011, Eggeman 2012), I adapted the method to address species-specific movements. I identified transitions between migration and residence based upon variation in NSD. Using pronghorn ecology as a guide, I determined that migration occurred when an individual had a NSD between 1% greater than the average winter range (in terms of NSD) and less than 95% of the average summer range to account for increased summer range areas versus smaller winter range areas used by northern pronghorn to conserve energy (Suitor 2011). In other words, an individual began spring migration (or ended fall migration) when NSD exceeded (returned to within) 101% of the average winter NSD and ended spring migration (or began fall migration) when NSD reached (dropped below) 95% of the average summer NSD. Additionally, these refinements allowed exploration of potential fawning-associated movements in which females move a substantial distance after giving birth. I considered these fawning-associated movements as special cases that are identified at the end of spring migration. For these individuals, I used the maximum (rather than the average) NSD for the summer range. When exploring for driven movements that potentially occurred, I used the same process in calculating spring migration dates but applied the algorithm after the end of fall migration.

Having identified start/stop dates delimiting movements, I next identified specific relocations during these time intervals. To this end, a set of standardized rules were used to further hone the start/stop of movements that may not have been otherwise identified through graphical interpretation (Appendix 2.1). In this way, I was able to extract seasonal migrations and long-distance movement relocations from datasets of annual relocations of individuals.

Expanding on the classifications defined in Bunnefeld et al. (2011), I classified movements as migratory, mixed-migratory, resident, migratory/resident with driven movement or migratory/mixed-migratory with fawning-associated movements. A migratory strategy implies that an individual moved between two distinct seasonal ranges in a calendar year, whereas a mixed-migratory strategy suggests that an individual used three geographic areas in a year (i.e. the location of the winter range changed). Another important biological consideration I addressed was the differentiation between fall migrations and driven movements. I assumed that fall migrations had been completed once relocations had clustered for greater than 30 days (i.e. had reached a winter range), and therefore were not considered as a stopover. Subsequent movements by an individual were considered driven movements (i.e. initiated due to extreme environmental gradients) until the next suitable winter range had been reached. In this way, an individual could make only one fall migration but afterwards could partake in multiple driven movements during the winter. For my purposes, I did not consider individuals classified as resident in this analysis.

Stopover Site Analysis

I used the adehabitatLT package (Calenge 2011) in R 2.15.2 (R Core Team 2012) with the Gueguen (2001) method to discriminate stopover sites from movement pathways along the overall spring and fall migratory pathways for individual animal years. Similar to the movement classification, this method used the NSD of the overall pathway and partitions sequential observations into homogenous segments that resulted in identifying stopover sites (i.e. resting/feeding states) from movement pathways. Based on exploratory analysis, I found a minimum migration path duration of nine days was needed for the model to appropriately run using the mid-day observation points to partition the overall pathway (P. Luckas - personal communication). Many of the analyzed individual migration animal years had durations shorter than nine days. For pathways that had ≥ 9 days of data (hereafter Above), I used each day's mid-day observation point to evaluate pathway partitions. For pathways that had < 9 days of data (hereafter Below), I used all observation points along the pathway to evaluate pathway partition. Within the Above and Below groups, additional sub-categories were identified based on combinations of being either long-distance (LDM) or short-distance (SDM) migration and daily relocation rates. LDM's and SDM's were differentiated by assessing if the distance movement was ≥50 km (Johnson et al. 2005). This resulted in a total of six migration categories.

The Gueguen (2001) method partitions an individual movement into segments characterized by homogenous behavior and allows the user to restrict the number of partitions in the movement to be evaluated. I evaluated four partition cases for each individual's seasonal migration pathway to identify up to three possible stopover sites selected by an individual. In the first case, no restrictions were placed on identified partitions; this is the program default and up to ten partitions may be delineated. In the second case, movements were restricted to three partitions to potentially identify one stopover (i.e. movement – stopover – movement). In the third case, movements were restricted to five partitions to potentially identify two stopovers. In the fourth case, movements were restricted to seven partitions to potentially identify three stopovers. I explored migration distances and movement rates for LDM and SDM individuals, as well as daily relocation rates, to determine the mean distance and standard deviation (inputs into the Gueguen method) for each individual's migratory pathway and evaluated partition similarities among individuals across all four partition cases to find consistent start and end relocations for identified stopover sites. Mean distances and standard deviations were kept constant within each of the six migration categories. Results identified the day (for Above) or relocation (for Below) of migratory state partition of individuals. Results not only partitioned stopovers sites along the overall migratory pathway but also identified segmentations along the migratory pathway, based on movement rate between relocations. This was particularly true for Below migrations, so I was conservative in designating stopover sites for these migratory paths.

Finally, partition results for individual migratory pathways were assessed across all four partitioning scenarios. I interpreted results to designate stopover sites by evaluating and matching partition patterns across all four cases for each migratory pathway using day (for Above) or relocation (for Below). I was cautious to accept identified stopover sites ≤ 2 days. In these instances (*n*=2), stopover sites were accepted only if all partition cases identified relocations as plausible stopover sites and the individual's migratory trajectory changed > 45° along the overall pathway.

Pronghorn Movement Metrics

Once movement periods were identified for individuals, I extracted the sequence of GPS locations making up each movement path to calculate subsequent movement metrics, per each movement type. All movement metric analyses were conducted using ArcGIS 10.1 toolboxes (ESRI 2012). First, I estimated the NSS population's mean seasonal migration start/stop dates and mean migratory duration as well as fawning-associated movements and driven movements. For each path, I then calculated Euclidean distance (straight line distance between consecutive mid-day points), measured pathway distance (both in km), ratio of displacement (a measure of movement sinuosity), movement rates in km/hour for both the measured Euclidean distance and "measured pathway distance," i.e. the length of the overall pathway vector and mean bearing. I arbitrarily characterized a movement as a LDM or SDM by assessing distance traveled using the Euclidean distance. Ratio of displacement was calculated by dividing the Euclidean distance by the measured pathway distance. This provides a measure of sinuosity where results are between 0-1. The closer the ratio is to 1, the less sinuous (or more direct) the movement (Benhamou 2004). Movement rates were determined by first dividing either the Euclidean distance or "measured pathway distance" by the duration of each movement (i.e. approximately 2 or 4 hours). I estimated population-level means, medians and standard deviations of each metric per movement period, except calculating only the mean for bearing. The population's mean bearing required additional steps to transform this circular metric into a linear metric. Once I transformed degrees into radians per individual, I used trigonometry to calculate population-level means and converted resulting solutions back to bearings (Batschelet 1981). In addition, I calculated start/stop dates, mean duration and, movement metrics for fall and spring stopover sites. To investigate annual pronghorn movement metric variation, I ran ANOVA and analysis of deviance tests on individuals separated by capture year for each movement classification. Finally, I used correspondence analysis and subsequent between-class analysis (BCA) to discriminate and graphically interpret between possible groupings based on calculated movement metrics of individuals. I used permutation tests to assess statistical significance of BCA groupings (Dray et al. 2014). The two-dimensional graphs produced by BCA do not provide labels for the axis because they represent synthetic variables created to represent as much of the variation in the original data as possible (McCune and Grace 2002).

RESULTS

Classifying Pronghorn Movements

I gathered sufficient data to study movements for 170 animal years and of these, 94 (55%) exhibited seasonal migrations (identified as either migratory or mixed-migratory) and 76 (45%) were considered resident. Of the 94 animal years considered migratory, 58 (62%) were classified as migratory and 36 (38%) were classified as mixed-migratory. In addition, 11 (12%) fawning-associated movements and 32 (34%) driven movements were identified from the 94 animal years considered migratory. Of the 76 animal years considered residents, 15 (20%) included driven movements (Figure 2.2). I restricted further analysis to migratory animal years and resident animal years that undertook driven movements. In total, I analyzed 94 spring migrations, 70 fall migrations, 11 fawning-associated movements and 53 driven movements (six individuals initiated two driven movements per animal year) (Table 2.1).

Stopover Site Analysis

A total of 164 spring and fall migrations were analyzed. Of these migrations, 97 (66 Spring, 31 Fall) or 59% were categorized as Above and 67 (28 Spring, 39 Fall) or 41% were categorized as Below, respectively. Overall, 89 migrations (51 Spring, 38 Fall) or 54% were considered long-distance movements (LDM's) moving an average of 105.6 km (Range = 50.8 km - 260.4 km), while 75 (43 Spring, 32 Fall) or 46% were considered short-distance movements (SDM's) moving an average of 31.7 km (Range = 9.4 km – 49.9 km), respectively.

Forty-five stopover sites were identified among 36 migrations that included at least one stopover (22% of all migrations). The mean overall duration was 9.8 days (Range = 2-27 days, SD = 5.92). Spring stopovers (n=34) averaged 9.6 days (Range = 2-23 days, SD = 5.63), while fall stopovers (n=11) averaged 10.4 days (Range = 2-27 days, SD = 7.02). Of the 36 movements where stopover sites were identified, 27 (75%) were during the spring and 9 (25%) were during the fall (Figure 2.3a). In addition, 33 (92%) of the 36 migrations occurred within long-distance migrants and only 3 (8%) occurred within short-distance migrants. Finally, I found that nine identified migrations (7 Spring, 2 Fall) or 25% had two stopover sites within the movement period (Figure 2.3b).

Pronghorn Movement Metrics

For 94 spring migratory animal years, I found the mean and median duration of spring migration to be 20 days and 15 days (Range = 1-64 days, SD = 16.3), respectively. The mean duration coincided with spring migration starting March 22 and ending April 10. Mean and median Euclidean distance moved during spring migrations was 77.1 km and 56.7 km (SD = 54.7), respectively. Mean and median "measured distance" was 162.4 km and 111.9 km (SD = 134.4), respectively. Among Euclidean distance results for individual animal years, 51 (54%) were considered long-distance movements. The mean and median ratio of displacement for the NSS population was 0.55 and 0.51 (SD = 0.2), respectively. The mean and median movement rates were 0.22 km/hour and 0.18 km/hour (SD = 0.14) for Euclidean distance and 0.37 km/hour and 0.35 km/hour (SD = 0.13) for "measured pathway distance," respectively. Finally, the mean bearing for the entire NSS population during spring migration was 356.6° (Range = 359.9° - 173°), almost due north (Table 2.2).

For 70 fall migratory animal years identified, I found the mean and median duration of fall migration to be 11 days and 7 days (Range 2-53 days, SD = 10.8), respectively. The mean duration coincided with fall migration, starting October 31 and ending November 10. Mean and median Euclidean distance during fall migrations were 64.6 km and 54.6 km (SD = 46.5), respectively. Mean and median "measured distance" was 108.6 km and 86 km (SD = 88.9), respectively. Among Euclidean distance results for individual animal year, 38 (54%) were considered long-distance movements. The mean and median ratio of displacement for the NSS population was 0.67 for both (SD = 0.26). The mean and median movement rates were 0.35 km/hour and 0.28 km/hour (SD = 0.25) for Euclidean distance and 0.50 km/hour and 0.46 km/hour (SD = 0.27) for "measured pathway distance," respectively. Finally, the mean bearing for the entire NSS population during fall migration was 176.2° (Range = 20.7° – 180.2°), almost due south (Table 2.2).

For the 11 fawning-associated movement animal years identified, I found the mean and median duration of fawning-associated movements to last 7 days and 6 days

(SD = 5.4), respectively. The mean duration coincided with fawning-associated movements starting June 10 and ending June 16. Mean and median Euclidean distance during fawning-associated movements were 43.2 km and 45.2 km (SD = 17), respectively. Mean and median "measured distance" was 97.7 km and 78.6 km (SD = 81.8), respectively. Using Euclidean distance results for individual animal years, 4 (36%) were considered long-distance movements. The mean and median ratio of displacement for the NSS population was 0.61 and 0.57 (SD = 0.29), respectively. The mean and median movement rates were 0.44 km/hour and 0.38 km/hour (SD = 0.37) for Euclidean distance and 0.66 km/hour and 0.61 km/hour (SD = 0.30) for "measured pathway distance," respectively. Finally, the mean bearing for the entire NSS population was 86.3° (Range = 4.4° – 211.2°), almost due east (Table 2.2).

For the 53 driven movement animal years identified, I noted that either GPS collars fell off or individuals died (due to extreme conditions) prior to the completion of these movements. Despite these observed limitations, I deemed it worthwhile to calculate summary metrics. I found the mean and median duration of driven movements to last 10 days and 6 days (SD = 11.32), respectively. The mean duration coincided with driven movements starting December 23 and ending January 1. Mean and median Euclidean distance during driven movements were 41.2 km and 30.6 km (SD = 35.5), respectively. Mean and median "measured distance" was 65.8 km and 43.8 km (SD = 62.3), respectively. Using Euclidean distance results for individual animal years, 14 (26%) were considered long-distance movements. The mean and median ratio of displacement for the NSS population was 0.71 and 0.76 (SD = 0.19), respectively. The mean and median movement rates were 0.26 km/hour and 0.23 km/hour (SD = 0.16) for Euclidean distance and 0.35 km/hour and 0.32 km/hour (SD = 0.17) for "measured pathway distance," respectively. Finally, the mean bearing for the entire NSS population was 175.8° (Range = 32° – 179.6°), almost due south (Table 2.2).

I further investigated differences between driven movements based on whether the individual was migratory or resident in a given year. I found the mean and median duration of both migratory and resident driven movements to last 10 days and 6 days (SD = 11.9, 10.3), respectively (t = -0.21, *p* = 0.829, df = 36). These mean durations coincided with migratory driven movements starting December 21 and ending December 30 while resident driven movements started December 29 and ended January 7 (t = -1.4, *p* = 0.169, df = 38 for start dates, t = -1.24, *p* = 0.222, df = 38 for end dates, respectively). Mean and median Euclidean distance during migratory driven movements were 44.2 km and 30.8 km (SD = 39.2) and 34.7 km and 25.9 km (SD = 25.8) for resident driven movements, respectively (t = 1.05, *p* = .0298, df = 45). Mean and median "measured distance" during migratory driven movements were 68.4 km and 42.5 km (SD = 67.9) and 60.4 km, and45.6 km (SD = 49.6) for resident driven movements, respectively (t = 0.483, *p* = 0.631, df = 42). The mean and median ratio of displacement for migratory driven movements was 0.74 and 0.76 (SD = 0.16) and 0.66 and 0.76 (SD = 0.23) for resident driven movements, respectively (t = 1.26, *p* = 0.218, df = 24). The mean and median movement rates using Euclidean distance for migratory driven movements were 0.28 km/hour and 0.25 km/hour (SD = 0.17) and 0.2 km/hour and 0.16 km/hour (SD = 0.13) for resident driven movements, respectively (t = 1.87, *p* = 0.068, df = 39). The mean and median movement rates using "measured distance" for migratory driven movements were 0.38 km/hour and 0.34 km/hour (SD = 0.19) and 0.29 km/hour and 0.27 km/hour (SD = 0.13) for resident driven movements, respectively (t = 2.05, *p* = 0.046, df = 44). Finally, the mean bearing for migratory driven movements was 171° (Range = 32° - 183°), while for resident driven movements, the bearing was 185.7° (Range = 275.1°-179.6°), both in southerly directions (Table 2.2).

Finally, for spring (*n* = 34) and fall (*n* = 11) stopover animal years identified, I found the mean and median duration of spring stopovers to last 9.6 days, and 8 days (SD = 5.6) and fall stopovers to last 10.3 days and 8 days (SD = 7), respectively. The mean duration coincided with spring stopovers starting April 5 and ending April 14 while fall stopovers started October 6 and ended October 15. Mean and median Euclidean distance for spring stopovers was 3.5 km and 2.7 km (SD = 2.7) while fall stopovers were 2.8 km and 2.4 km (SD = 2), respectively. Mean and median "measured distance" for spring stopovers was 40.6 km and 26.7 km (SD = 36), while fall stopovers were 38.2 km and 33.9 km (SD = 36.6), respectively. The mean and median ratio of displacement during spring stopovers was 0.12 and 0.07 (SD = 0.09) while fall stopovers were 0.12 and 0.09 (SD = 0.1), respectively. The mean and median movement rate using Euclidean distance during spring stopovers was 0.02 km/hour and 0.02 km/hour (SD = 0.01) while fall stopovers were 0.01 km/hour and 0.01 km/hour (SD = 0.01), respectively. The mean and median movement rate using “measured distance” during spring stopovers was 0.16 km/hour and 0.15 km/hour (SD = 0.07), while fall stopovers were 0.14 km/hour and 0.13 km/hour (SD = 0.07), respectively. Finally, the mean bearing during spring stopovers was 28.8° (Range = 3.2° – 172.2°) in a northeasterly direction, while during fall stopovers the mean bearing was 166.2° (Range =56.5° – 182.1°) in a southerly direction (Table 2.2).

I found annual variation in movement metrics of some movement classifications using ANOVA and analysis of deviance tests. Based on individuals analyzed from distinct captures years, I found that annual variation was most identified in start/end dates and overall distances. Movement metrics such as duration, displacement ratio and movement rates (both using Euclidian and measured distances) typically exhibited insignificant annual variation (Table 2.3, Appendix 2.2). Fall migrations and driven movements seemed to show the most annual variation in movement metrics.

Using BCA, I found three general groupings of the various movements from movement distances, duration, displacement and rate metrics (Figure 2.4a). Although some variance was observed, individuals that undertook fall migration, fawning-associated movements and driven movements were associated as one general group. Spring and fall stopovers were classified as a second group, while spring migration formed a third distinct group. Between-class variance was 31.5% while 68.5% of variance can be explained by observations within groups (*p* = 0.001) (Figure 2.4b).

DISCUSSION

Pronghorn Migration, Movements and Stopover Sites

At the end of summer annually, pronghorn are typically in good body condition with respect to nutritional intake and fat reserves to sustain themselves for the impending rut and winter months (Parker et al. 2009). Fall migrations may be prompted by environmental cues such as temperature, snow depth or forage moisture content (Pennycuick 1975, Hoskinson and Tester 1980, Dalton 2009, Suitor 2011). It was evident that pronghorn may first make exploratory movements at the end of summer, sometimes moving long distances from summer range, only to return to summer ranges before engaging in migration. These movements may be an effort to test the availability of suitable conditions or may be the result of agonistic social interactions between sexes during rut (Kitchen 1974, Byers 1997). Consequently, fall migration start/stop dates varied more than spring migrations dates as seen in other ungulates (Cagnacci et al. 2011). As observed in the increased ratio of displacement and movement rates, fall migrations were rapid and linear movements to winter ranges where sustenance in the form of evergreen sagebrush and juniper and shelter from harsh conditions were provided. I compared movement metric results reported for pronghorn in the NSS to other pronghorn studies across North America. Overall, I found similar results for timing and duration of migration but variation in distance travelled. In Idaho, pronghorn began spring migration from late February to late March, which lasted an average of 49 days with mean distance travelled 44 km. Fall migration typically began October 1 and lasted through November 25 (Hoskinson and Tester 1980). In Wyoming, Sawyer et al. (2005) reported that spring migration on average lasted 73 days while mean fall migration lasted 19 days. The mean roundtrip migration was 177.2 km. In another study, Sheldon (2005) reported that spring migration on average occurred from April 2 – April 20, lasting 18 days, with a mean distance of 82 km at rate of 6 km/day in a northwesterly direction. On average, fall migration occurred from October 9 – October 20, lasting 11 days, with a mean distance of 55 km at a rate of 9 km/day in a southeasterly direction. In North Dakota, spring migration on average occurred from March 20 – April 10 with a mean distance of 74.6 km. Fall migration on average occurred from October 22 – November 9 with a mean distance of 63.1 km (Kolar et al. 2011). Compared to other long-distance ungulate migrations, pronghorn demonstrate similar metrics for distance travelled. In my study, the longest roundtrip migration was 887 km, based on movements between relocations. This distance is comparable to the 400-600 km and 400-2400 km roundtrip migrations undertaken by wildebeest (Thirgood et al. 2004) and saiga (Bekenov et al. 1998), respectively. Barren-ground caribou undertake in extremely long migrations, with mean roundtrip distances of 3031 km reported (Fancey et al. 1989).

Many migratory individuals in this partially migratory population were classified as mixed-migrants while others displayed fidelity to winter range. Of 70 individuals where full annual migrations were recorded, 36 (51%) used the mixed-migratory strategy and did not return to the same winter range. Presumably, individuals move only as far as necessary to locate acceptable winter range conditions, thus conserving energy for the ensuing winter (Nicholson et al. 1997, Cagnacci et al. 2011). As a result, the azimuth and magnitude of fall migration destinations determines the orientation of the following return spring migration to fawn and summer range. In addition, only 25% of identified stopover sites were during the fall migratory period, in accordance with the view that fall migration represents a faster, more directed movement than spring migration (Sawyer et al. 2005, Sawyer and Kaufmann 2011). I suggest that individuals opportunistically used stopovers during fall to increase chances of arriving at winter range in good condition.

I fortuitously collected multi-year data on13 individuals. Of these, three individuals switched movement strategies (i.e. switched from mixed-migrant classification to resident classification) from one year to the next. An individual’s decision to move annually may be more flexible and adaptable than previously considered and therefore not an innate behavior (Gaillard 2013). Across the NSS, pronghorn typically grouped together in the fall and moved to suitable winter range. Moving together as a group may decrease energetic costs of moving through snow, since individuals migrate in a single-file line (Parker et al. 2009). During the fall, group migration in pronghorn may involve a social element, where related individuals follow kin to possibly take advantage of learned destinations by more experienced individuals (Barnowe-Meyer et al. 2013). I suggest during the fall migration period individuals switch movement strategies based on flexibility in winter range selection and learn through social interactions. Pronghorn, and other ungulates, must prepare for future unknown winter conditions. Although advantageous for multiple reasons, the act of migration in itself depletes energy reserves (Parker et al. 2009). It may be advantageous for individual pronghorn and other ungulates to switch movement strategies in a spatiotemporal variant system. More long-term studies are required to tease apart the various migration mechanisms at play to determine whether migration is passed down to related kin through learned behavior, is an innate behavior of the individual, or is annually flexible in response to varying ecological gradients (Sweanor and Sandegren 1988, Nelson 1998, Hebblewhite and Merrill 2011, Gaillard 2013).

Spring migration of pronghorn involves return movements back to fawning ranges, to which pronghorn show high fidelity (Wiseman et al. 2006). Fawning range along with accompanying summer range are the anchor locations during an individual's annual life cycle. During spring migration, pronghorn engage in consistent movements interspersed with stopovers to track high quality forage to recover from the previous winter and prepare for fawning (Fryxell and Sinclair 1988, Hebblewhite et al. 2008, Mysterud 2013). During spring, pronghorn had the longest movement durations, the longest distances traveled, the highest path sinuosity and slowest movement rates of all identified movement classifications. Although no data was collected on pronghorn densities, individuals on comparatively smaller winter ranges typically encounter increased forage competition than while on summer ranges. As a result, density-dependent competition may lead to earlier spring migration initiation dates (Mysterud et al. 2011). Likewise, once pronghorn group together after the rut in fall, density-dependent forage competition may also lead to earlier migration initiation dates or increased movement rates to winter range (Mysterud et al. 2011).

Similar to other migrating ungulates, pronghorn utilized stopovers sites during migration (Saher and Schmiegelow 2005, White et al. 2010, Sawyer and Kauffman 2011, Seidler et al. 2014). In pronghorn, 76% of stopover sites were identified during this period. Engaging in slow, steady movements interspersed with stopovers may be advantageous for pronghorn. During spring migration, fetal growth demands of female pronghorn is high; therefore, reducing energy expenditure and maximizing intake of high quality forage through slow, sinuous movements may improve reproductive success (Webster et al. 2002, Owen-Smith et al. 2010, Avgar et al. 2014). The northerly bearing during spring migration takes advantage of increasing forage productivity, which occurs later at higher latitudes as spring progresses (Myneni et al. 1997). Thus, the use of stopover sites during spring migration provides pronghorn an opportunity to track and match spatiotemporal gradients in plant phenology and access high quality resources (Sawyer and Kauffman 2011).

From GPS relocations and graphical interpretation, I identified distinct fawning-associated movements made by collared pronghorn approximately three weeks after parturition, speculatively with a fawn at heel. Although these movements occurred during springtime, fawning-associated movements were on average the shortest in duration, more direct and had much higher movement rates than observed during spring migration. Fawning occurs synchronously across the NSS pronghorn population where individuals fawn in isolation and neonates are considered “hiders” (Gregg et al. 2001, Olson et al. 2005). After pronghorn give birth, females and fawns aggregate into nursery herds during the late spring and summer (Kitchen 1974). Because no data were collected on fawning success in my study, the rationale for observed fawning-associated movements would be merely speculative. However, future research should investigate these movements in further detail.

In addition to seasonal migratory and fawning-associated movements, I examined driven movements, which may be undertaken to escape adverse environmental conditions and possible starvation. Accordingly, I did not expect stopover sites associated with driven movements and did not investigate possible stopovers during these movements. In the NSS, driven movements may be initiated as a response to extreme low temperatures, high wind speeds and increased snow accumulation. For example, individuals captured in Alberta from 2003-2006 experienced typical winter conditions based on long-term climatic data (Environment Canada 2010) (Table 2.4). Only one individual was classified as undertaking a driven movement. However, individuals captured in Montana and Saskatchewan from 2008-2010 experienced exceptionally harsh winter conditions with respects to long-term climatic data. During that period, there were both decreased mean and maximum temperatures and record snow accumulations for the area (Environment Canada 2010, NOAA 2014) (Table 2.4). As a result, 46 individuals initiated driven movements, and included both migrants and residents. Pronghorn morphology makes this species highly sensitive to deep snow accumulation, as they have the lowest mean chest height and highest foot-loading index (ratio of weight to surface area of the foot) of any ungulate (Telfer and Kelsall 1984). To compensate for these morphological constraints, pronghorn escape severe conditions by moving at accelerated rates until conditions improve. For example, one individual undertook a 22.5 km driven movement during a six-hour period; a mean movement rate of 3.7 km/hour. These movements during extreme winter events and other stochastic environmental events across pronghorn range (drought, fire, etc.) allow pronghorn populations to persist in the NSS. Although many of the collared pronghorn either died while making driven movements or their collars fell off during the movement itself, seven driven movements were at least 100 km in length.

It is difficult to conclude exactly when or how far pronghorn will travel before they stop. On average, driven movements were almost directly south and these movements exhibited the highest ratio of displacement, i.e. highest linear movements, for all movement types investigated. In extreme winter conditions, pronghorn make rapid driven moves directly south to find better conditions. Physical structures such as roads, fences, railroads and their indirect associations (traffic, noise, etc.) may increase time taken by pronghorn to make long-distance movements. As a result, increased movement costs likely have negative consequences (predation, starvation, over-exposure) for individuals and populations (Barrett 1982, Gavin and Komers 2006, Harrington and Conover 2006, Jones 2014).

I investigated possible differences in movement metrics between migrant and resident individuals that undertook driven movements. Of 53 driven movements for which I calculated movement metrics, 32 were undertaken by migrants and 15 by residents. I found that the rate of driven movements by migratory pronghorn were significantly faster, and on average these individuals started driven movements eight days earlier than driven movements of resident individuals. Given this finding, I suggest that individuals that have previously undergone seasonal migrations have either gained experience and are more willing to move long distances, or they have learned that movement is a favorable strategy for survival through social processes such as culturally transmitted information or conspecific attraction (Bauer et al. 2011). However, more research is needed to test this hypothesis. Individuals that move in response to environmental stimuli may be better suited to handle severe winter conditions, which are common at the northern periphery of pronghorn range. From a population perspective, it is therefore imperative to facilitate these seasonal movements through the use of various management tools (barrier modifications, movement structures, habitat enhancements, community education, etc.), so that individuals and their offspring are better equipped to navigate fluctuating environments and stochastic events (Sawyer et al. 2013).

Annual variation in movement metrics by movement classifications was tested for to explore temporal influences. More often than not, metrics did not significantly vary on an annual basis. However start/stop dates and overall distances did show significant annual variation, in particular for fall migration and driven movements. Annual variation in these two movement classifications may indicate that pronghorn respond to deteriorating conditions on seasonal range, providing pronghorn flexibility to find improved conditions and improving survival prospects across unpredictable environmental gradients (Martinka 1966, Hoskinson and Tester 1980).

The use of BCA highlighted similarities and differences between movement classifications, based on individual movement metrics. I found that attributes of movements during fall migration, fawning-associated, and driven movements were similar, while spring migration attributes were distinct from others. Finally, spring and fall stopovers had distinctly different metrics from other movements. To offset risks of mortality from harsh environmental conditions and predation (i.e. increase survival rates), pronghorn moved directly and at accelerated rates during fall migrations, fawning-associated and driven movements. These tactics are similar to responses by other ungulates to predation and varying environmental factors (Owen-Smith et al. 2005). Spring migration is a return movement to fawning range and thus is particularly linked to an individual's reproductive success. Spring migration was grouped independently from other groups based on higher duration and magnitude of the movement in keeping with tracking a temporal latitudinal gradient of high quality forage. Analogous movements have been reported for elk (*Cervus elaphus candensis*) in mountainous areas that follow a temporal-elevational gradient in forage quality (Hebblewhite et al. 2008). Finally, both spring and fall stopover sites were grouped together from calculated movement metrics.

Stopovers sites are areas that ungulates use to feed on high quality forage for reproductive success and maintenance (Parker et al. 2009, Sawyer and Kauffman 2011). However, based on similar spring and fall stopover metrics, pronghorn stopover sites may demonstrate greater association with individual maintenance requirements (i.e. rest, nutritional replenishment) acquired during migration events (Dingle and Drake 2007). More research is needed to make robust conclusions.

Movement Management and Conservation

As with other ungulates, pronghorn have adapted to track and respond to environmental gradients across large landscapes by selecting to either engage in seasonal migrations and long-distance movements or remain as year-round residents (Fryxell and Sinclair 1988, Hebblewhite et al. 2008, Mueller et al. 2008, Jones et al. 2015). Jones et al. (2015) found that a higher proportion of pronghorn captured in croplands tended to use a resident strategy. Alternatively, an individual's selection of strategy (i.e. migrant or resident) may be an intrinsic tradition, learned and passed down from the mother or others in a group context (Sweanor and Sandegren 1988, Barnowe-Meyer et al. 2013). In the NSS, 55% of collared pronghorn underwent seasonal migrations (i.e. occupied discrete seasonal ranges). This migratory frequency is similar to other studies of pronghorn in North Dakota (Kolar et al. 2011), South Dakota (Jacques et al. 2009) and Wyoming (White et al. 2007, Beckmann et al. 2012). Of the 55% that underwent migrations, 54% (using Euclidean distance) of the migrations were considered long-distance movements (LDM's > 50 km). In my study, thirty individuals made seasonal migrations of ≥ 200 km, far exceeding distances reported in previous pronghorn studies. The NSS region is the northern limit of pronghorn range. I was able to infer latitudinal influences on this pronghorn population as the mean azimuth for most collared pronghorn was almost due north during spring while in contrast, fall migration was almost due south. Return spring migrations to fawning sites may follow the "green wave" of high quality forage, which occurs at increasing latitudes as spring progresses.

The spatiotemporal insights into pronghorn migration and long-distance movements given here provide a basis for population management. Across the NSS, anthropogenic development may threaten the landscape integrity and connectivity necessary for long-distance migrants through habitat loss and fragmentation. As a first step, I suggest migrations and long-distance movements should be managed seasonally, in addition to managing species spatial requirements. For example, annual spring migrations typically occur in a predictable and synchronous manner and can be managed accordingly. Similarly, driven movements occur in response to recognizable, extreme winter conditions and other stochastic events, and can be opportunistically managed as conditions dictate. Management practices such as opening gates, fence modifications and creating opportunities to cross roads and railroads could facilitate pronghorn movement at the northern limit of their range. In addition, stopover sites are a significant component of migration and should be conserved and managed (Sawyer and Kauffman

2011). As discussed by Seidler et al. (2014), human-induced stopover sites have been identified that may cause a mismatch between the timing of maximum forage quality and stopover use; therefore, more attention should be given to facilitate continued movement across linear anthropogenic features (Sawyer et al. 2013).

Finally, it is apparent that migration and long-distance movements made by pronghorn are important strategies at the northern periphery of the species' range. Over half of the collared individuals underwent seasonal migration and the majority of these movements were LDM's. During my study, mortality rates of collared pronghorn were 31%, which is a significant proportion of the population. Higher mortality rates at the periphery rather than at the core of a species range is credible (Gaston 2008). Managing and conserving landscapes to support long-distance migration could assist in mitigating mortality by providing opportunities for pronghorn to locate and use discrete optimal habitat.

The use of NSD provided a fitting metric for classifying migration and long-distance movements in pronghorn while also identifying stopover sites. This framework can be used by researchers to classify and identify migration components in pronghorn and other migratory species. In my study, once NSD was calculated for each individual's particular movement, subsequent movement classification and stopover analysis was simplified. Presently, the adehabitatLT package identifies various movement types while also differentiating movement pathways by rates; that is, the package may identify two or more movement pathways segments along one continual movement pathway. In future instances, the package could be refined to determine specific movement types (i.e. migratory pathway or stopover site). Finally, results presented here can be used to predict multi-scale movement patterns across the NSS by modeling the influence of a series of temporal and spatial parameters across the system. Movement models can be translated into maps so that stakeholders can prioritize management opportunities (Squires et al. 2013; see chapter 3). In addition, I could investigate stopover sites requirements across the migratory pathway to monitor potential spatial and temporal characteristics of these areas for conservation.

Table 2.1: Movement classification totals for each movement type (migratory, mixed-migratory or resident) in a partially migratory population of pronghorn across the NSS from 2003-2011.

Movement Classification (*n*)	**Spring Mig.**	**Fall Mig.**	**Fawn Move.**	**Driven Move.**	**Spring Stop**	**Fall Stop**
Migratory (58)	58	34	5	21	13	5
Mixed-migratory (36)	36	36	6	15	14	4
Resident (76)	NA	NA	NA	17	NA	NA
TOTAL (170)	94	70	11	53	27	9

Table 2.2: Summary of pronghorn movement metrics for each movement classification across the NSS from 2003-2011.

Movement Type (*n*)	Mean Start Date	Mean Stop Date	Mean & Median Duration (Days)	Mean & Median Euc. Dis. (km)	Mean & Median Meas. Dis. (km)
Spring (94)	22-Mar	10-Apr	20 & 15	77.1 & 56.7	162.4 & 111.9
Fall (70)	31-Oct	10-Nov	11 & 7	64.6 & 54.6	108.6 & 86
Fawn (11)	10-Jun	16-Jun	7 & 6	43.2 & 45.2	97.7 & 78.6
Driven - Migrant (36)*	21-Dec	30-Dec	10 & 6	44.2 & 30.8	68.4 & 42.5
Driven - Resident (17)*	29-Dec	7-Jan	10 & 6	34.7 & 25.9	60.4 & 45.6
Spring Stopover (34)	5-Apr	14-Apr	10 & 8	3.5 & 2.7	40.6 & 26.7
Fall Stopover (11)	6-Oct	15-Oct	10 & 8	2.8 & 2.4	38.2 & 33.9

Movement Type (*n*)	Mean & Median Displace. Ratio	Mean & Median Euc. Dis. Rate (km/h)	Mean & Median Meas. Dis. Rate (km/h)	Mean Bearing°	Mean General Direction
Spring (94)	0.55 & 0.51	0.22 & 0.18	0.37 & 0.35	356.6	North
Fall (70)	0.67 & 0.67	0.35 & 0.28	0.5 & 0.46	176.2	South
Fawn (11)	0.61 & 0.57	0.44 & 0.38	0.66 & 0.61	86.8	East
Driven - Migrant (36)*	0.74 & 0.76	0.28 & 0.25	0.38 & 0.34	171	South
Driven - Resident (17)*	0.66 & 0.76	0.2 & 0.16	0.29 & 0.27	185.7	South
Spring Stopover (34)	0.12 & 0.07	0.02 & 0.02	0.16 & 0.15	28.8	Northeast
Fall Stopover (11)	0.12 & 0.09	0.01 & 0.01	0.14 & 0.13	166.2	South

* Metrics may not be accurate due to in many instances, animal died or collar fell off during driven movement

Table 2.3: Summary movement metric results using ANOVA and analysis of deviance tests for each pronghorn movement classification to investigate annual variation in movement metrics for pronghorn across the NSS from 2003-2011.

Season	**Start Date**	**Stop Date**	**Duration**	**Euc. Dist.**	**Meas. Dist.**	**Displace. Ratio**	**Euc. Dis. Rate**	**Meas. Dis. Rate**
Spring Migration	Yes	Yes	No	Yes	No	No	No	No
Fall Migration	Yes	Yes	Yes	Yes	Yes	No	No	No
Fawn Movement	Yes	Yes	No	No	No	No	No	No
Driven Movement	No	No	Yes	Yes	Yes	Yes	No	No
Spring Stopover	No	No	No	No	No	No	No	No
Fall Stopover	Yes	No	No	No	No	No	No	No

Note:
"Yes" indicates a significant difference ($p < 0.05$) between years for each metric,
"No" indicates no significant differences between years for each metric

Table 2.4: Capture year (2003-2011) and long-term (20 year) winter climatic conditions that indicate temperature and snowfall at two weather stations across the NSS.

Location	Winter (Nov-Mar)	Capture Year	Mean °C	Mean °C Max	Mean °C Min	Snowfall (cm)
Medicine Hat, AB	2003-2004	1	-5.0	0.1	-10.1	87.2
Medicine Hat, AB	2004-2005	2	-3.1	3.4	-9.6	82.4
Medicine Hat, AB	2005-2006	3	-2.0	3.5	-7.5	89.5
Medicine Hat, AB	2006-2007	NA	-3.2	3.1	-9.5	0
Medicine Hat, AB	**1981-2010**	**NA**	**-4.5**	**1.2**	**-10.3**	**67.3**
Glasgow, MT	2007-2008	4	4.7	16.3	-6.7	58.4
Glasgow, MT	2008-2009	5	0.4	10.7	-9.9	93.5
Glasgow, MT	2009-2010	6	1.0	10.9	-8.8	73.2
Glasgow, MT	2010-2011	NA	-3.2	5.8	-12.1	264.4
Glasgow, MT	**1981-2010**	**NA**	**4.3**	**14.3**	**-5.8**	**76.7**

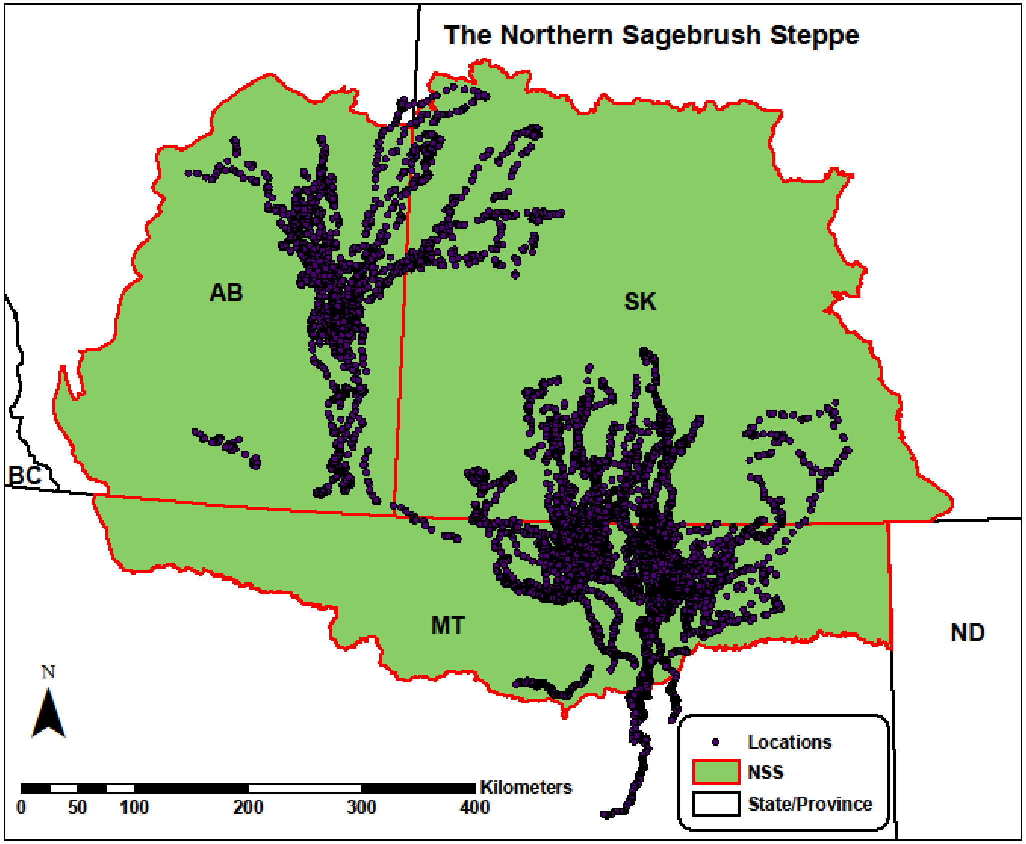
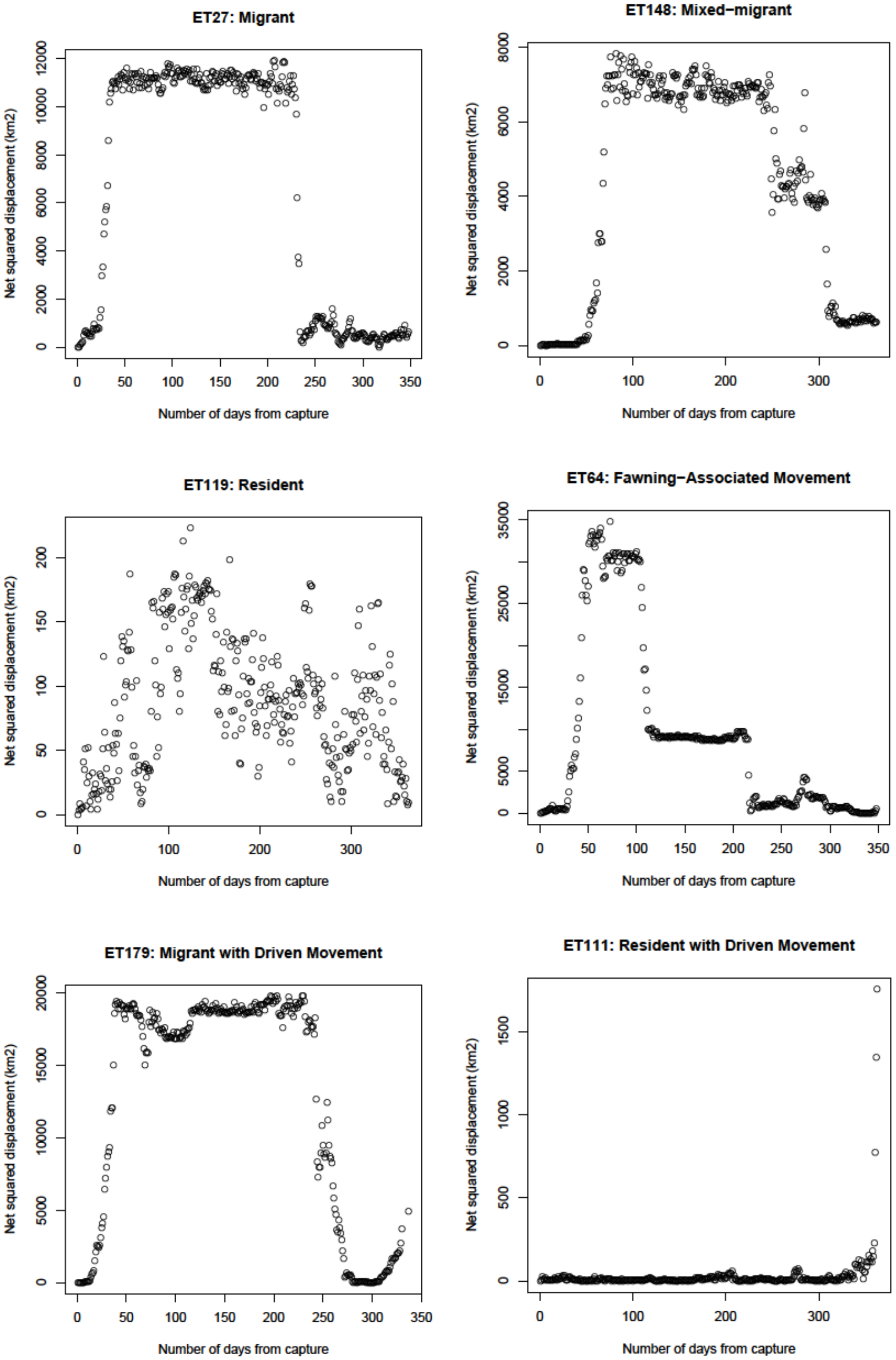


Figure 2.1: The Northern Sagebrush Steppe with pronghorn migration/movement locations per individual, 2003-2011.


ET27: Migrant

ET148: Mixed−migrant

ET119: Resident

ET64: Fawning−Associated Movement

ET179: Migrant with Driven Movement

ET111: Resident with Driven Movement

Figure 2.2: Graphical examples of each movement classification based on daily NSD for pronghorn across the NSS. Note that all pronghorn were captured during the winter time (December-March) of the respective capture year. Open circles depict daily relocations per individual.

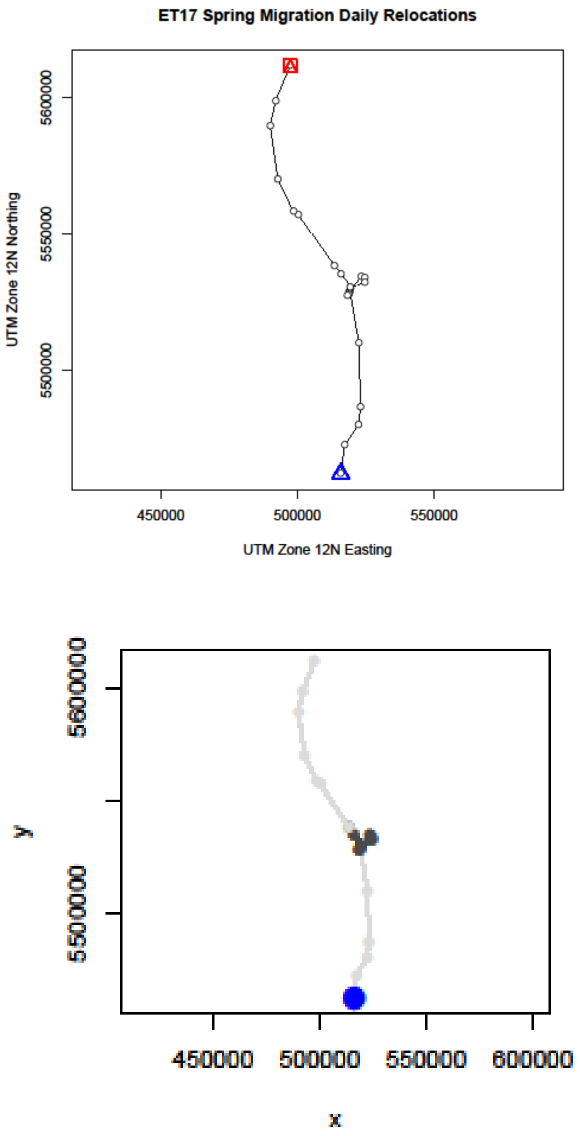


Figure 2.3: Example of graphical result to identify stopover sites in pronghorn across the NSS. The top panel shows the daily relocations during spring migration of pronghorn ET 17 where the blue triangle and red square depicts start and stop of migration. The bottom panel exhibits the migration sectioned to identify stopover sites; in this case, one stopover site is identified.

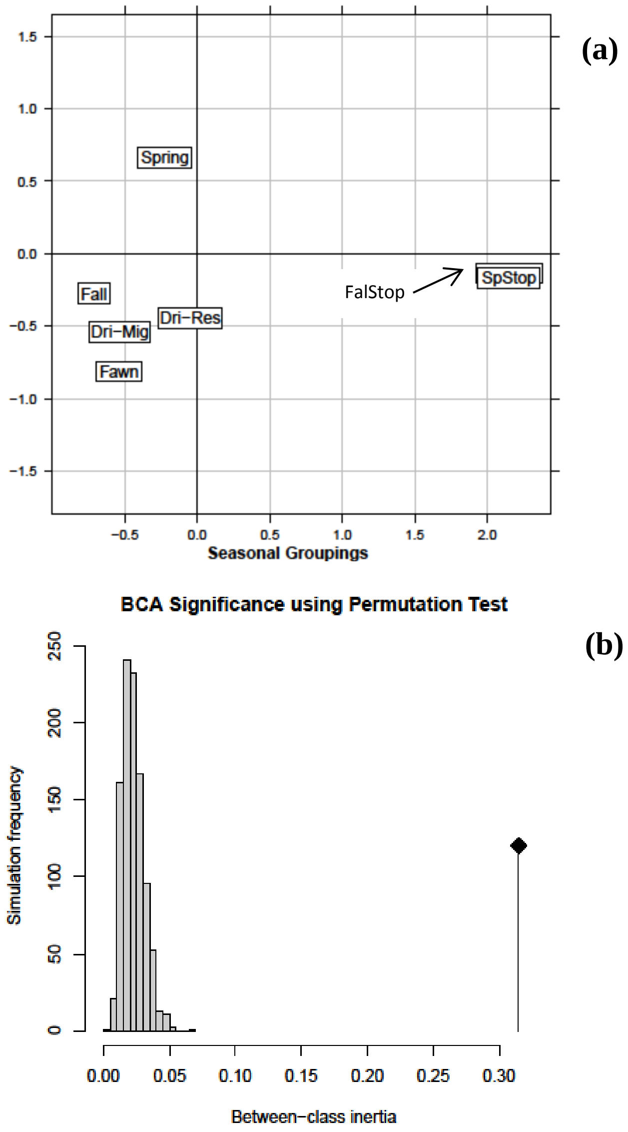


Figure 2.4 (a-b): Between-class analysis results. (a) Depicts three distinct groupings of movement classification based on individual movement metrics. Grouping metrics include duration (days), Euclidean distance (km), displacement ratio and movement rate (km/h). (b) Histogram of 999 simulation values to test differences between groups using permutation test. The observed value displayed as the vertical line at the right of the histogram is 0.315, indicating the between-class inertia (variance explained between groups). The observed between-class inertia value is significantly different from random, simulated values (p=.001) demonstrating that based on movement metrics, groups are significantly different.

CHAPTER 3: MULTI-SCALE SELECTION OF MIGRATION PATHWAYS BY PRONGHORN IN RELATION TO ENVIRONMENTAL GRADIENTS AND ANTHROPOGENIC FACTORS

INTRODUCTION

Ecological processes occur at multiple spatiotemporal scales and as a result, wildlife respond to landscape heterogeneity at different scales to varying degrees (Peterson et al. 1998, Boyce 2006). A relevant scale is characterized by both its grain and extent, referring to the finest level of spatial resolution and the size or duration of an ecological observation, respectively (Turner et al. 1989, Wheatley and Johnson 2009). Johnson (1980) first defined orders of selection to denote a hierarchy of scale regarding wildlife habitat selection, from broadest to finest spatial areas. The finest ordered scale of selection is nested within a broader scale so that fine scale decisions depend on broad scale decisions; thus, factors selected at broader scales are interpreted as limiting to species distributions (Foreman 1995, Rettie and Messier 2000, Kie et al. 2002). Often, habitat selection studies examine an animal's response to multiple ecological processes and anthropogenic factors that may vary across scales (Rettie and Messier 2000, Schaefer et al. 2000, Johnson et al. 2004, DeCesare et al. 2012). Movement selection by wildlife is a tactic for satisfying life-history requirements and may be perceived at various orders of scale yet does not fit neatly as a hierarchal process (Ims 1995, Chetkiewicz et al. 2006). As with modeling habitat selection, fine ordered scales of movement may be nested within a broader order of scale. Unlike modeling habitat selection, movement selection is sequential; in other words, a pathway is dependent on the length and turning angle of the preceding step or steps, and there are diverse stimuli and biological requirements that affect movement (i.e. foraging, migration, dispersal, etc.) (Thurfjell et al. 2014). Furthermore, the broadest scales of movement selection may be understood as ecological processes (e.g. connectivity) that theoretically unite seasonal habitats over extended periods. Similar to predicting multi-scalar habitat selection, analytical approaches can be used to predict movement selection at individual and population levels (Sawyer et al. 2009*b*, Thurfjell et al. 2014). Researchers can design multi-scalar movement studies, by framing the grain and extent of the relevant scale, to predict wildlife spatiotemporal responses across large areas (Schaefer et al. 2000, Bowyer and Kie 2006, Chetkiewicz et al 2006, Thurfjell et al. 2014).

Migration in ungulates is an adaptive strategy that can be defined as repeated movements by individuals or population segments to discrete seasonal ranges used at different times of the year (Baker 1978, Berger 2004, Dingle and Drake 2007). Ungulate migrations occur worldwide and have been shown to be in response, largely, to precipitation and resulting forage productivity in Africa (Wilmshurst et al. 1999), Asia (Singh et al. 2010) and North America (Hebblewhite et al. 2008). In addition, migrations occur so that individuals or population segments can escape predators, to offset density-dependent factors, to improve physical condition before breeding and/or to improve long-term reproductive success (Fryxell and Sinclair 1988, Bolger et al. 2007, Avgar et al. 2014). Depending on the length of migration, ungulates may use stopover sites to serve as a critical role amid migration to energetically recover and amass reserves to complete the journey (Bolger et al. 2007, Sawyer et al. 2009*a*, Sawyer and Kauffman 2011). Stopover sites have been found in areas of higher forage productivity with lower densities of anthropogenic features than migratory pathways (Sawyer and Kaufmann 2011, Seidler et al. 2014). As such, migration itself is a movement behavior and a habitat selection strategy (Gaudry et al. 2015).

Globally, grassland communities face continued direct and indirect ecological threats from anthropogenic development disrupting natural ecological processes and diminishing wildlife populations (Hobbs et al. 2008). Conversion of native landscapes to agricultural lands and infrastructure such as roads, power lines and fences cause direct habitat loss, fragments the landscape, and either partially impedes or completely blocks animal movement (Trombulak and Frissell 2000, Chape et al. 2003, Fahrig, 2003, Forrest 2004, Harrington and Conover 2006). The continuous demand for energy from oil and natural gas resource extraction exacerbates these effects (Copeland 2009). Migratory ungulates galvanize ecological processes across large grassland areas (Fryxell and Sinclair 1988, Harris et al. 2009), and are globally threatened by increasing human activities in grasslands, including wildebeest (Thirgood et al. 2004), Mongolian gazelles (Mueller et al. 2008), saiga (Berger et al. 2008), and pronghorn (Berger 2004, Beckmann et al. 2012). Broad-scale analytical approaches are needed to address threats by designing management and conservation applications for sustaining ungulate long-distance movements, including migrations.

Both environmental and anthropogenic factors influence ungulate habitat and migratory pathway selection. Spatial variability in landcover types and topography has been shown to influence selection (Nicholson et al. 1997, Johnson et al. 2002, DeCesare and Pletscher 2006, Sappington et al. 2007). In addition, temporal factors such as plant phenology (Mysterud et al. 2001, Hebblewhite et al. 2008, Mueller et al. 2011) and snow depth (Sweeney and Sweeney 1984, Turner et al. 1994, Ball et al. 2001) have been demonstrated to impact ungulate habitat selection. Finally, anthropogenic features such as roads and oil and natural gas development affect ungulate distributions at various scales (Sawyer et al. 2006, Johnson et al. 2005, Sawyer et al. 2009*b*, Hebblewhite 2011, Polfus et al. 2011, DeCesare et al. 2012). Regarding anthropogenic features specifically, variable selection at broader scales ought to influence migratory pathway selection more significantly than at finer scales. Ungulate resource selection is first made broadly, and so finer scale decisions are limited and as a result, responses to anthropogenic features may be muted (Polfus et al. 2011, DeCesare et al. 2012).

The pronghorn (*Antilocapra americana*) is an indigenous ungulate species that ranges across the prairies, intermountain valleys and sagebrush steppes of Western North America where populations are usually partially migratory (Berger 2004, White el al. 2007, Kolar et al. 2011). In Chapter 2, I reported that individual pronghorn initiated migrations during the fall and spring and used stopover sites. Four migration states were distinguished to include fall migratory pathways, fall stopover sites, spring migratory pathways and spring stopover sites at their northern range limit in the Northern Sagebrush Steppe (NSS; Figure 3.1). Migratory pronghorn in the NSS undergo a general migratory pattern of migration between southern ranges when plants senescence in fall to more northerly summer ranges during spring (Bruns 1977, Barrett 1984, Suitor 2011). Pronghorn are considered intermediate/mixed feeders tending towards concentrate feeders and most likely feed on forage with the highest available crude protein content during a given season (Hofmann 1989, Schwartz et al. 1981). During spring return migration to fawning locations, pronghorn are believed to track quality forage, primarily forbs and grasses (Wiseman et al. 2006). Once fawning occurs, pronghorn consume a variety of native and cultivated forage throughout the summer at the height of plant production. During summer, fat reserves are replenished until plant senescence occurs again.

Here, I examine multi-scale migration pathway selection of pronghorn between discrete summer and winter ranges in the Northern Sagebrush Steppe. Based on pronghorn distribution literature, I predicted that pronghorn will avoid higher densities of anthropogenic features such as roads and oil and gas wells during migration (Gavin and Komers 2006, Beckmann et al. 2012). I reviewed a number of methods to assess anthropogenic variables effect on pronghorn migratory pathway selection and found deficiencies in assessing human-induced development cumulatively across a landscape. Previous studies and management guidelines used arbitrarily designated buffer sizes or “distance to” measurements to represent the spatial breadth of impact of linear or point anthropogenic variables on pronghorn resource selection (Environmental Law Institute 2003, Sheldon 2005, Dalton 2009). Studies utilizing “distance to” measurements only account for the nearest attribute to infer ungulate response to a given variable (Sawyer et al. 2006, Sawyer et al. 2009*b*). In highly developed or fragmented areas, it is more appropriate to spatially measure density to infer response to a given variable. Recent studies have begun to use spatial analysis in ArcGIS (ESRI 2012) to ascertain a search radius that best describes an ungulate’s response to various densities of a given parameter (Polfus et al. 2011, DeCesare et al. 2012).

This approach allows the species response to varying search radii to dictate the appropriate density of each variable to use in modeling efforts.

I propose that during migration pronghorn select for native grassland forage such as grasses and forbs in less rugged areas to maintain visual acuteness and energy reserves required for migration (Nicholson et al. 1997, Sawyer et al. 2005). Partially based on their dietary niche as intermediate feeders, pronghorn will move with spatiotemporal gradients in forage productivity (phenology) and decreasing snow cover. Finally, they will avoid areas of higher density of anthropogenic features (i.e. roads and wells). I expected pronghorn will respond differently to these factors depending on migration season (i.e. fall or spring migration pathway selection). I predicted that pronghorn will select stopover sites along the migratory pathway that are higher in forage quality and in areas with lower anthropogenic densities than random.

Finally, I predict that road and well features will have a significant influence on multi-scalar migration pathway selection by pronghorn and that selection at broader scales is more influenced by these features than at finer scales. As found by Gavin and Komers (2006), I predict pronghorn will respond most to intermediate road densities to balance tradeoffs associated with high quality forage located near roads versus lower densities of movement barriers far from roads. I predict that pronghorn will exhibit a negative linear relationship to increasing densities of wells, where as well density increases, pronghorn will more strongly avoid those areas.

As relevant scales of interest are hierarchically nested, broader order scales can provide the spatial context for extrapolating and mapping fine-scale model results (Johnson et al. 2004). As with habitat selection studies, I predict that different factors influence pathway selection at broader scales than at finer scales. Theoretically, within a multi-scalar case-control sampling regime, each fine scale control location ecologically may be considered a case location at the next broader scale, so that identical data is utilized independently at multiple scales (Johnson et al. 2006, Northrup et al. 2013). Once multi-scalar models have been produced, integrating results into one map for conservation and management purposes across an entire study area would be useful (Johnson et al. 2004). Multi-scalar models have been found to more accurately predict habitat selection than single scale models for species (Meyer and Thuiller 2006), and recent studies have depicted multi-scale model results into one integrated map output for caribou (DeCesare et al. 2012). However, similar hierarchically nested movement models have not been completed for ungulate migration, nor have multi-scalar integrative map outputs been achieved. These gaps provide excellent opportunities for research consideration.

In this chapter, I developed parsimonious selection models for fall and spring migration pathways that incorporate measurable natural and anthropogenic factors likely to influence migrations at relevant scales of selection. I then mapped high priority migration pathways by integrating multi-scalar migration models into one map output. I also modelled seasonal movement states (i.e. stopover sites versus migration pathways) and investigated selection variations between the two. Finally, I assessed anthropogenic feature influences in multi-scalar models. I propose that the methods used here contribute to approaches for integrating multi-scalar migration pathway selection that are useful for conserving and managing migrations for transboundary pronghorn populations.

METHODS

Sampling Framework

The study area, capture, and data collection methods were described previously in chapter 2. I adapted Meyer and Thuiller (2006) hierarchical habitat selection criteria for movement selection to assess multi-scale selection. First, at the third-order scale, I considered each relocation or case point as a ‘step’ along a migratory pathway. A step selection function (SSF) estimates selection by wildlife moving throughout an area by linking consecutive animal locations (i.e. steps), where each step at a certain time is paired with random available locations that are distributed from the identical starting point by step length and turning angles (Fortin et al. 2005, Chetkiewicz et al. 2009, Forrester et al. 2009, Thurfjell et al. 2014). To associate case points with corresponding control points at a 5:1

ratio, I used Geospatial Modelling Environment (GME) (Beyer 2013) based on the proceeding movement step and bearing leading up to each point. For each individual's migratory state, I paired each case point with five generated control points using GME. I explored five approaches to match the appropriate bearings, turn angles and steps lengths of each case point to the eventual corresponding set of control points by season and individual (Appendix 3.1). The five approaches included: 1) Turn angle distribution constrained 180° (Whittington et al. 2011) and step length empirical distribution for each individual and season; 2) Turn angle distribution constrained 90° and step length empirical distribution for each individual and season; 3) Turn angle and step length empirical distributions for each individual and season; 4) Turn angle and step length distributions based on standard deviation of all individuals by season; 5) Turn angle based on "Wrapped Cauchy" distribution and step length based on "Weibull" distribution. I elected to use empirical distributions by individual as it treats individuals separately, accounts for seasonal variation and does not limit movement direction (Fortin et al. 2005, Forester e al. 2009). I selected 25 bins per turn angle and step length distributions to provide finer resolution of the data. I then merged the resulting control line endpoints to the corresponding case points into one complete geodatabase (Figure 3.2a).

To assess selection of migration pathways at the second-order scale, I adjusted the case/control point design to sample across the entire NSS, while conjointly having points tied to the finer third-order scale. To achieve this, I considered the control points at the third-order scale as second-order case points because, ecologically, these points could be considered 'used' at this broader scale (DeCesare et al. 2012). I created random second-order control points (Saunders 2007) at a 1:1 ratio and paired with designated second-order case points. Each control point was also given a 0.2 weight to equally weight and match control to case observations during modeling efforts (Ferrier et al. 2002). This scheme generated 208,190 locations sampled, resulting in extensive coverage of the NSS (Figure 3.2b).

Resource Variables

Spatial Variables

In cooperation with Northern Sagebrush Steppe Initiative (NSSI) partners and cooperators I created regional environmental and anthropogenic spatial layers across the NSS. These included 30 m^2 resolution landcover and digital elevation model (DEM) raster layers, a well location point layer, and a road location and two scales of hydrology line layers. During model building, I set landcover type 'Agriculture' as the reference variable so that the resulting sign of each categorical variable's coefficient were in relation to it. Two additional landcover types, 'Recently burned' and 'Mixed conifer and deciduous forest,' were so minimal across the NSS that they were not included in modeling efforts, thus becoming reference variables as well. To be clear, the 'Agriculture' landcover type includes cultivated areas and dryland crops. The 'Pasture and perennial crop' landcover type includes perennial croplands, irrigated cropland and tame pastures. From a broad-scale context, the 'Agriculture' landcover type could serve as a proxy for a higher occurrence of fragmentation while 'Grassland' landcover type serves as a proxy for unfragmented parcels of land. Full documentation of NSSI GIS layers is provided in Appendix 1.1. Unless otherwise indicated, a suite of subsequent spatial layers was created from these base NSSI layers using Spatial Analysis Toolbox in ArcGIS 10.1 as detailed below (ESRI 2012).

The DEM "decimal surface" raster layer created by Violette (2011), acted as the base layer to create additional 'Aspect', 'Slope', and 'Vector ruggedness measure (VRM)' NSS layers. The resulting aspect raster layer was in compass direction from 0°-360°. To provide a more linear measure, I created a subsequent raster layer that converted degrees into radians. Once in radians, I converted this layer into "Northness" using the equation Northness = Cosine ((Aspect in degrees * PI)/180) (Zar 1999). This provided a linear measure of aspect from -1 to 1. The VRM layer was created using Terrain Tools Toolbox, developed by Sappington et al. (2007). VRM measures terrain ruggedness in a manner less correlated with slope. It measures ruggedness based on variability in aspect and the gradient component of slope, contributing to a multivariate representation of topography

(Sappington et al. 2007). As a result, ruggedness values can range from 0 (no terrain variation) to 1 (complete terrain variation), where typical natural terrains range between 0-0.4.

The NSSI well location, road location and two scales of hydrology spatial layers were used to determine the appropriate density of each of these variables at the third-order scale, based on pronghorn response to varying search radii. Results from each variable's analysis were used to create raster layers at the appropriate density for use in ensuing modeling efforts. Both road and well density serve as proxies for the underlying mechanism that influences pronghorn migratory pathway selection. For example, increased road and well densities increase vehicle traffic and noise, which simulate natural predators. Pronghorn are more likely influenced by the vehicles on the roads, not by the roads or wells themselves. In addition, roads (to include well access roads) allow increased access to hunting by humans and natural predators by fragmenting the landscape and decreasing concealment areas (James and Stuart-Smith 2000). For each variable at the third-order scale, I first designated varying search radii to create a series of 30 m^2 density rasters at 50 m, 100 m, 200 m, 300 m, 400 m, 500 m, 750 m, 1000 m, 1500 m, and 2000 m, respectively. A priori variables included 'All roads,' 'Paved roads,' 'Unpaved roads,' 'Hydro250 (1:250,000),' 'Hydro1M (1:1,000,000),' 'Well density-AB,' 'Well density-MT/SK,' 'Well density-all'. Initially, I pooled spring and fall migratory occurrence data across all individuals and fit linear fixed-effects regression models in R 2.15.2 (R Core Team 2012) to identify the most appropriate density that pronghorn respond to using the set of density rasters and Akaike's Information Criterion (AIC) scores to compare models by variable. Briefly, AIC provides a method for model selection by estimating model fit against a suite of candidate models. The model with the lowest AIC score is considered the preferred model (Burnham and Anderson 2002).

Once confident in pooling data, I used mixed-effect logistic regression models (GLMMs) with a random intercept for each individual to obtain final AIC scores per variable at a population level (Hebblewhite and Merrill 2008). I plotted each variable’s AIC score for each density raster to determine the density that most influenced pronghorn migration at the third-order scale (Figure 3.3a-e). Extra steps were required to determine the appropriate well density that pronghorn responded to at the third-order scale. I first considered well locations separated by jurisdiction to: 1) account for distinct differences in well densities (i.e. wells are ubiquitous and in higher numbers across the Alberta portion of the NSS contrasted with clumped distributions across the Montana and Saskatchewan portions of the NSS) and; 2) account for temporal variation in data collected from collared pronghorn by jurisdiction. Additionally, I pooled well locations across the NSS to evaluate well density on a regional basis. The AIC scores from the GLMMs were then plotted and I determined that analyzing well density separately by jurisdiction provided similar results to pooling well density across jurisdictions, i.e. AIC scores were < 2 between jurisdictional and pooled data. To maintain consistency between other spatial layers, I used well density across the NSS (not by jurisdiction) for subsequent modeling efforts (Figure 3.3f).

Finally, following previous modeling literature for ungulates (Leblond et al. 2011, Dussault et al. 2012), I used the 1000 m search radius density rasters for each a priori variable for second-order scale analysis. Once the appropriate raster layers were created for each spatial variable at each scale, I populated both third and second-order geodatabases for all case/control points using GME (Beyer 2013).

Temporal Variables

I addressed potential influence of temporal variation in wells being drilled, forage productivity and snow cover across the NSS relative to pronghorn movement selection by using a suite of methods to create additional spatiotemporal GIS layers. First, I refined a “Temporal Nearest Distance” tool (Koenig 2010) that calculates the nearest neighbor distance between two points of consideration within a temporal window (Appendix 3.2). The temporal variation in wells being drilled serves as a proxy to test the influence from increased vehicle traffic and noise at a given location while the well is being drilled. For my purposes, this equated to finding the closest well being drilled to each case/control point within a certain timeframe. To be conservative and to account for the difference in development regulatory statures by jurisdiction, the script used a temporal window of eight days on either side of the identified drilling date provided in the NSSI well location layer to account for surveying, on-site activities and cleanup of each well site. The resulting field in third and second-order geodatabases describes a distance to nearest drilled well for each case/control point within a 16-day period.

I used MODIS 16-day composite normalized difference vegetation index (NDVI) images (composite denoting the best quality NDVI reading over a 16-day time period is assigned as the NDVI value within a particular pixel) from 2000 through 2011 with a spatial resolution of 250 m^2 to temporally measure forage productivity across the NSS. NDVI serves as a broad-scale significant proxy for measuring vegetation productivity, particularly across grasslands (Kawamura et al. 2005, Pettorelli et al. 2005). Data was mosaicked and pre-processed using cloud-correction algorithms described in Kang et al. (2005). I used a suite of "Spatial-temporal Habitat Analysis Tools" to collect, clip and process NDVI satellite imagery for use at multiple temporal and spatial scales (Zimmer 2012). For my purposes, 16-day satellite tiles (*n*=272) were collected and clipped to the NSS boundary to investigate temporal variance in forage productivity. In addition, tiles corresponding to the equivalent 16-day period over the 12-year period were added together with the resulting means used to create decadal satellite tiles (*n*=23) across the NSS for mean NDVI value. I created a series of scripts in Python 2.7 to add NDVI values for each case/control point into new fields in multi-scale geodatabases (Python Software Foundation 2013). Generally, these scripts first added an integer field to each case/control point which indicates the number of days from Julian Day 1 (January 1). This integer value was used for both NDVI annual and decadal variables to determine the appropriate 16-day temporal composite raster from which to extract the corresponding values. The resulting NDVI values were between -1 and 1, with a value of 1 corresponding to the highest forage quality possible. Finally, I used MODIS 16-day composite tiles to plot mean NSS NDVI bi-monthly values by year to investigate annual variation of plant phenology across the NSS.

I used MODIS 8-day composite snow extent (composite denoting the best quality snow extent reading over an 8-day time period is assigned as the land cover value within a particular pixel of the snow extent raster) images of 500 m^2 spatial resolution to measure snow presence and accumulation across the NSS (NSIDC 2006). I clipped, interpolated and evaluated imagery to create 8-day composite tiles (*n*=544) of both snow cover per pixel (0, 1) and snow accumulation from 2000 through 2011 (Zimmer 2012). In addition, tiles corresponding to equivalent 8-day periods were added together over the 12-year period with the resulting means used to create decadal satellite tiles (*n*=46) across the NSS to assess mean snow presence and accumulation for a given area. I created a series of scripts to add snow cover and accumulation values for each case/control point into new fields in multi-scale geodatabases. As with NDVI, these scripts first added an integer field to each case/control point which indicates the number of days from Julian day 1 (January 1). This integer value was used to identify the corresponding image date and year for annual snow cover and date for decadal snow accumulation to determine the appropriate 8-day temporal composite raster from which to extract values. Finally, I used MODIS 8-day composite tiles to plot mean NSS snow extent weekly values by year to investigate annual variation of snowcover across the NSS.

Variable Selection

I screened candidate variables for multi-collinearity using sequential steps in R 3.0.1 to retain variables for modeling efforts (R Core Team 2013). I first conducted a correlation analysis to identify pairs of variables exhibiting values $\geq |0.7|$. In these instances, the variable that explained the most variation (determined with a univariate logistic model) was retained (Saher and Schmiegelow 2005). I then performed univariate analysis separated by individual and migratory season which treated the individual as a sampling unit (Sawyer et al. 2006). Throughout the process, *p*-values >0.10 for a given variable were used as cut-offs for removal from future analysis. Additionally, I included quadratic terms for ‘All roads,’ ‘Paved roads,’ and ‘Slope’ variables to account for possible non-linear responses by pronghorn (Gavin and Komers 2006, Beckmann et al. 2012). I generated graphical predictions to assess the probability of pronghorn use for each of these variables and their quadratics to identify possible differences between the two. I found significant differences for ‘All roads, ’‘Paved roads,’ and ‘Slope’ variables. I created raster layers for these variables’ quadratics (accounting for varying search radius density by scale) and included values to final multi-scale geodatabases using GME (Beyer 2013). I also assessed two interaction terms (‘Well density-all’*‘Grassland’ and ‘Nearest well’*‘Grassland’) to test if pronghorn responded to well density or well drilling in grasslands differently than other habitat types because of increased well densities on large intact grassland parcels on CFB Suffield lands in AB and on BLM lands in MT. Exploratory analyses showed insignificant interaction effects, and accordingly, these interaction terms were excluded from subsequent analysis. I estimated average, population-level 75% confidence intervals for each variable to determine use in subsequent multi-variable analyses. Of the 33 candidate variables inspected, a total of 21 were retained for subsequent multi-scale modeling efforts (Table 3.1).

Data Analysis

Screening

Individual migratory pathways with < 20 observations (*n*=23) were not considered for further analysis due to insufficient data (Hosmer and Lameshow 2000). I selected < 20 observations as a cut-off because many individuals’ migratory states would not have been included with a higher observation cut-off. Instead, I considered it necessary to include as many individual migratory pathways as possible to infer biologically informative results. I pooled an individual’s migration if there were two years of data during that particular seasonal migration (*n*=7). Although seasonal migrations are annual events, in these cases they were completed by the same individual and so should not be considered a separate sample unit (i.e. the individual is the sampling unit) (Fieberg et al. 2010). I randomly withheld 20% of individuals for each seasonal migratory pathway modeling effort as a mechanism (i.e. testing data) to gauge movement prediction accuracy at multiple scales (Fielding and Bell 1997, DeCesare et al. 2012). The remaining 80% of individual seasonal migratory pathways were used in model building as training data. I considered separate study sites (i.e. AB or MT/SK) to separate training from testing data sets to ensure that a proportional number of individual movement states were withheld from each study site. The training sets included 67 spring migration pathways (20 AB, 47 MT/SK) and 43 fall migration pathways (12 AB, 31 MT/SK), while the testing sets included 17 spring migration pathways (5 AB, 12 MT/SK) and 11 fall migration pathways (3 AB, 8 MT/SK) (Table 3.2). Stopover site locations were excluded from migration pathways and were not included in multi-scalar movement modeling because I considered individuals were selecting habitat resources at these locations where migration has paused to accumulate energy reserves or as the result of anthropogenic features, and thus analogous to resource selection function modeling (Sawyer et al. 2009*a*, Sawyer and Kauffman 2011, Seidler et al. 2014).

Third-order Models

I used SSFs to calculate the probability of pronghorn use at the third-order scale along seasonal migratory pathways (Fortin et al. 2005). Similar to a resource selection function (RSF) models used to predict multi-scale habitat use (Boyce 2006), an SSF uses conditional logistic regression (Compton et al. 2002) to predict the probability of use for a given movement location. I used matched-case conditional fixed-effect logistic regression in R 2.15.2 (R Core Team 2012) (Saher and Schmiegelow 2005, Hebblewhite et al. 2008) and a two-stage approach for seasonal migratory pathway on training data to build global models (Sawyer et al. 2006, Sawyer et al. 2009*b*, Fieberg et al. 2010). I used two-stage modeling (following Fieberg et al. 2010) instead of mixed-effects matched-case design to account for individual animals as the appropriate sample unit to estimate population coefficients that were determined using Eqs. 1-3 to estimate inverse variance weighted mean coefficients (β; Murtaugh 2007) averaged across individuals i within migratory state j for each variable k and season s (e.g., DeCesare et al. 2012):

$$\text{Eq.1: } \hat{\hat{\beta}}_{jks} = \sum_{i=1}^{N} w_{ijks}\hat{\beta}_{ijks} \ ,$$

Where w_{ijks}s is a seasonal individual parameter weight estimated as

$$\text{Eq.2: } w_{ijks} = \frac{1 \Big/ \left[\mathrm{SE}\left(\hat{\beta}_{ijks}\right)\right]^2}{\sum_{i=1}^{N}\left(1 \Big/ \left[\mathrm{SE}\left(\hat{\beta}_{ijks}\right)\right]^2\right)} \ .$$

and standard errors are estimated as

$$\text{Eq. 3: } \mathrm{SE}\left(\hat{\hat{\beta}}_{jks}\right) = \sqrt{\frac{\sum_{i=1}^{N} w_{ijks}\left(\hat{\beta}_{\mathrm{ijks}} - \hat{\hat{\beta}}_{jks}\right)}{N-1}} \ .$$

Thus, a final global model was produced for each seasonal migratory pathway. To test variable significance for inclusion in global population-level models I calculated *t*-tests at level $p \leq 0.05$. Finally, I grouped individuals by capture year to find average coefficients with 95% confidence intervals to investigate annual variation in pronghorn migratory pathway resource selection.

Second-order Models

I used population level mixed-effect models (GLMMs) to predict probability of pronghorn use at the second-order scale for each seasonal migration (Hebblewhite and Merrill 2008). I used a random intercept to account for heterogeneity between individuals for final population coefficient estimates. I withheld the same 'testing data' individuals that were identified for third-order model analysis, for second-order model analysis. I fit GLMMs with the logit link in R 3.0.1 (R Core Team 2013) using pooled individual data for each seasonal migration. I then used manual backwards stepwise logistic regression to individually withdraw insignificant variables, $p > 0.05$, until the model was reduced to include significant variables, with corresponding z-score, to obtain final global model estimates (Pearce and Ferrier 2000).

Stopover Site Analysis

I used migratory state results reported in Chapter 2 to predict the probability of a location being a stopover site from the overall migratory pathway for this pronghorn population. I used R 3.0.1 (R Core Team 2013), to fit GLMMs on case data only, to evaluate differences between seasonal stopover sites and migratory pathways. I used manual backwards stepwise methods to eliminate insignificant explanatory variables, $p \geq 0.05$ until all continuous variables were found significant for fall and spring seasons. I then used predicted values for migratory pathway case data during both seasons to generate ten equal-frequency bins to assort stopover site case data within each bin. I used k-folds cross validation again to evaluate seasonal predictability of stopover sites from migratory pathways.

Anthropogenic Influence across Multiple Scales

I investigated possible influences of anthropogenic variables on migration pathways at both third and second-order scales. Anthropogenic variables of interest included road and well variables retained for multi-scale model evaluation. I used AIC to evaluate model support between models with and without these anthropogenic variables included (Burnham and Anderson 2002). I used R 3.0.1 (R Core Team 2013) to fit fixed-effect logistic regression at the third-order scale, by seasonal migration on each individual's final model to estimate anthropogenic factors' influence on overall model performance (DeCesare et al. 2012). Fixed-effect logistic regression was performed to estimate AICc (AIC corrected for small sample size) on an individual's "base" model (those without anthropogenic variables) and "human" model (those with anthropogenic variables). The ΔAICc was calculated between base and human models to find the weight of evidence, *w* (0-1), by individual. Models with higher *w* exhibit increased support in influencing migratory pathway selection at each scale. I then calculated the population's mean *w* by each seasonal migration for base and human models to identify which model was most supported overall. At the second-order scale, I ran global GLMMs for each seasonal migration to estimate anthropogenic influence on overall model performance at this scale. I calculated AICc on both base and human models to find ΔAICc between global models. Finally, the weight of evidence, *w*, was calculated to compare anthropogenic influences on seasonal migration at this scale.

Migration Spatial Predictions

I created and illustrated spatial predictions of the global third-order model, which allowed for the conditionality of the third-order step selection function (e.g. dependent on the second-order) and addressed time-varying covariates. Although third-order movement selection was restricted to its availability within the NSS (Mysterud and Ims 1999), I was able to map probability of seasonal migration pathways across the NSS. Creating conditional statements in GIS allowed me to estimate pixel values in areas across the NSS that were not sampled, based on each explanatory variable's minimum and maximum pixel values at the third-order scale (Table 3.3). These values are a mechanism to constrain interpolation of both seasonal migrations' global model within these thresholds and thereby do not extrapolate values into areas of the NSS that were not sampled (DeCesare and Pletscher 2006, DeCesare et al. 2012).

Because of the inclusion of time-varying covariates in spatial prediction of the global third-order models, I had to specify spatial constraints to temporal covariates. I identified individual migratory start and end dates for seasonal migrations and calculated the mean across all individuals (*n*=94 for spring, *n*=70 for fall) to identify a representative spatial raster to map NDVI during spring and fall time periods. Mean spring migration started on March 22 and ended on April 10 (20 days) whereas mean fall migration started on October 31 and ended on November 10 (11 days) across the NSS. I identified the 16-day decadal NDVI raster that best captured these mean spring and fall migratory time periods. For spring, I used the NDVI decadal raster that covered March 22 – April 6 time period. For fall, I used the NDVI decadal raster that covered November 1 – November 16 time period. I did not include a raster to represent the 'Nearest drilled well' variable using the "Condition Function" to produce final maps. For each case/control point, the parameter was a measure of the distance to nearest drilled well within a 16-day window. Because of the temporally varying nature of each parameter record, creating a spatial composite from numerous drilling events was problematic.

I created and illustrated spatial predictions of the global second-order model across the entire NSS, and used a similar approach for time-varying NDVI and drilling covariates as the global third-order model. Because second-order case/control points spanned the entire NSS, there was no need to find minimum and maximum values for each variable (Johnson et al. 2004). As a result, second-order maps provide the spatial context for ensuing scale-integrated mapping. For both third and second-order maps, I estimated predicted movement values for each raster as

Eq.4: $w_{js}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + ... + \beta_k x_k)$,

and used a linear stretch to rescale predicted values between 0 and 1 (Johnson et al. 2004, DeCesare et al. 2012):

Eq.5: $\hat{w}_{js} = \left(\frac{w_{js}(x) - w_{min}}{w_{max} - w_{min}} \right)$.

Following DeCesare et al. 2012, Eq. 1, I multiplied the third-order and second-order scaled map to create a Scale-Integrated Step Selection Function (ISSF) map output. I used the linear stretch, Eq. 5, to rescale ISSF predicted values between 0 and 1 (Johnson et al. 2004, DeCesare et al. 2012). Lastly, I reclassified predicted values into equal-frequency bins from 1-10 (10 being highest value) in R 2.15.2 (R Core Team 2012) to clarify map interpretation. All spatial modeling was performed in ArcGIS 10.1 (ESRI 2012).

Model Validation

I followed validation procedures outlined by Boyce et al. (2002) and DeCesare et al. (2012) to evaluate third- and second-order top models in predicting pronghorn seasonal migrations. I used k-fold cross validating following Boyce et al. (2002) to validate predictive performance, and estimated the Spearman rank correlation between the predicted probabilities of occurrence in 10 ordinal habitat categories, and the observed frequency of validation data within each category (Boyce et al. 2002). I conducted validations both on training and testing data for models of each scale, such that independent data were included to evaluate performance of each model (Fielding and Bell 1997). Spearman rank correlations were also calculated for ISSF spatial predictions by comparing the frequency of both third- and second-order case points to equal-bins of ISSF maps within the respective zone of availability for each scale.

RESULTS

Road, Hydrology and Well Density Analysis

I determined the radius within which to measure density for or against road, hydrology, and well explanatory variables at the third-order scale according to the relative strength of selection (Figure 3.3a-f). For all road variables (all, paved, unpaved), the 100 m density layer had the lowest relative ΔAIC scores across each category. For hydrology variables, the 50 m density layer was most appropriate at the 1:250,000 scale, while the 750 m layer elicited the lowest relative ΔAIC score at the 1:1,000,000 scale. To determine the appropriate well density, results were inconclusive for both the separate jurisdiction analysis and NSS wide analysis. Exploratory results showed that as well densities increased, fixed-effect estimates were variable in sign and magnitude. In addition, the lowest relative ΔAIC scores per well density differentiated slightly, compared to hydrologic and road variables. To keep methods consistent across variables and for cross-boundary management implications, I calculated well density selection using all well locations across the NSS. The resultant graph, however, demonstrated similarly low relative ΔAIC scores for the three largest search radii, leading to subjective interpretation. Pronghorn did not avoid higher well densities in a negative, linear manner but in a more asymptotic response. As a result, I selected the 1000 m raster as the optimum well density for third-order modeling efforts because subsequent density rasters (i.e. 1500 m, 2000 m) provided negligible statistical differences between relative ΔAIC scores.

Multi-Scale Models, Spatial Predictions and Validations

For each pronghorn, I evaluated all estimable model coefficients for each migratory pathway, and retained significant variables ($p < 0.05$) in multi-variable models for fall (Appendix 3.3) and spring (Appendix 3.4). I then estimated population-level third-order models with the average of individual coefficients, using *t*-tests to evaluate population-level variable significance for seasonal migratory pathways (Table 3.4). At third-order scales, pronghorn select for distinctly different attributes during migratory periods. Results indicated that during both seasonal migrations paved roads, paved roads^2, NDVI, density of hydrology (1:1000000), VRM, water and deciduous forest in relation to agriculture, were found to be significant variables. However, the sign for each of the above variables' coefficients may switch between fall and spring migrations; only VRM (-) and water (+) had consistent signs across season. During fall migration, the most influential significant continuous variables were density of hydrology 1:1,000,000 (+), VRM (-), density of paved roads (-), NDVI (-) and density of paved roads^2 (+). In relation to anthropogenic features, pronghorn selected for intermediate densities of paved roads. The most influential categorical variables in reference to agricultural landcover included water (+), development (+) and deciduous forest (+) landcover types. During spring migration, the most influential significant continuous variables (based on *t*-values) were density of hydrology 1:1,000,000 (-), density of paved roads (+) along with density of paved roads^2 (-), VRM (-) and density of wells (-). In relation to anthropogenic features, results can be interpreted that pronghorn select an intermediate density of paved roads and selected against increased noise, monitoring efforts and fragmentation at well sites. The most influential categorical variables were in reference to agricultural landcover and included deciduous forest (-), shrubland (+) and exposed (+) landcover types.

I found annual variation in NDVI across the NSS by interpreting graphs of bi-monthly NDVI values (Figure 3.4). Variation was most noted during peak height of the growing season (June – July) and late summer into fall (August – October). NDVI values varied little during the winter and spring seasons during my study. I also found annual variation in snowcover across the NSS by interpreting graphs of weekly snow extent values (Figure 3.5) Variation was most noted during January – February, April – May, and October – November of each year of my study. Snowcover exhibited slight annual variation during March, June – September, and December of my study. In addition, I noted annual variation in pronghorn third-order migratory pathway resource selection during fall and spring by individuals grouped by capture year (Table 3.5 and Table 3.6). However, most 95% confidence intervals of each variable's coefficient during each capture year indicated that results were insignificant.

The final spatial predictions for third-order scale seasonal migratory pathways across the NSS with rescaled predictive values between 0-1 are provided in Figure 3.6a-b. Neither training nor testing data sets significantly validated third-order seasonal migratory pathway models based on Spearman rank correlations (Figure 3.7). As a result, third-order models by themselves would perform poorly for predicting fall and spring migration pathways.

Results for second-order scale models were much clearer than at the third-order scale. During fall movement, pronghorn strongly selected for grasslands, intermediate slopes, south-facing aspects along with exposed areas. They avoided higher road densities (both paved and all), water and, to a lesser extent, higher well density and rugged terrain (Table 3.7). Regarding anthropogenic features (road and well density), pronghorn selected against increased vehicle use, noise, fragmentation and access pressures from these features. During spring migration, pronghorn strongly selected for grasslands, NDVI, intermediate slopes, exposed areas, south-facing aspects and increased distances from drilled wells, while strongly avoiding higher road density, higher well density, large drainages and, to a lesser extent, pastures and perennial crops, water and rugged terrain (Table 3.8). Regarding anthropogenic features (road and well density, distance to well drilling), pronghorn selected against increased vehicle use, noise, fragmentation and access pressures from these features.

'Grasslands' was the most important variable for where pronghorn selected migration pathways during both seasons, based on z-scores of corresponding coefficients. The 'Grasslands' landcover type may serves as a proxy for unfragmented areas. Pronghorn consistently avoided coniferous and deciduous forests, and open water. As for topography, pronghorn generally selected intermediate gradient slopes along south-facing aspects and low ruggedness while migrating across the NSS. Increased densities of large rivers, streams and creeks at the 1:1,000,000 scale significantly (positively) influenced pronghorn fall migratory pathway selection but negatively influenced selection during spring migration. NDVI was an important variable that pronghorn selected for during spring migration but was not significant during fall migration. As for anthropogenic variables, both increased densities of roads and wells were significant factors in predicting pronghorn seasonal migration. Increased densities of all roads were the strongest factor pronghorn avoided during spring migration and, in addition, was a strong factor pronghorn avoided during fall migration. In addition, pronghorn avoided increased densities of paved roads during fall migration. Quadratic terms of all road densities and paved road densities did not provide meaningful differences from those offered by linear terms. Increased well densities were a significant negative influence avoided during both fall and, in particular, spring migration. Additionally, during spring migration, pronghorn selected migratory pathways that were at increased distances from drilled wells.

The final spatial predictions for second-order scale seasonal migratory pathways across the NSS with rescaled predictive values between 0-1 are provided in Figure 3.8a-b. Both training and testing data sets statistically validated second-order models using Spearman rank correlations (Figure 3.9). In particular, spring migratory pathway models (both training and testing) resulted in 1's for correlation. Furthermore, using testing data showed high significance levels in predicting probability of occurrence for second-order seasonal migratory pathways across the NSS.

Stopover Site Analysis

I found significant differences between migratory pathways and stopover sites calculated from GLMMs. During fall migration, the five variables with the highest z-scores in order from strongest to weakest were NDVI (+), nearest well (-), pasture and perennial crop (-), grassland (-), and well density (-) (Table 3.9). These predictor variables are those that pronghorn select most strongly for or against while selecting a stopover site during fall migration, realizing that landcover variables are in relation to agricultural landcover. Pronghorn selected for areas of high forage productivity and against high well densities with associated drilling impacts (i.e. increased vehicle use, noise, fragmentation and access) as well as against native and pasture landcover types. Additional significant contributors toward predicting stopover sites from fall migratory pathways included aspect (+), slope^2 (-), slope (+), VRM (-), all roads (-), shrubland (-), and wetland (-). Results from topographic variables infer that pronghorn select stopover sites that are on north-facing, intermediate slopes with less ruggedness than from the remaining migratory pathway. Pronghorn are more sensitive to roads while using stopover sites in the fall than during the migration pathway. Finally, pronghorn avoided other native landcover types (shrub and wetland) while identifying fall stopover sites from migratory pathways.

During spring migration, the five variables with the highest z-scores in order from strongest to weakest were NDVI (+), aspect (+), shrub (-), exposed (-), and well density (-) (Table 3.10). These predictor variables are those that pronghorn selected most strongly for or against while electing a stopover location during spring migration, realizing that landcover variables are in relation to agricultural landcover. An additional significant contributor towards predicting stopover sites from spring migratory pathways included grassland (-). Pronghorn selected for high forage productivity areas during spring stopovers versus the remaining migratory pathway, with north-facing slopes, and against high well densities and native landcover types.

I used equal-frequency bins of seasonal migratory pathway predicted values and binned stopover locations within each of these bins to validate results using Spearman rank correlations. I found increasing stopover site locations as the bins (1-10) categorizing predicted values increased. Rho values were highly correlated and significant for fall ($\rho = 0.982$, $p = 4.85\text{E-}07$) and spring ($\rho = 0.879$, $p = 0.002$) (Figure 3.10). Generally during migration, pronghorn selected stopover sites with high quality forage (based on NDVI scores that serve as a broad-scale proxy) on north-facing slopes while avoiding well attributes (high densities and wells being drilled) and native landcover types. Using results from the GLMM approach, I could discriminate variable influences on pronghorn stopover site selection from migratory pathways during seasonal migration.

Anthropogenic Influence across Multiple Scales

I used AICc scores to compare support between models with and without anthropogenic variables included at third and second-order scales. At the third-order scale, I averaged individuals' weight of evidence, *w*, for both migratory seasons to produce a population level comparison. For both seasons, mean weights of evidence were higher for models without anthropogenic variables included and thus are the more supported models (Appendix 3.5 -Appendix 3.6). Generally, adding road and well variables did not influence pronghorn migratory pathway selection at third-order scales. At the second-order scale, I used population level GLMMs to calculate AICc for both migratory seasons. For both seasons, the weights of evidence were calculated to be 1 for models with anthropogenic variables included and, accordingly, are highly supported as the best performing models (Appendix 3.7). Results indicate that at second-order scales, roads and wells strongly influenced pronghorn migratory pathway selection. In general, results indicate that selection at second-order scales is the foremost driver between these two nested scales. Pronghorn seasonal migratory pathway selection is limited by anthropogenic influences at broader scales. However, at finer scales, these anthropogenic factors are not as limiting to a step-by-step choice (i.e. at third-order scale selection) (Table 3.11).

Scale-Integrated Spatial Predictions and Validation

In general, final ISSF models (Figure 3.4 a-b, Appendix 3.8) displayed similar core areas for both fall and spring migrations across the NSS. However, I deduced subtle differences from broad-scaled maps that included greater distribution of selection areas during fall migration. Pronghorn also follow larger rivers and streams during fall migration, where they avoided these features during spring. I found varying results with scale-integrated map performance for validating multi-scale seasonal migration across the NSS. ISSF models exhibited lower performance at predicting third-order selection than third-order models. Additionally, Spearman rank correlations on testing data were weaker than those using training data (Figure 3.12). Only during spring migration did ISSF models outperform third-order models at predicting pronghorn selection (Table 3.12).

However, both second-order and ISSF models exhibited high performance for predicting second-order pronghorn selection (Figure 3.13). Specifically, second-order models outperformed ISSF models using testing data during spring migration, while during fall migration, ISSF models outperformed second-order models using testing data as a means of gauging pronghorn multi-scalar selection (Table 3.12). I provide Figure 3.5 as a close-up example of ISSF model performance during spring migration, demonstrating model fit for both training and testing data.

DISCUSSION

Multi-Scale Migratory Pathway Selection

I used a hierarchically nested sampling design and modeling methods to predict pronghorn migratory pathway selection at multiple scales across the NSS. I considered that using a nested approach was necessary because finer scale selection is conditional on selection made at broader scales (Rettie and Messier 2000, Meyer and Thuiller 2006). Because wildlife perceive and utilize habitat at various scales (Johnson et al. 2004, Wheatley and Johnson 2009), it is important to identify key selection parameters that may differ in effect between scales.

Location data collected over a six-year period were used to develop predictive models for seasonal migration across the NSS. Because data were collected across a large spatiotemporal scale, I used a variety of techniques to assess explanatory variables, which most reflect influential spatiotemporal dynamics to migratory pathway selection. First, since pronghorn perceive and utilize landscapes at various scales, I considered it imperative that observed pronghorn behaviors dictate the relevant density of various linear and point parameters for modeling influences on migration pathway selection (Polfus et al. 2011, DeCesare et al. 2012). Second, I used satellite imagery to capture temporal variability to assess important environmental factors’ influence on seasonal migratory pathway selection. As with other ungulates, pronghorn move in response to environmental fluctuations across the landscape (Hoskinson and Tester 1980, Dalton 2009, Poor et al. 2012). Other researchers, for instance, have found tracking quality forage to be the most important determinant of ungulate migration (Hebblewhite et al. 2008, Mueller et al. 2008, Mysterud 2013). Therefore, I considered that when modeling an ecologically discrete time period (i.e. seasonal migrations) it is critical that temporal changes to environmental gradients across the landscape be addressed. I examined annual variation in NDVI and snow extent values across the NSS as these model variables change temporally. Annual variation was observed across the NSS for both variables, most notably during the fall period (October-November). These annual variations may be a prominent factor in finding significant yearly differences in start/stop dates and overall distances in pronghorn fall migration and driven movements in Chapter 2. I also found annual variation in third-order migration pathway selection by pronghorn. Although insignificant, results illustrate the importance of considering annual fluctuation in environmental gradients and how these variation influence resource selection. Researchers and managers intending to use the spatial predictions presented here must recognize that they integrate an average of the overall variation in NDVI and snowcover variables.

During the candidate variable screening process, both annual and decadal snow variables were found to be insignificant factors during pronghorn migratory pathway selection across the NSS. At the same time other research has found that snow occurrence and depth affect pronghorn movements (White et al. 2007, Dalton 2009, Jacques et al. 2009). Although this still may be the case across the NSS, the MODIS imagery for snow occurrence was at a 500 m^2 resolution/pixel and so likely is too coarse to truly model its potential effects on pronghorn migration. As remote sensing techniques improve, researchers will be better equipped to test snow distribution and depth on large-scale wildlife studies.

In addition, natural gas wells have been shown to impact wildlife use and distribution, specifically during distinct seasons (i.e. winter, migration, birthing, and/or mating rituals) (Sawyer et al. 2006, Aldridge and Boyce 2007, Sawyer et al. 2009*b*). As a result, I further investigated potential effects on migrating pronghorn by temporally determining the closest drilled well to each pronghorn location during migration. This variable gauged pronghorn response to a discrete landscape influence and served as a proxy for indirect effects associated with drilling (i.e. increased traffic, increased noise).

I found specific densities of anthropogenic and hydrologic features that influence pronghorn response at third-order scales when measured with varying search radii. Pronghorn selection was strongest at a 100 m search radius while interacting with roads. This is consistent with pronghorn risk-avoidance behaviors reported by Gavin and Komers (2006). Pronghorn appeared to respond to roads opportunistically, as roadsides may provide some high quality forage (many roadsides are partial ditches with wetter soils than adjacent areas) yet may also be perceived as a direct threat owing to vehicle traffic.

Pronghorn responded to intermediate densities of large rivers and streams across the NSS using 750 m search radii. Pronghorn may balance use of high forage quality provided by mesic soils in the surrounding floodplain with exposed soils and rugged topography, which contour larger rivers and streams. Pronghorn exhibited an asymptotic positive response for well densities and was strongest with the 1000 m search radius, which was inconsistent with the negative response I had predicted. This confounding result may be due, in part, to pronghorn selections at higher ordered scales. At second-order scales, migratory pronghorn were found to significantly select for grasslands within the multi-use landcover matrix across the NSS. Finer scale decisions subsequently were limited to a degree within grasslands. The majority of large grassland parcels in the NSS are owned by state, provincial and federal agencies and so pronghorn selected these areas first at the broader scale. However, these lands are managed for a suite of natural resource uses. As a result, the highest densities of wells are found in agency-owned grassland parcels, which pronghorn use disproportionately more than other landcover types across the region.

At third-order scales, pronghorn selected to migrate through non-rugged terrain with intermediate slopes. Pronghorn responses to most remaining parameters at this scale varied across seasons, with the exception of selecting for water (i.e. ephemeral ponds/lakes) for drinking, which were dotted across the landscape. During fall migration, pronghorn significantly avoided all road types, against areas of higher forage productivity and select for areas following large riverine systems. During spring migration, pronghorn significantly avoided all roads combined but they separately selected for paved roads. This may be due to high quality forage found along paved roads, as paved roads are paralleled by ditches that hold water longer during the spring in this semi-arid landscape. Pronghorn avoided higher well densities and selected for areas that likely had higher forage quality during the spring, which is consistent with other ungulate spring migrations (Johnson et al. 2002, Saher and Schmiegelow 2005, Hebblewhite 2008).

Validation results on both training and testing data exhibited poor model performance at the third-order scale. Poorer model performance at finer scales has also been noted in other multi-scale wildlife studies (Johnson et al. 2005, DeCesare et al. 2012) and may be expected for a highly adaptable and vagile species such as pronghorn. Pronghorn can move rapidly through multiple, available landcover types across NSS. Undoubtedly, pronghorn prefer specific attributes during discrete time periods, such as selecting for highly productive areas during spring migration. However, when confronted with sub-standard forage quality or habitats, pronghorn are able to move through areas quickly. For example, accelerated pronghorn migration rates during fall occurred while migrating in concert with other individuals and most likely provided prompt arrival onto winter range (Chapter 2). Alternatively, during spring, pronghorn selected migratory steps that increased protein intake from high quality forage.

Second-order scale results more clearly identified pronghorn seasonal migratory pathway selection across the NSS. General similarities and contrasts between variables during pronghorn spring and fall migration were noted. Pronghorn select most strongly for grasslands, followed by intermediate slopes along south-facing aspects and exposed areas. Migratory pronghorn strongly selected for grassland landcover types in part for forage opportunities they provide during spring, but more likely because grasslands provide large, unfragmented tracts to migrate through that are relatively undisturbed by humans. Alternatively, pronghorn that were captured in agriculture landcover types were more likely to remain resident in part because of increased energy and vigilance required from increased encounters with anthropogenic features (Jones et al. 2015). Pronghorn most strongly avoided increasing road densities, followed by increased well densities, increased ruggedness, water, coniferous and deciduous forests. Fall migration in pronghorn is more rapid and is more directional than spring migration (Chapter 2). At the second-order scale, pronghorn seemingly selected for the most linear, un-fragmented path to winter range, through native grassland cover, exposed (barren ground) areas and following major drainages, while avoiding high road densities.

There has been speculation that pronghorn initiate fall migration with the onset of snow (Dalton 2009). However, Hoskinson and Tester (1980) found that fall migration was initiated due to decreased moisture content in forage. I found that snow presence, snow accumulation or forage productivity were not significant factors influencing fall migration pathway selection. Once migration was fully initiated, pronghorn preferred large parcels of un-fragmented native prairie in less rugged areas along south-facing aspects (i.e. aspects with decreased tendency for snow accumulation). Migratory pathway selection during fall confirmed that individuals and/or groups are inclined to migrate in an undistracted fashion to arrive at winter destinations successfully (Dalton 2009, Barnowe-Meyer et al. 2013).

Increased road and well densities, along with the accompanying infrastructure, may act as partial or complete barriers to migration, contribute to unnatural fragmentation to the landscape, and may be perceived as direct threats to pronghorn (Sheldon 2005, Gavin and Komers 2006, Kolar et al. 2011, Beckmann et al. 2012). Particularly during fall migration, pronghorn significantly avoided paved roads; a period when increased urgency to arrive at winter range occurs. Paved roads, associated infrastructure and the accompanying high-speed high-vehicle density may act to fragment the landscape more than any other measured factor. Besides cities and towns, barriers to movement (fences, railroads, high speed traffic) occur at much higher densities along paved roads than any other area across the NSS (Poor et al. 2014). Thus, conservation and management approaches should be designed to allow for continued movement across/around these obstructions.

During spring migration, pronghorn across the NSS are highly selective for grasslands with increasing forage productivity (Suitor 2011, Poor et al. 2012). Ungulates have been observed to follow the “green-wave” along increasing elevation gradients (Hoskinson and Tester 1980, Hebblewhite et al. 2008, Mysterud 2013). In the NSS this phenomenon was evident with increasing latitudes, i.e. green-up started earlier in the south than in the north of the study region. Individuals may undertake migrations to coordinate timing with slowly advancing plant phenology and thus, displayed slower rates of movement with higher sinuosity (Chapter 2). Spring migration is an important time for providing females with foraging opportunities to regain condition after long, difficult winters. During spring, forbs and grasses are at peak protein levels, which provide critical nutrition and energy for impending fawning and fawn rearing (Parker et al. 2009). The need to reach fawning grounds in good physical condition may explain why pronghorn bypass areas of human use (i.e. high density roads, high density wells, areas with active drilling), that could be perceived as challenges to migration and threatening to the individual (Sawyer et al. 2009*a*, Suitor 2011, Beckmann et al. 2012). Pronghorn selected intermediate slopes on south-facing aspects (typically the most snow-free in northern latitudes) in less rugged terrain away from large riverine systems. Migrating pronghorn preferred topographically gentle and open landscapes because they increase range of view from predators and reduce energy expenditure during movement bouts (Nicholson et al. 1997, Johnson et al. 2002).

Stopover Site Selection

I investigated differences between stopover sites along pronghorn seasonal migratory pathways. By using mixed-effect modeling, I explored parameter influence on stopover site selection during fall and spring migration. During both migratory periods, pronghorn most strongly selected for areas that have high NDVI (forage productivity) and north-facing slopes. In contrast to migratory pathways, pronghorn avoided grasslands, shrublands, and areas with high well densities. This pattern is consistent with the results of previous studies in which pronghorn selected stopover sites that provided high density nutritious forage and remained resident until local forage resources were depleted (Sawyer and Kauffman 2011, Seidler et al. 2014). Pronghorn selected north-facing slopes significantly more during stopovers than while moving along the migratory path. At northern latitudes, north-facing slopes receive less sunlight than south-facing slopes. Therefore, during the fall north-facing slopes may accumulate snow or hold moisture longer so, in turn, grasses and forbs have delayed senescence. Advantageously during spring, water and snow may accumulate here for longer periods of time so that forbs and grasses promptly germinate and are available to pronghorn.

Pronghorn additionally avoid increased well densities at stopover sites. Although not specifically addressed for stopover sites, Beckmann et al. (2012) found that pronghorn showed reduced use of habitat within the most heavily developed areas of natural gas fields in Wyoming. Increased noise, fragmentation and traffic may unsettle pronghorn during periods when they are resting and/or critically feeding on high quality forage. As a result, pronghorn selected fall stopover sites in underdeveloped road areas and farther away from drilled wells. Topographic variables were found to be significant during fall stopovers but not during spring stopovers. Pronghorn may be more destination-driven during fall migration and thus are more aware of energetic expenditures than during spring.

Interestingly, pronghorn strongly avoided native habitat at stopover sites versus along a migratory pathway. As discussed in Chapter 2, stopover sites are not used as often in fall as in spring. However, when pronghorn do select to stop during migration, they appear to be taking advantage of higher quality forage available in these areas. Often during migration seasons, the highest quality forage is in irrigated agricultural fields with perennial crops such as alfalfa and certain legumes. Stopover site use during spring in particular may assist in increasing overall individual fitness; that is, these sites replenish female body tissue reserves after winter months and contribute to meeting the nutritional demands of late-stage pregnancy (Sawyer and Kauffman 2011). Because stopovers are discrete sites along a migration path, they can be considered of high conservation value (Saher and Schmiegelow 2005, Sawyer and Kauffman 2011). Yet results indicate that across the NSS, pronghorn select stopover sites along the migratory pathway within human-altered landcover types. This may indicate that the migratory pathway itself may be more important for long-term population persistence than any specific stopover sites (Berger 2004). Seidler et al. (2014), for instance, found that if migration patterns were altered, pronghorn still used stopover sites within close proximity to road features. Pronghorn opportunistically utilize highly productive areas to stopover while migrating, and, as noted in other ungulates, individuals may use the same sites annually (Sawyer and Kauffman 2011). However, I suggest that across the NSS that pronghorn are not restricted to specific stopover locales where resource types (i.e. space, specific forage) are limited as may occur in other species (Alerstam et al. 2003, Calvert et al. 2009, Bowlin et al. 2010). Therefore, I encourage conservation efforts involving work with farmers and ranchers to conserve ungulate stopovers along predicted migratory pathways.

Future research may be able to more accurately describe and test stopover site predictability for pronghorn with improvements to spatiotemporal data and the using metrics presented here. For example, finer resolution and detailed landcover classification or shorter temporal windows between MODIS tiles will increase predictive model accuracy. In addition, FRAGSTATS analysis could investigate the effect of parcel size and distribution of available landcover types on migration pathway selection. Add to this, intriguing behavioral questions remain to untangle. Future research on multi-generation and individual multi-year data is needed to test pronghorn stopover use as a learned trait in encountering specific sites or to determine whether stopover sites can be predicted at highly productive locales. These questions pertaining to pronghorn and other species will assist in understanding stopover site ecology for future management of migratory ungulates.

Anthropogenic Influences across Multiple Scales

Roads and oil/natural gas wells are anthropogenic factors with both direct and indirect effects on wildlife and ecosystem processes (Trombulak and Frissell 2000, Burennan and Kuvlesky 2005, Aldridge and Boyce 2007, Hebblewhite 2011). As a result, anthropogenic developments have led to modifications in ungulate seasonal habitat and movement selection (Johnson et al. 2005, Hebblewhite et al. 2006, Polfus et al. 2011, Lendrum et al. 2012, Lendrum et al. 2013). I examined how these anthropogenic variables contribute to pronghorn selection at multi-scales during seasonal migration by calculating AIC scores for models with and without road and well variables.

At the third-order scale, the strongest models for migration pathway selection did not include anthropogenic features. During fall migration, model selection was over six times stronger for models without anthropogenic variables, while during spring migration, models without anthropogenic variables were four times stronger. I inferred that road and oil/natural gas well variables did not influence pronghorn movement selection at this scale. Pronghorn exhibited mixed responses to paved roads while negatively responding to the ‘All roads’ variable at this order. However, tradeoffs in selection close to roads suggest that topography and forage quality are more significant in determining pronghorn selection at third-order scales. Based on personal observations and information gleaned during my discussions with land managers I found that gas well structures in Montana and Saskatchewan tended to be small metal shacks with effluent pipes leading to an outside holding pond. In Alberta, most natural gas wells, especially in CFB Suffield, are not much more than a wellhead sticking out of the ground. Pronghorn have acute eyesight and are highly responsive to visual stimuli (Kitchen 1974, Gavin and Komers 2006). I observed that well sites with metal shacks and effluent piping were monitored and maintained more frequently than wellhead sites, which involved personnel arriving in vehicles and managing each site for long extents of time. I interpreted results of my study to signify that pronghorn migratory pathway selection at the third-order scale was influenced by well density and not by variation in well types. However, research is needed to address pronghorn selection between well types across varying landcover types and scales. At the third-order scale, pronghorn selection was modelled using either two- or four-hour time period "steps" across the landscape. The pronghorn's capacity to constantly and rapidly move allows individuals to minimize exposure, specifically in response to oil/natural gas extraction, to less than ideal conditions during migration. Within a relatively short period, pronghorn may transverse areas to access more favorable conditions if required.

At second-order scales, pronghorn migratory pathway selection was greatly affected by anthropogenic development. Weights of evidence for seasonal models equaled 1, which unequivocally demonstrated that the best performing models included anthropogenic variables. As in other studies, overall selection is driven first by broader scale conditions and then refined by finer scale decisions, specifically regarding human influences on the landscape (Apps et al. 2004, DeCesare et al. 2012). My results show this to be accurate for pronghorn migratory pathway selection as well. Habitat loss and fragmentation by roads and oil/natural gas development can lead to increased energy needed for pronghorn to remain vigilant, and consequently can affect the direction, distance and timing that pronghorn migrate (Beckmann et al. 2012, Seidler et al. 2014). Continued anthropogenic development across the landscapes, specifically in the NSS, may continue to incrementally degrade migratory pathways. As reported in Chapter 2, a significant proportion of pronghorn across the NSS are migratory and so managing landscapes to support migration is important for pronghorn conservation.

Multi-Scale Mapping for Transboundary Management

Ungulates perceive and select habitat attributes at multiple scales, and appropriately, wildlife and habitat managers attempt to determine which scale is most important for management (Rettie and Messier 2000, Johnson et al. 2005). Ungulates should elect to move through the landscape dependent on multi-scale requirements (Chetkiewicz et al. 2006, Thurfjell et al. 2014). Here I demonstrate that pronghorn selected a suite of parameters at multiple scales during seasonal migrations. In addition, I show that these scales of migratory pathway selection are hierarchically nested within each other from broader to finer scales, as in habitat selection studies (Johnson et al. 2004, Meyer and Thuiller 2006). I applied integrated-scale resource selection mapping methods developed by DeCesare et al. (2012) to merge multi-scalar migration model outputs and account for pronghorn ecological requirements at various scales.

The use of integrated-scale maps will contribute to the goal of managing for wildlife and habitats at multiple scales. These composite maps can facilitate stakeholder awareness and support (from resource managers to private industry), while concurrently addressing species needs more appropriately. In their own right, I found second-order map outputs to be useful in managing landscapes for pronghorn migration across the NSS. However, for both training and testing sets, ISSF maps either outperformed or performed equivalently to second-order map outputs in half the cases, while the other half of ISSF maps performed just below second-order maps. Results should be robust as individual seasonal migrations were completely withheld as testing data. ISSF spatial predictions for pronghorn seasonal migrations, to my knowledge, are the first multi-scale movement-based map outputs for conservation and landscape planning initiatives.

Overall, second-order models appear to have a much greater influence on scale-integrated maps compared with third-order models of pronghorn seasonal migration. ISSF maps helped mute predictive variability for individuals at the third-order scale to predict seasonal migration pathways for large landscapes. Therefore, the second-order selection seems to be the relevant scale for conservation planning to support pronghorn migration across the NSS. I found support that scales of migration pathway selection are hierarchically nested, similar to habitat selection patterns made by other ungulates where decisions made at finer scales are conditional to selections initially made at broader scales (Rettie and Messier 2000, Kie et al. 2002, DeCesare et al. 2012). I used equal frequency bins in Spearman rank correlation tests to compare both third and second-order predictive values against ISSF maps. Second-order case points were consistently increasing within subsequent increasing ISSF map predictive value bins for seasonal migrations, whereas third-order case points were erratic across season and training/testing data. Therefore, second-order models are inferred to influence generated ISSF maps to a greater extent than third-order models. In addition, multi-scalar models both with and without anthropogenic features were calculated to find weight of evidence, *w*, for each model at two scales. Models including anthropogenic features had low support at the third-order scale yet had the highest possible *w* at second-order scales, indicating that anthropogenic features greatly affect migration pathway selection at this scale. Numerous other studies have found that anthropogenic features influence ungulate habitat selection patterns (Johnson et al. 2005, Hebblewhite et al. 2006, Polfus et al. 2011, Lendrum et al. 2012, Lendrum et al. 2013).

In ungulate populations, migration is an important life history strategy that has gained international attention for management and conservation (Berger 2004, Harris et al. 2009). Currently, researchers are making remarkable advancements in methods for studying ungulate migration metrics and pathway selection. For example, Naidoo et al. (2014) identified the longest migration in Africa made by Burchell's zebras spanning multiple countries. As a result, movement modeling and, in particular, migration modeling has accelerated over the past decade (Chetkiewicz and Boyce 2009, Sawyer and Kaufmann 2011, Mysterud 2013, Thurfjell et al. 2014). It is apparent that for wildlife management, efforts must be applied to migration spatiotemporally, which possibly span great distances and long time periods (Mueller et al. 2008). Fortuitously, across ungulate taxa migration generally occurs during the same times of year, during the fall and spring. This makes managing for migration temporally consistent on an annual basis.

The Northern Sagebrush Steppe is a transboundary region encompassing the northern extent of the North American Great Plains. Accordingly, it is also the northern extent of many species' ranges. Due to the international nature of the region, multiple and occasionally contradictory laws and policies govern land use practices. Collection of ecological data can be inconsistent and difficult to share. Additionally, the sheer size of the region (over 315,000 km^2) ensures cultural and environmental variability. Nevertheless, the habitat and the species that depend on it span the international border. These factors make the NSS an important area for cooperative efforts to conserve ecological assets, including shared wildlife populations and ecological processes. Marked pronghorn were found to migrate between the NSS jurisdictions. During my study, collared pronghorn made the longest ungulate migrations observed in the lower 48 states of the U.S.A. In general, multi-scalar modeling of migratory ungulates may assist to identify species movement priorities in landscape level planning. Moreover, scale-integrated step selection function (ISSF) map outputs defined and expressed here provide a critical step in guiding management and conservation priorities across the NSS and, plausibly, other broad regions to address continued declines in global ungulate migrations.

Table 3.1: Candidate variables retained through screening process for multi-scalar modeling efforts of pronghorn migratory pathways across the NSS from 2004-2010.

Candidate Variable	Type	Correlation Analysis†	Univariate Analysis†
Well Density	Continuous	Yes	Yes
Well Density^2	Continuous	N/A	No
Nearest Well	Continuous	Yes	Yes
Nearest Well^2	Continuous	N/A	No
All Roads	Continuous	Yes	Yes
All Road^2 Density	Continuous	N/A	Yes
Paved Road Density	Continuous	Yes	Yes
Paved Road^2 Density	Continuous	N/A	Yes
Unpaved Road Density	Continuous	No	No
Hydro. Den. 1:250000	Continuous	Yes	No
Hydro. Den. 1:1000000	Continuous	Yes	Yes
Snowcover Annual	Continuous	Yes	No
Snowcover Decadal	Continuous	No	No
NDVI Annual	Continuous	Yes	Yes
NDVI Decadal	Continuous	No	No
VRM	Continuous	Yes	Yes
Slope	Continuous	Yes	Yes
Slope^2	Continuous	N/A	Yes
Aspect	Continuous	Yes	Yes
Grassland	Categorical	Yes	Yes
Shrubland	Categorical	Yes	Yes
Pasture & Perenial Crop	Categorical	Yes	Yes
Agriculture*	Categorical	Yes	No
Water	Categorical	Yes	Yes
Exposed	Categorical	Yes	Yes
Development	Categorical	Yes	Yes
Wetland	Categorical	Yes	Yes
Conifer Forest	Categorical	Yes	Yes
Deciduous Forest	Categorical	Yes	Yes
Mixed Forest*	Categorical	Yes	No
Recently Burned*	Categorical	Yes	No
Well Den. x Grassland	Continuous	N/A	No
Nearest Well x Grassland	Continuous	N/A	No

†Yes/No denotes if variable was retained for subsequent modeling efforts after separate correlation and univariate analysis

*Denotes the use as a reference variable in modeling efforts

Table 3.2: Pronghorn withheld for testing multi-scalar migratory pathway selection models across the NSS from 2004-2010.

Pronghorn	Season	Study Site
59	Fall	AB
60	Fall	AB
64	Fall	AB
110	Fall	MT/SK
137	Fall	MT/SK
139	Fall	MT/SK
156	Fall	MT/SK
157	Fall	MT/SK
158	Fall	MT/SK
161	Fall	MT/SK
182	Fall	MT/SK
17	Spring	AB
28	Spring	AB
31	Spring	AB
39	Spring	AB
51	Spring	AB
113	Spring	MT/SK
129	Spring	MT/SK
131	Spring	MT/SK
134	Spring	MT/SK
136	Spring	MT/SK
165	Spring	MT/SK
179	Spring	MT/SK
185	Spring	MT/SK
187	Spring	MT/SK
192	Spring	MT/SK
201	Spring	MT/SK
1939	Spring	MT/SK

Table 3.3: Minimum/maximum pixel values for each continuous variable in pronghorn global third-order migratory pathway selection models across the NSS from 2004-2010.

Fall Migratory Pathway:

Variable	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	Near Well	Well Den.	Hydro. Den.	NDVI	VRM	SLOPE	SLOPE^2	ASPECT
Min	0	0	0	0	20.64229	0	0	-0.1832	0	0	0	-1
Max	0.017	0.00029	0.023	0.0005	400831.4	0.000032	0.00153	0.795	0.066	29.6	874.6	1

Spring Migratory Pathway:

Variable	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	Near Well	Well Den.	Hydro. Den.	NDVI	VRM	SLOPE	SLOPE^2	ASPECT
Min	0	0	0	0	86.5	0	0	-0.169	0	0	0	-1
Max	0.013	0.00018	0.014	0.0002	359587.7	0.000036	0.00193	0.795	0.036	23.2	536.8	1

Table 3.4: Pronghorn third-order global model variable coefficients for fall and spring migratory pathway selection with corresponding *t*-values and *p*-values across the NSS from 2004-2010.

Coefficients:

Season	Paved Rd.	Paved Rd.^{2}	All Rd.	All Rd.^{2}	Near Well	Well Den.	Hydro. Den.	NDVI	VRM	SLOPE	SLOPE^2
Fall	-1059.1	103299.5	-62.3	10020.6	0.00002	-43866.1	1.4	-0.2	-112.5	0.08	-0.005
Spring	536.4	-66718.5	-55.9	7649.4	-0.00001	-25059.4	-1012.0	2.6	-83.4	0.04	-0.001

Season	ASPECT	GRASS	SHRUB	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
Fall	-0.19	-0.04	0.18	0.11	0.18	0.10	0.15	0.47	-17.79	0.87
Spring	-0.05	0.13	0.15	0.15	-0.05	0.42	0.24	0.95	1.82	-0.21

***t*-values:**

Season	Paved Rd.	Paved Rd.^{2}	All Rd.	All Rd.^{2}	Near Well	Well Den.	Hydro. Den.	NDVI	VRM	SLOPE	SLOPE^2
Fall	3.83	2.31	1.62	1.56	0.50	1.01	8.52	3.59	3.86	0.36	0.03
Spring	220.25	217.13	2.86	3.27	1.55	7.04	690.06	2.65	9.31	4.95	2.10

Season	ASPECT	GRASS	SHRUB	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
Fall	0.88	1.14	0.36	1.13	1.76	28.37	1.05	10.35	0.00	2.83
Spring	0.95	2.22	6.49	4.35	2.82	2.18	5.94	1.76	0.00	26.31

***p*-values*:**

Season	**Paved Rd.**	**Paved Rd.^{2}**	**All Rd.**	**All Rd.^{2}**	**Near Well**	**Well Den.**	**Hydro. Den.**	**NDVI**	**VRM**	**SLOPE**	**SLOPE^2**
Fall	0.00086	0.03218	0.113	0.126	0.622	0.32	2.37E-10	0.0009	0.00038	0.723	0.978
Spring	5.6E-62	2.8E-52	0.006	0.002	0.126	1.36E-09	5.74E-117	0.0101	1.2E-13	5.5E-06	0.040

RED indicates $p \leq 0.05$

Season	**ASPECT**	**GRASS**	**SHRUB**	**PPCROP**	**WETLAND**	**WATER**	**EXPOSED**	**DEVELOP**	**CONIF**	**DECID**
Fall	0.382	0.259	0.723	0.263	0.090	1.9E-14	0.304	1.782E-09	1	0.011
Sping	0.348	0.030	2.7E-08	5.82E-05	0.007	0.038	4.439E-07	0.086	1	1.1E-18

RED indicates $p \leq 0.05$

Table 3.5: Annual mean third-order coefficients with 95% confidence intervals for fall migratory pathway selection from 2004-2010. Results indicate selection contained annually variability during the study period.

	Paved Rd.	**Paved Rd.^{2}**	**All Road**	**All Road^2**	**NearWell**	**Well Den.**	**Hydro. Den.**
2004							
n=1							
Mean	2870.0	-1043000.0	47.1	89.7	-0.00002	70830.0	485.3
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	2870.0	-1043000.0	47.1	89.7	-0.00002	70830.0	485.3
95%-CI	2870.0	-1043000.0	47.1	89.7	-0.00002	70830.0	485.3
2005							
n=7							
Mean	17738.5	-21477088.0	79.8	-23844.3	-0.00006	-104630.0	-23638.5
SD	39161.0	39352128.0	520.2	107328.5	0.00009	152612.4	40072.7
95%+CI	94494.0	55653082.8	1099.4	186519.6	0.00012	194490.3	54904.1
95%-CI	-59017.1	-98607258.8	-939.9	-234208.2	-0.00023	-403750.3	-102181.1
2006							
n=4							
Mean	-496.0	-926000.0	351.4	-75035.0	0.00004	-149885.0	-1576.7
SD	6756.9	1325132.2	619.8	98517.8	0.00003	75824.9	1026.6
95%+CI	12747.5	1671259.1	1566.1	118059.9	0.00011	-1268.1	435.5
95%-CI	-13739.5	-3523259.1	-863.3	-268129.9	-0.00002	-298501.9	-3588.8

	NDVI	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
2004							
n=1							
Mean	5.623	596.2	0.303	-0.023	0.094	0.365	-18.140
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	5.623	596.2	0.303	-0.023	0.094	0.365	-18.140
95%-CI	5.623	596.2	0.303	-0.023	0.094	0.365	-18.140
2005							
n=7							
Mean	-1.059	84.6	0.079	-0.051	-0.174	2.362	0.872
SD	4.259	1441.7	0.390	0.060	0.211	5.933	0.600
95%+CI	7.288	2910.3	0.843	0.066	0.240	13.991	2.048
95%-CI	-9.407	-2741.2	-0.685	-0.168	-0.587	-9.267	-0.304
2006							
n=4							
Mean	-6.078	-194.2	0.268	-0.050	-0.142	4.037	-18.365
SD	5.923	890.5	0.227	0.052	0.276	7.649	10.763
95%+CI	5.532	1551.2	0.714	0.052	0.399	19.029	2.731
95%-CI	-17.688	-1939.5	-0.177	-0.153	-0.684	-10.955	-39.461

	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
2004							
n=1							
Mean	0.220	-17.820	-17.900	-18.340	0.153	-18.020	-17.980
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	0.220	-17.820	-17.900	-18.340	0.153	-18.020	-17.980
95%-CI	0.220	-17.820	-17.900	-18.340	0.153	-18.020	-17.980
2005							
n=7							
Mean	-5.673	-3.820	-11.139	22.555	-4.110	-18.390	-16.130
SD	9.057	12.238	9.583	16.975	14.905	6.951	6.097
95%+CI	12.079	20.167	7.644	55.826	25.104	-4.766	-4.181
95%-CI	-23.425	-27.807	-29.922	-10.716	-33.324	-32.014	-28.079
2006							
n=4							
Mean	-5.621	-11.826	-18.050	-20.640	-1.295	-16.840	-18.300
SD	7.958	10.799	9.193	10.320	13.848	8.420	10.708
95%+CI	9.977	9.339	-0.032	-0.413	25.846	-0.337	2.687
95%-CI	-21.219	-32.992	-36.068	-40.867	-28.436	-33.343	-39.287

	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	NearWell	Well Den.	Hydro. Den.
2008							
n=1							
Mean	NA	NA	-407.4	52650.0	0.00009	-2059000.0	-751.9
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	NA	NA	-407.4	52650.0	0.00009	-2059000.0	-751.9
95%-CI	NA	NA	-407.4	52650.0	0.00009	-2059000.0	-751.9
2009							
n=13							
Mean	2921.4	-1498428.6	-5824.6	775574.2	0.00018	-54088.5	-7253.2
SD	14141.1	3400673.6	10621.3	1505390.4	0.00019	1021210.6	27530.9
95%+CI	30637.9	5166891.6	14993.0	3726139.3	0.00055	1947484.3	46707.4
95%-CI	-24795.2	-8163748.8	-26642.3	-2174991.0	-0.00020	-2055661.2	-61213.7
2010							
n=15							
Mean	72532.2	-14111575.0	-11189.2	1701398.5	-0.00009	-3590435.7	-20308.7
SD	87005.3	13752353.9	41948.4	6610751.4	0.00016	11741650.2	39370.2
95%+CI	243062.6	12843038.6	71029.8	14658471.3	0.00023	19423198.7	56856.9
95%-CI	-97998.2	-41066188.6	-93408.1	-11255674.3	-0.00040	-26604070.1	-97474.3

	NDVI	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
2008							
n=1							
Mean	-1.620	-131.2	-0.139	0.008	-0.247	-0.397	0.358
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	-1.620	-131.2	-0.139	0.008	-0.247	-0.397	0.358
95%-CI	-1.620	-131.2	-0.139	0.008	-0.247	-0.397	0.358
2009							
n=13							
Mean	-2.371	-310.0	0.068	-0.002	-0.214	1.903	0.307
SD	9.918	303.4	0.371	0.039	0.360	5.380	7.875
95%+CI	17.069	284.7	0.795	0.074	0.491	12.448	15.743
95%-CI	-21.811	-904.6	-0.660	-0.079	-0.919	-8.643	-15.128
2010							
n=15							
Mean	1.293	-227.0	0.086	-0.031	-0.260	1.379	-8.096
SD	4.556	668.6	0.340	0.063	0.365	5.602	11.886
95%+CI	10.222	1083.4	0.752	0.092	0.455	12.358	15.200
95%-CI	-7.636	-1537.3	-0.580	-0.155	-0.975	-9.601	-31.391

	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
2008							
n=1							
Mean	-1.078	-0.005	NA	-15.360	NA	NA	NA
SD	NA	NA	NA	NA	NA	NA	NA
95%+CI	-1.078	-0.005	NA	-15.360	NA	NA	NA
95%-CI	-1.078	-0.005	NA	-15.360	NA	NA	NA
2009							
n=13							
Mean	-2.445	-6.806	-13.220	1.144	-23.383	NA	-15.264
SD	10.416	7.673	3.667	7.865	18.259	NA	9.131
95%+CI	17.970	8.233	-6.034	16.559	12.405	NA	2.634
95%-CI	-22.861	-21.846	-20.406	-14.271	-59.171	NA	-33.161
2010							
n=15							
Mean	-6.025	-12.771	-17.072	-3.210	-14.192	NA	-5.111
SD	9.538	8.744	8.704	11.989	8.522	NA	10.333
95%+CI	12.669	4.368	-0.012	20.289	2.511	NA	15.142
95%-CI	-24.719	-29.910	-34.132	-26.709	-30.894	NA	-25.363

Table 3.6: Annual mean third-order coefficients with 95% confidence intervals for fall migratory pathway selection from 2004-2010. Results indicate selection contained annually variability during the study period.

	Paved Rd.	**Paved Rd.^{2}**	**All Road**	**All Road^2**	**NearWell**	**Well Den.**	**Hydro. Den.**
2004							
n = 6							
Mean	6625.8	-4445146.0	-1564.1	249780.0	0.00002	316615.0	-3523.2
SD	17325.5	9369419.7	3584.7	583246.0	0.00018	1037908.3	8383.6
95%+CI	40583.7	13918916.6	5461.9	1392942.1	0.00037	2350915.3	12908.6
95%-CI	-27332.1	-22809208.6	-8590.1	-893382.1	-0.00033	-1717685.3	-19955.0
2005							
n=7							
Mean	-12633.1	2423700.0	-142.7	10195.7	0.00003	-123844.3	-33428.8
SD	15474.8	2546930.1	466.2	64359.4	0.00012	189163.1	38798.7
95%+CI	17697.5	7415683.0	771.0	136340.0	0.00027	246915.3	42616.6
95%-CI	-42963.8	-2568283.0	-1056.5	-115948.6	-0.00021	-494603.9	-109474.2
2006							
n=6							
Mean	-4471.3	338210.0	-3614.4	493436.3	-0.00016	-84319.7	-1106.9
SD	3504.9	283771.0	8759.2	1199042.7	0.00012	121519.7	1010.6
95%+CI	2398.3	894401.2	13553.6	2843560.1	0.00008	153859.0	874.0
95%-CI	-11341.0	-217981.2	-20782.4	-1856687.4	-0.00039	-322498.4	-3087.7

	NDVI	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
2004							
n = 6							
Mean	7.605	-4991.9	0.121	0.032	0.056	3.289	-3.972
SD	8.030	10552.5	0.228	0.077	0.220	7.714	7.865
95%+CI	23.345	15691.0	0.567	0.184	0.487	18.408	11.443
95%-CI	-8.134	-25674.8	-0.325	-0.120	-0.375	-11.830	-19.387
2005							
n=7							
Mean	0.938	-188.3	0.204	-0.025	-0.153	-1.027	2.294
SD	5.435	477.3	0.157	0.031	0.111	11.281	10.411
95%+CI	11.592	747.2	0.512	0.035	0.064	21.084	22.700
95%-CI	-9.715	-1123.8	-0.104	-0.085	-0.370	-23.138	-18.112
2006							
n=6							
Mean	-7.679	-484.9	0.618	-0.103	-0.033	6.985	-10.187
SD	20.388	1200.8	1.112	0.197	0.133	9.786	8.728
95%+CI	32.280	1868.6	2.796	0.283	0.227	26.165	6.921
95%-CI	-47.639	-2838.5	-1.561	-0.488	-0.293	-12.195	-27.295

	PPCROP	**WETLAND**	**WATER**	**EXPOSED**	**DEVELOP**	**CONIF**	**DECID**
2004							
n = 6							
Mean	0.319	-11.955	0.811	-12.745	120.559	NA	-16.670
SD	0.288	9.268	0.422	9.376	260.797	NA	6.805
95%+CI	0.883	6.211	1.638	5.633	631.721	NA	-3.331
95%-CI	-0.245	-30.121	-0.016	-31.123	-390.603	NA	-30.009
2005							
n=7							
Mean	-4.146	-11.573	-13.829	3.452	-17.120	-7.812	-16.685
SD	7.514	15.373	14.390	11.964	6.471	5.521	8.154
95%+CI	10.581	18.558	14.375	26.901	-4.437	3.009	-0.703
95%-CI	-18.873	-41.704	-42.033	-19.996	-29.803	-18.633	-32.667
2006							
n=6							
Mean	0.381	0.497	-3.306	-10.549	-15.243	-4.398	-8.580
SD	0.734	1.422	7.444	8.088	8.439	7.327	7.139
95%+CI	1.820	3.284	11.284	5.303	1.297	9.962	5.412
95%-CI	-1.059	-2.291	-17.896	-26.401	-31.784	-18.758	-22.571

	Paved Rd.	**Paved Rd.^{2}**	**All Road**	**All Road^2**	**NearWell**	**Well Den.**	**Hydro. Den.**
2008							
n=3							
Mean	865.3	NA	-2856.7	306590.0	-0.00020	-1752600.0	-2269.3
SD	499.6	NA	5663.8	640785.3	0.00018	959139.8	1447.0
95%+CI	1844.5	NA	8244.4	1562529.2	0.00015	127313.9	566.8
95%-CI	-113.9	NA	-13957.9	-949349.2	-0.00056	-3632513.9	-5105.5
2009							
n=27							
Mean	-12476.8	2210360.0	2700.5	-1709489.2	0.00001	-6437775.4	-10520.4
SD	24202.2	4357493.1	13823.1	7887032.5	0.00020	17885368.0	24295.6
95%+CI	34959.5	10751046.6	29793.8	13749094.5	0.00040	28617545.8	37099.0
95%-CI	-59913.2	-6330326.6	-24392.8	-17168073.0	-0.00039	-41493096.7	-58139.7
2010							
n=13							
Mean	-8209.2	925284.0	-2400.3	192593.2	-0.00022	-323559.2	-3865.9
SD	8264.4	2164393.9	6610.3	550887.0	0.00038	1160448.8	11143.7
95%+CI	7989.1	5167496.1	10555.9	1272331.7	0.00053	1950920.4	17975.8
95%-CI	-24407.4	-3316928.1	-15356.4	-887145.2	-0.00097	-2598038.9	-25707.6

	NDVI	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
2008							
n=3							
Mean	15.546	-583.7	0.010	0.016	-0.194	0.154	-8.192
SD	21.308	879.3	0.390	0.005	0.662	1.225	9.525
95%+CI	57.310	1139.7	0.776	0.026	1.102	2.555	10.478
95%-CI	-26.218	-2307.1	-0.755	0.006	-1.491	-2.248	-26.861
2009							
n=27							
Mean	1.429	-453.3	0.076	-0.012	-0.050	1.694	-4.064
SD	6.474	628.6	0.256	0.034	0.271	5.273	7.471
95%+CI	14.119	778.8	0.578	0.055	0.482	12.029	10.580
95%-CI	-11.260	-1685.4	-0.425	-0.079	-0.582	-8.642	-18.708
2010							
n=13							
Mean	2.140	-358.7	0.045	-0.020	0.026	4.719	3.080
SD	7.601	425.0	0.163	0.024	0.448	8.479	10.725
95%+CI	17.037	474.3	0.364	0.028	0.904	21.337	24.101
95%-CI	-12.757	-1191.7	-0.274	-0.067	-0.852	-11.899	-17.941

	PPCROP	**WETLAND**	**WATER**	**EXPOSED**	**DEVELOP**	**CONIF**	**DECID**
2008							
n=3							
Mean	0.692	-17.903	-17.090	2.139	-19.253	NA	-19.975
SD	0.753	2.630	9.867	1.984	3.664	NA	11.828
95%+CI	2.167	-12.749	2.249	6.028	-12.071	NA	3.207
95%-CI	-0.783	-23.058	-36.429	-1.750	-26.436	NA	-43.157
2009							
n=27							
Mean	-2.915	-11.639	-14.270	-1.117	-10.523	NA	-12.137
SD	7.276	8.569	8.053	8.143	25.844	NA	7.734
95%+CI	11.346	5.156	1.514	14.843	40.131	NA	3.022
95%-CI	-17.177	-28.434	-30.053	-17.078	-61.177	NA	-27.296
2010							
n=13							
Mean	2.736	-11.516	-15.677	-1.693	30.782	NA	-15.746
SD	13.660	7.976	6.913	5.308	51.123	NA	8.016
95%+CI	29.510	4.117	-2.128	8.711	130.983	NA	-0.036
95%-CI	-24.037	-27.148	-29.225	-12.097	-69.418	NA	-31.456

Table 3.7: Second-order global model variable coefficients for pronghorn fall migratory pathway selection with corresponding standard error, z-score and *p*-values across the NSS from 2004-2010.*

Variable	**β**	**SE**	**z-score**	***p*-value**
INTERCEPT	-0.39	0.06	-6.47	9.78E-11
WATER	-1.50	0.33	-4.52	6.09E-06
EXPOSED	0.70	0.19	3.67	0.00024
DEVELOP	0.53	0.34	1.53	0.125
SHRUB	0.11	0.12	0.89	0.374
WETLAND	-0.13	0.22	-0.59	0.556
GRASS	1.05	0.06	18.30	< 2E-16
PPCROP	0.16	0.08	1.92	0.05501
CONIF	-2.63	1.15	-2.28	0.0225
DECID	-0.58	0.34	-1.69	0.09073
VRM	-41.09	19.84	-2.07	0.03833
SLOPE	0.20	0.02	8.19	2.57E-16
SLOPE^2	-0.02	0.00	-7.71	1.29E-14
ASPECT	-0.27	0.03	-8.10	5.53E-16
Hydro. Den.	424.90	131.70	3.23	0.00125
Paved Rd.	-624.50	148.10	-4.22	0.00002
All Rd.	-362.70	46.20	-7.85	4.09E-15
Well Den.	-36680.00	13430.00	-2.73	0.0063

***** RED indicates $p \leq 0.05$

Table 3.8: Second-order global model variable coefficients for pronghorn spring migratory pathway selection with corresponding standard error, z-score and *p*-values across the NSS from 2004-2010.*

Variable	β	SE	z-score	*p* -value
INTERCEPT	-1.16	0.08	-15.40	< 2E-16
WATER	-0.95	0.21	-4.61	4.06E-06
EXPOSED	1.07	0.13	8.38	< 2E-16
DEVELOP	0.43	0.22	1.91	0.057
SHRUB	-0.17	0.08	-2.13	0.033
WETLAND	-0.07	0.14	-0.47	0.638
GRASS	1.07	0.04	28.54	< 2E-16
PPCROP	-0.31	0.06	-5.30	1.18E-07
CONIF	-2.57	0.64	-4.01	6.15E-05
DECID	-1.03	0.25	-4.19	2.83E-05
VRM	-53.60	13.49	-3.97	7.12E-05
SLOPE	0.14	0.02	9.00	< 2E-16
SLOPE^2	-0.01	0.0014	-9.84	< 2E-16
ASPECT	-0.12	0.02	-5.77	7.91E-09
Hydro. Den.	-887.80	99.19	-8.95	< 2E-16
All Rd.	-643.10	30.11	-21.36	< 2E-16
Well Den.	-78050.00	10330.00	-7.55	4.29E-14
Near Well	0.00	0.00	7.18	7.23E-13
NDVI	3.73	0.26	14.37	< 2E-16

***** RED indicates $p \leq 0.05$

Table 3.9: Mixed-effect model results for pronghorn stopover site selection during fall migration across the NSS from 2004-2010.*

Variable	β	SE	z-score	*p* -value*
INTERCEPT	-3.08	0.30	-10.23	< 2E-16
WATER	-13.86	1042.0	-0.01	0.989
EXPOSED	0.41	0.69	0.59	0.557
DEVELOP	-10.44	576.50	-0.02	0.986
SHRUB	-1.55	0.58	-2.66	0.008
WETLAND	-2.51	1.17	-2.14	0.032
GRASS	-0.95	0.14	-7.01	2.42E-12
P&P CROP	-1.95	0.23	-8.43	< 2E-16
DECID	0.99	1.45	0.69	0.493
VRM	-1590.00	549.10	-2.90	0.004
SLOPE	0.46	0.17	2.75	0.006
SLOPE^2	-0.12	0.04	-3.22	0.001
ASPECT	0.45	0.08	5.31	1.09E-07
All Road	-130.90	58.52	-2.24	0.025
Well Den.	-523700.0	83770.0	-6.25	4.08E-10
Near Well	-0.00001	0.00000	-8.92	< 2E-16
NDVI	7.75	0.65	11.87	< 2E-16

*RED indicates $p \leq 0.05$

Table 3.10: Mixed-effect model results for pronghorn stopover site selection during spring migration across the NSS from 2004-2010.*

Variable	**β**	**SE**	***z*-score**	***p* -value***
INTERCEPT	-4.79	0.40	-12.00	< 2E-16
WATER	0.17	1.00	0.17	0.867
EXPOSED	-1.58	0.41	-3.82	0.0001
DEVELOP	-0.08	0.62	-0.13	0.895
SHRUB	-1.81	0.44	-4.16	0.0001
WETLAND	-0.18	0.60	-0.30	0.763
GRASS	-0.18	0.08	-2.30	0.021
P&P CROP	0.24	0.13	1.76	0.079
DECID	0.19	4.59	0.04	0.967
CONIF	-10.14	1631.0	-0.01	0.995
ASPECT	0.25	0.05	5.34	9.22E-08
Well Den.	-249900.0	78180.0	-3.20	0.001
NDVI	4.39	0.62	7.13	1.02E-12

*RED indicates $p \leq 0.05$

Table 3.11: Pronghorn seasonal multi-scale migratory pathway selection using Base and Human models across the NSS from 2004-2010.*

Season	Order	Base (*w*)	Human (*w*)
Fall	Third	0.861	0.139
Fall	Second	0	1
Spring	Third	0.764	0.236
Spring	Second	0	1

*"Human" models include road and well variables whereas "Base" models do not

Table 3.12: Validation of single order migratory pathway selection models versus ISSF migratory pathway selection spatial predictions for pronghorn across the NSS from 2004-2010. Rho (ρ) indicates correlation between case points and model predictions from Spearman rank tests and *p* indicates the level of significance.

Season	Order	ISSF Yes/No*	Train/Test †	ρ	*p*§
Fall	3rd	No	Train	0.345	0.331
Fall	3rd	Yes	Train	0.321	0.368
Fall	3rd	No	Test	0.370	0.296
Fall	3rd	Yes	Test	0.165	0.650
Spring	3rd	No	Train	0.430	0.218
Spring	3rd	Yes	Train	0.818	0.007
Spring	3rd	No	Test	-0.273	0.448
Spring	3rd	Yes	Test	-0.758	0.016
Fall	2nd	No	Train	1	2.20E-16
Fall	2nd	Yes	Train	1	2.20E-16
Fall	2nd	No	Test	0.818	0.007
Fall	2nd	Yes	Test	0.988	2.20E-16
Spring	2nd	No	Train	1	2.20E-16
Spring	2nd	Yes	Train	1	2.20E-16
Spring	2nd	No	Test	1	2.20E-16
Spring	2nd	Yes	Test	0.891	0.001

*Indicates if the correlation was performed on the single scale model or on the multi-scalar (ISSF) model

†Indicates if validation test was performed on training or testing data

§RED indicates that $p \leq 0.05$

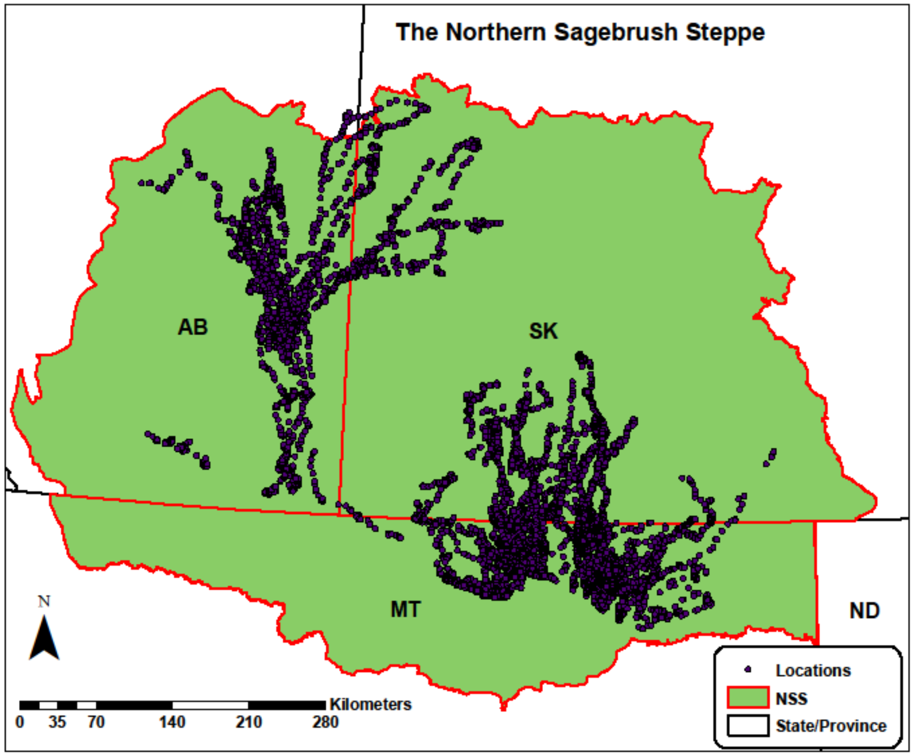


Figure 3.1: The Northern Sagebrush Steppe and GPS locations of fall (*n* = 70) and spring (*n* = 94) migrations achieved by female pronghorn recorded from 2004-2010.

(a)

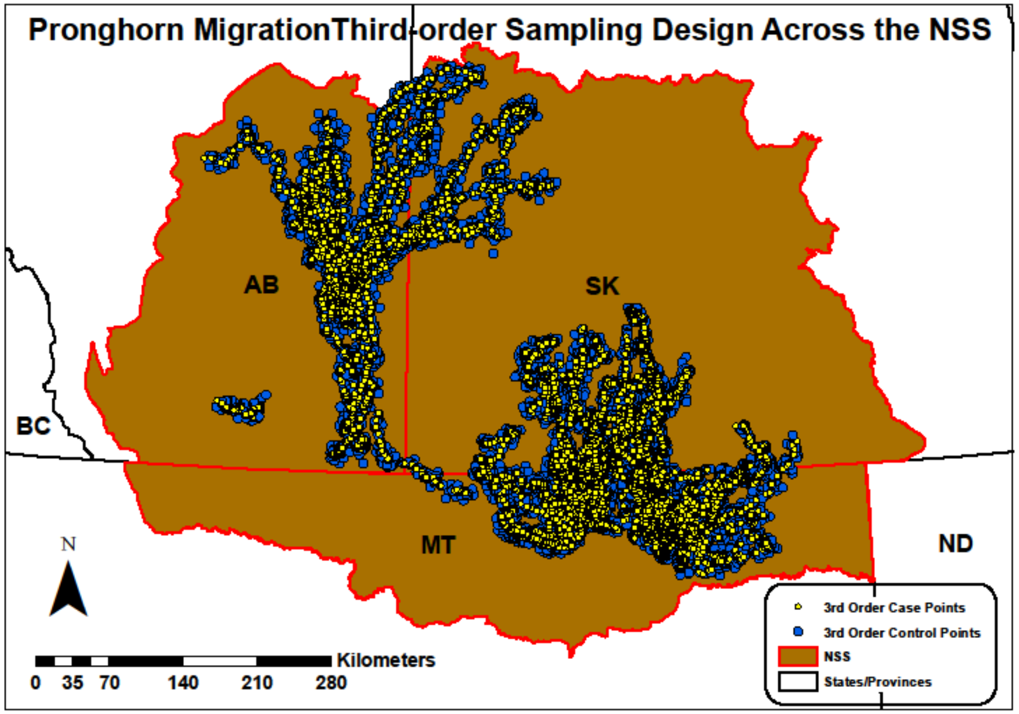
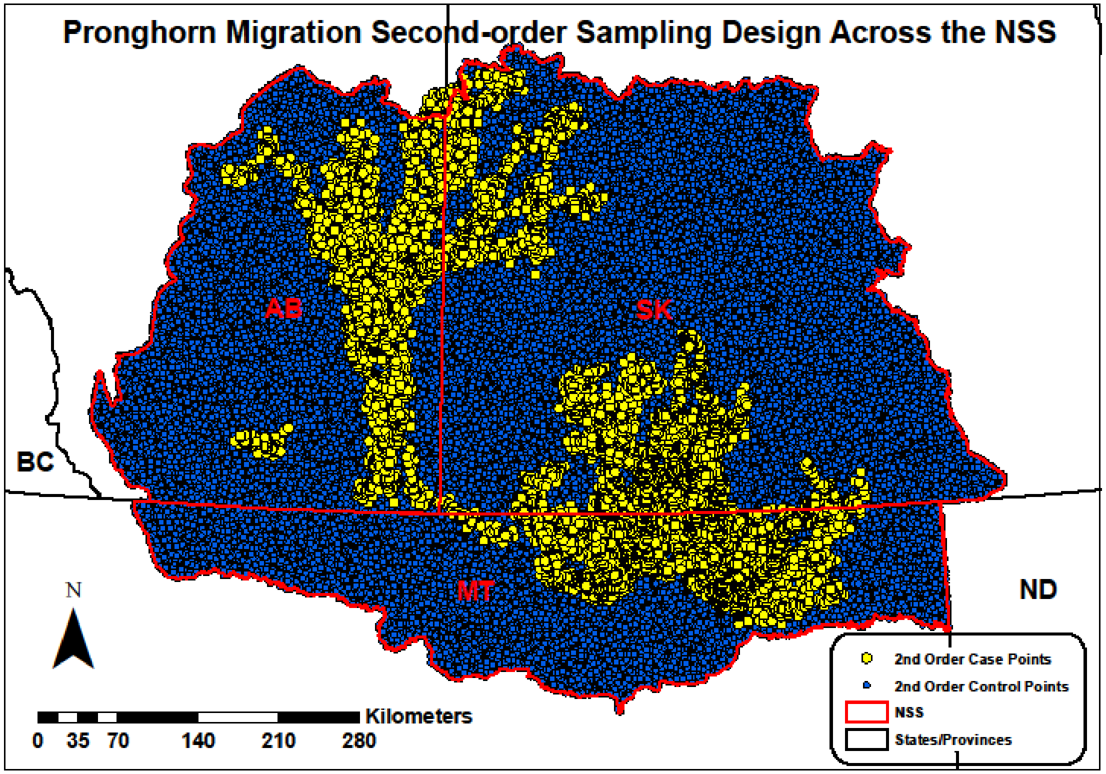


Figure 3.2 (a-b): Third-order (a) and second-order (b) scale sampling designs of pronghorn seasonal migration case/control points across the NSS. At the third-order scale, case points are matched with control points at a 5:1 ratio along a migration pathway. At the second-order scale, the third-order control points are used as case points and matched with random control points distributed across the NSS at a 1:1 ratio. This creates a hierarchically nested sampling design.

(b)


Pronghorn Migration Second-order Sampling Design Across the NSS
AB
SK
MT
BC
ND
N
Kilometers
0
35
70
140
210
280
2nd Order Case Points
2nd Order Control Points
NSS
States/Provinces

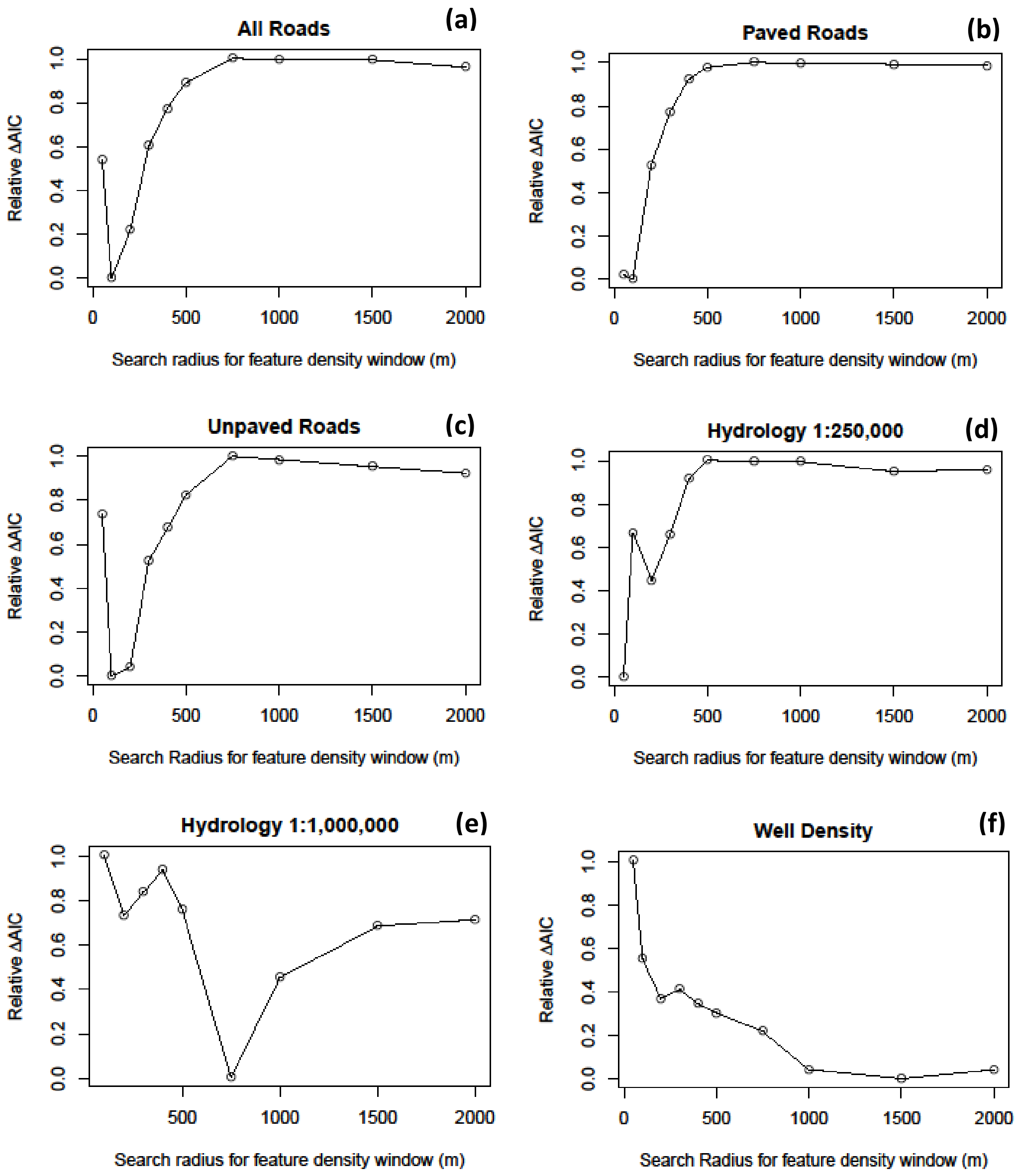


Figure 3.3 (a-f): Relative ΔAIC ($\Delta AIC/\Delta AIC_{max}$) for linear and point variables at the third-order scale. The search radius with the lowest relative ΔAIC score was considered for subsequent pronghorn migration pathway selection modeling at the third-order scale across the NSS, excluding Well Density due to major jurisdictional variation. Variables include (a) All Roads, (b) Paved Roads, (c) Unpaved Roads, (d) Hydrology 1:250,000, (e) Hydrology 1:1,000,000, (f) Well Density.

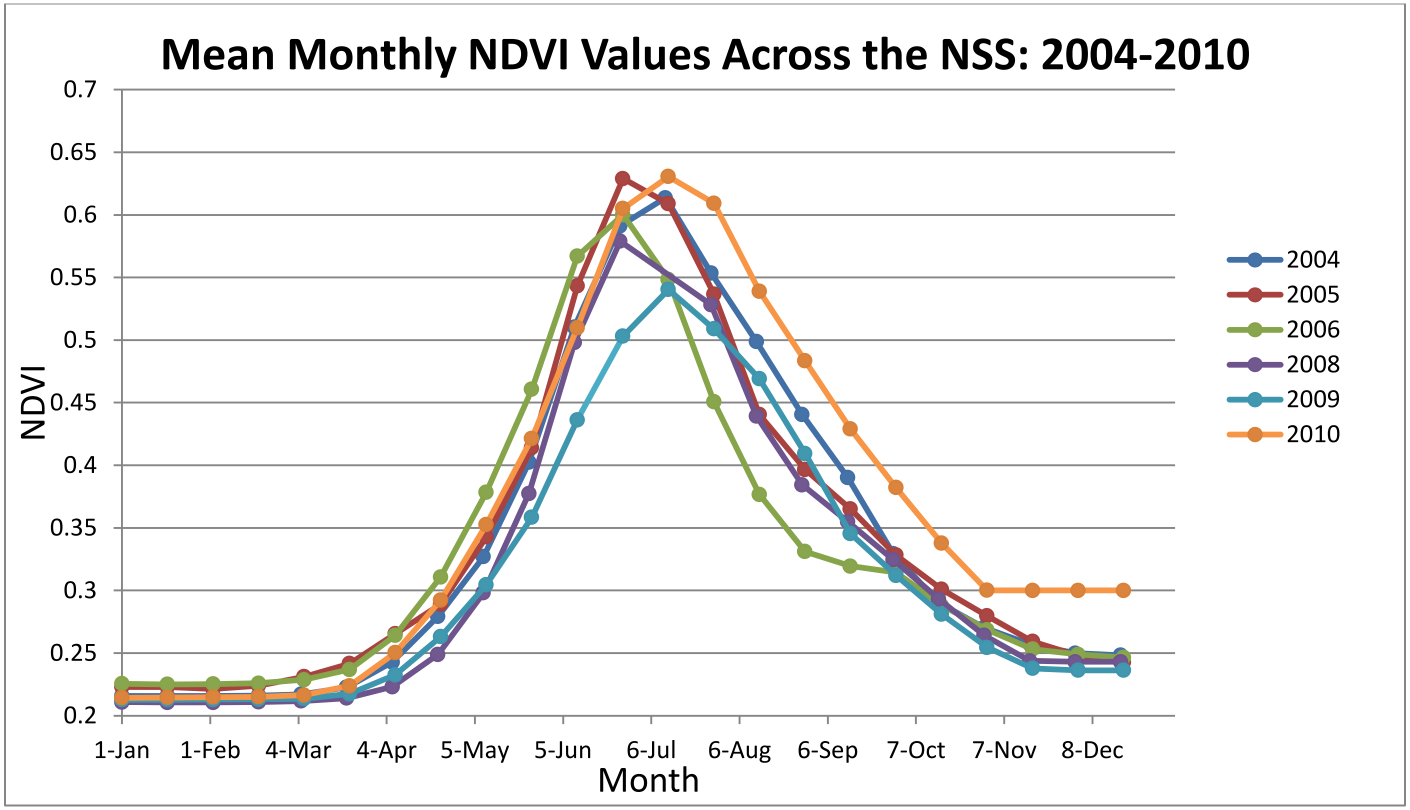


Figure 3.4: Mean monthly NDVI values across the NSS from 2004-2010. Overall, graph indicates little annual variability in winter and spring (January – May). However, peak NDVI levels vary annually in June-July and in addition are variable during late summer and into fall (August – October). By in large, little annual variability was seen in late fall into early winter (November – December).

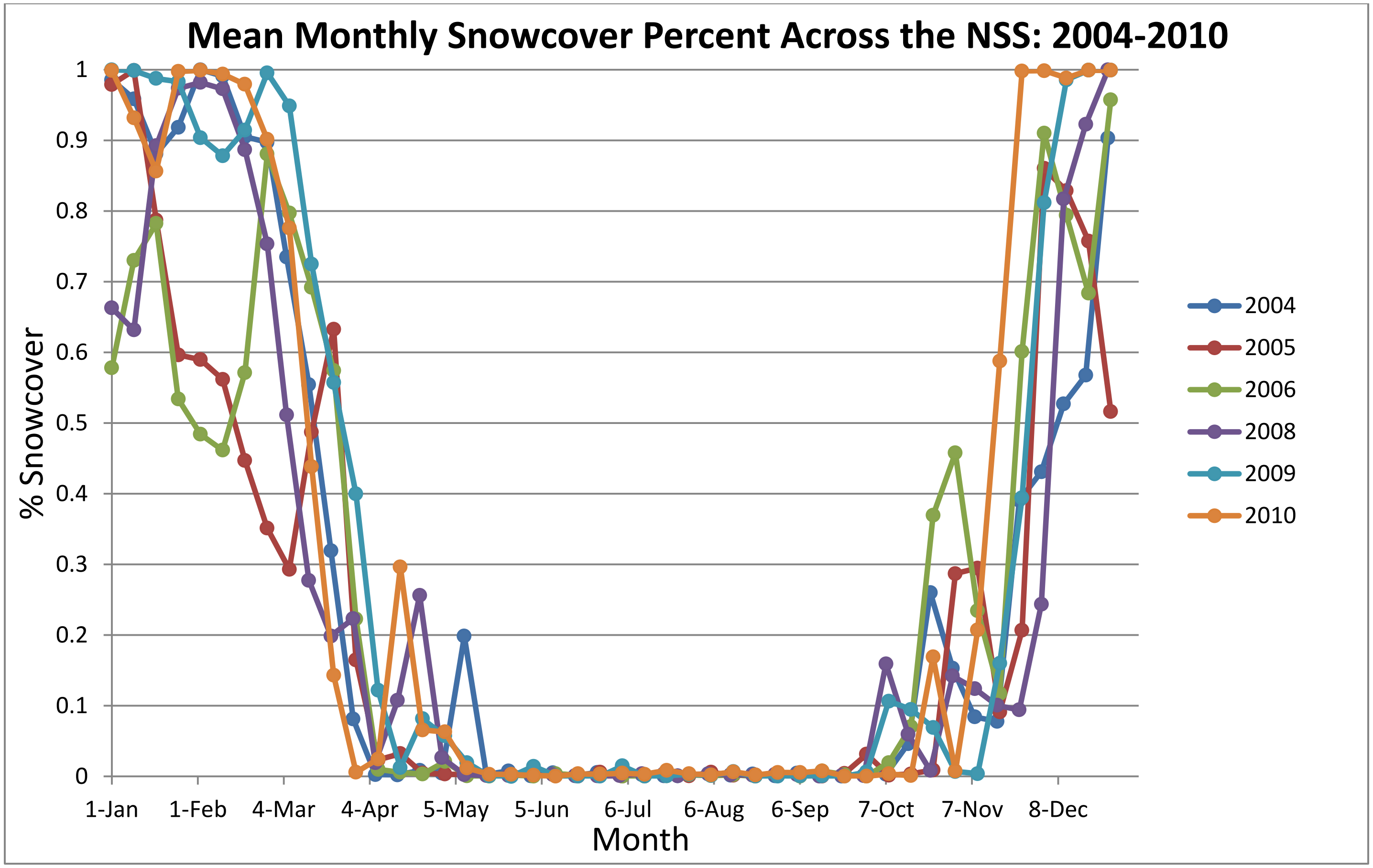


Figure 3.5: Mean monthly snowcover percentage across the NSS from 2004-2010. Results based on snow presence across a 500 m^2 area during an eight-day period. Annual variability was identified from January – February, April – May, and October – November. Little annual variability was identified in March, from June – September, and in December of each year.

(a)

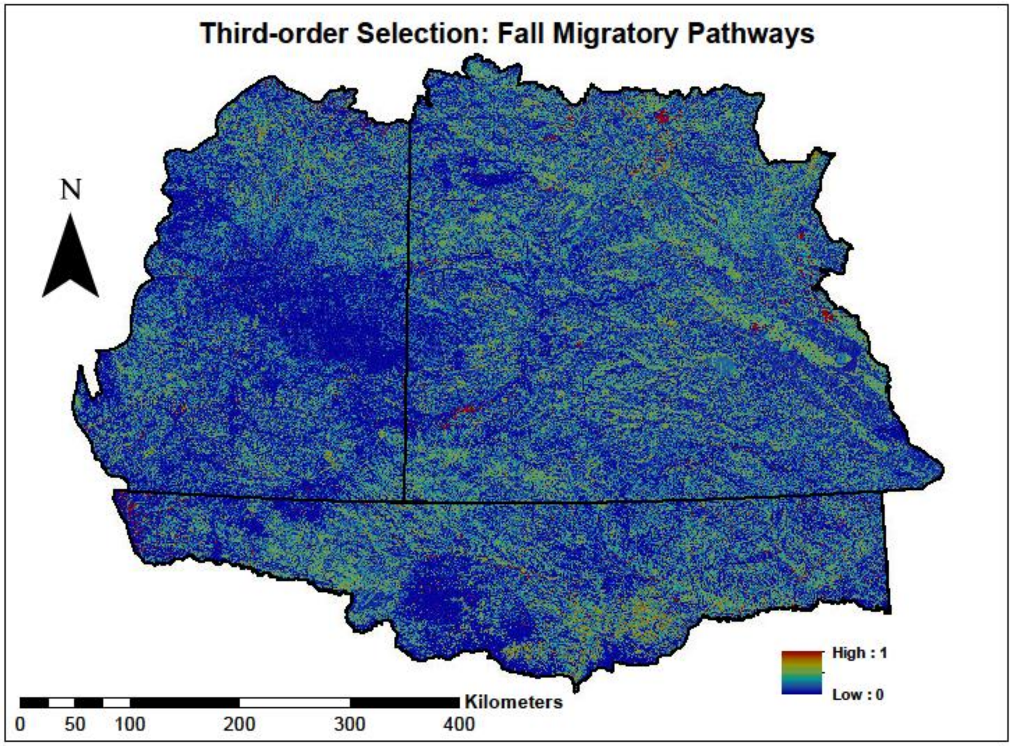
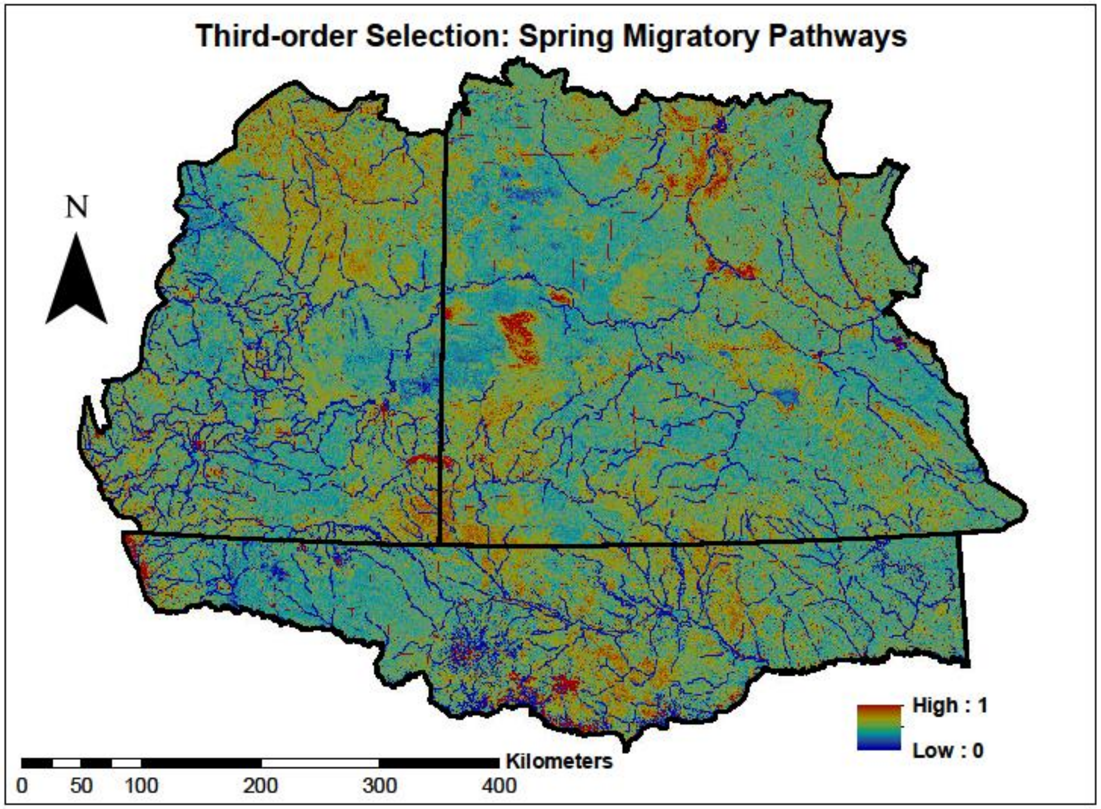
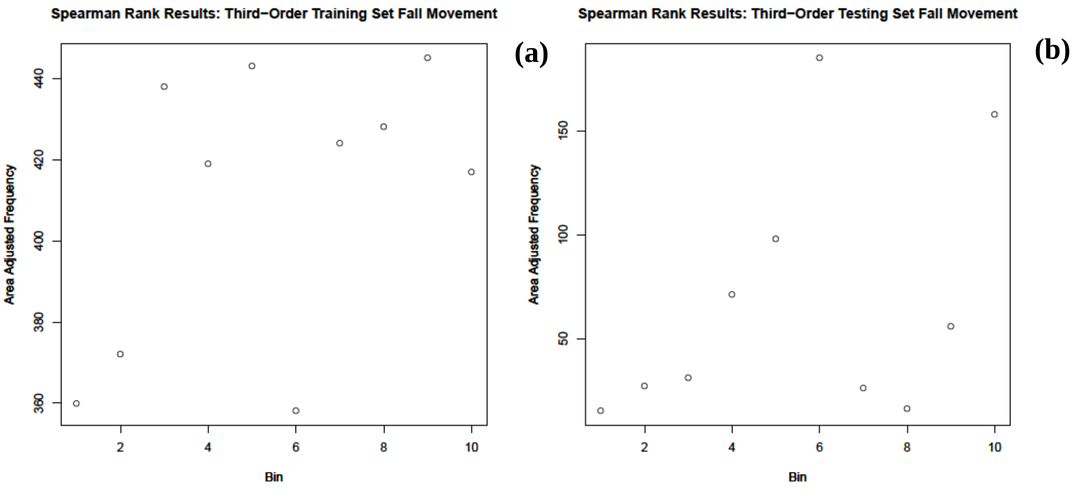


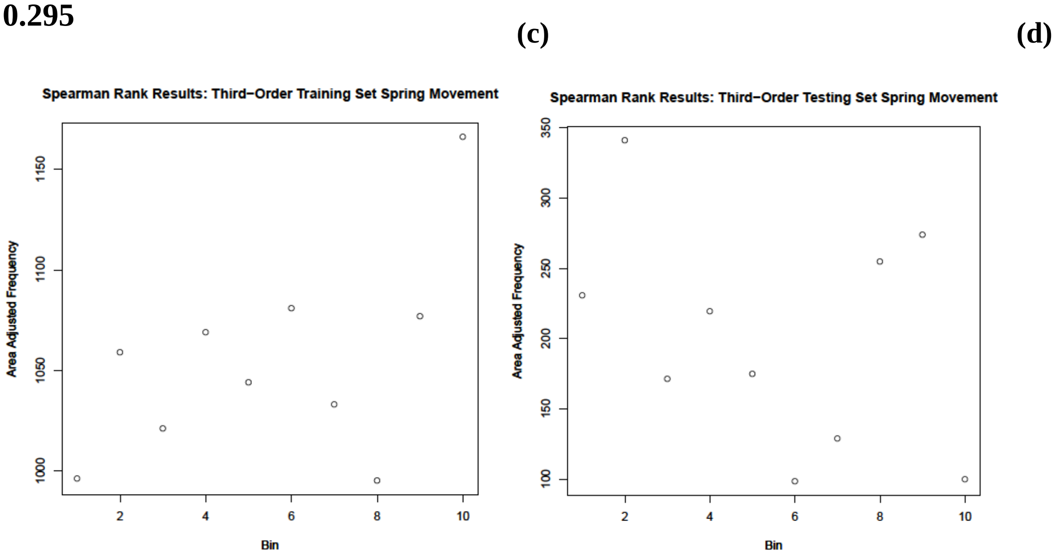
Figure 3.6 (a-b): Third-order fall and spring migratory pathway selection spatial predictions for pronghorn across the NSS from 2004-2010. Red pixels indicate high probability areas for seasonal migration pathway selection, while blue pixels indicate low probability areas.

(b)


Third-order Selection: Spring Migratory Pathways
N
High : 1
Low : 0
Kilometers
0
50
100
200
300
400



(a) Fall training data ρ = 0.345, *p* = 0.331; (b) Fall testing data ρ = 0.37, *p* = 0.295



(c) Spring training data ρ = 0.43, *p* = 0.218; (d) Spring testing data ρ = -0.272, *p* = 0.448

Figure 3.7: Spearman rank correlations for third-order fall and spring migratory pathway selection, using both training and testing data. Graphs (a) – (d) all indicate poor performance in predicting pronghorn probability of migratory pathway selection at this across the NSS, using data from 2004-2010.

(a)

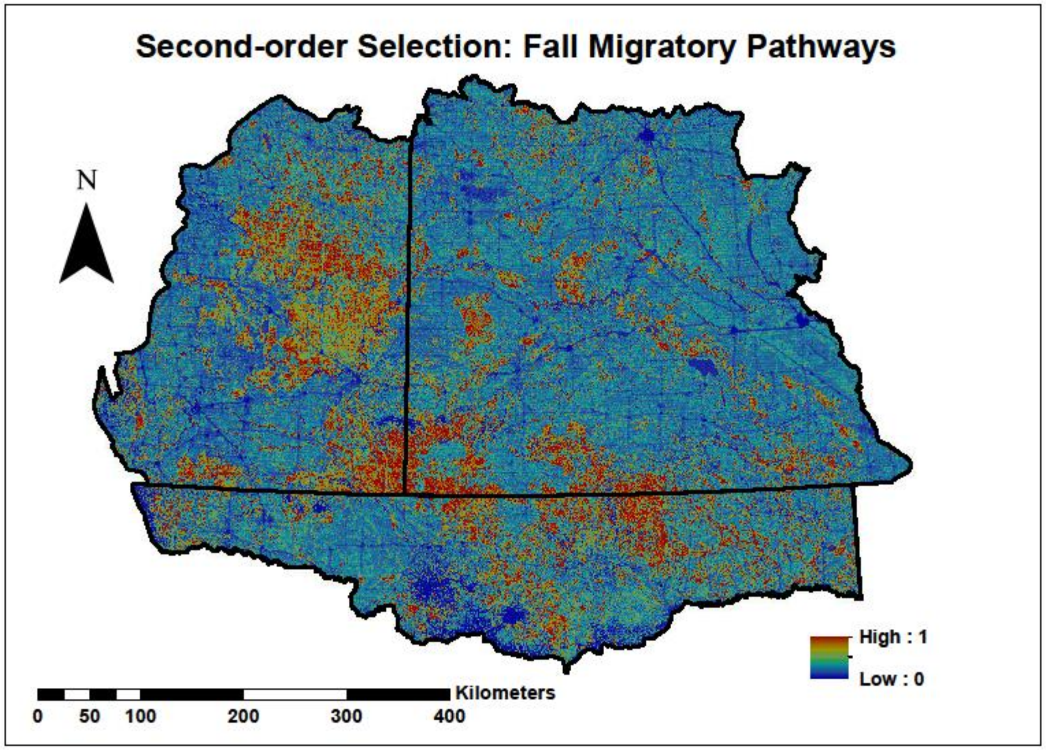
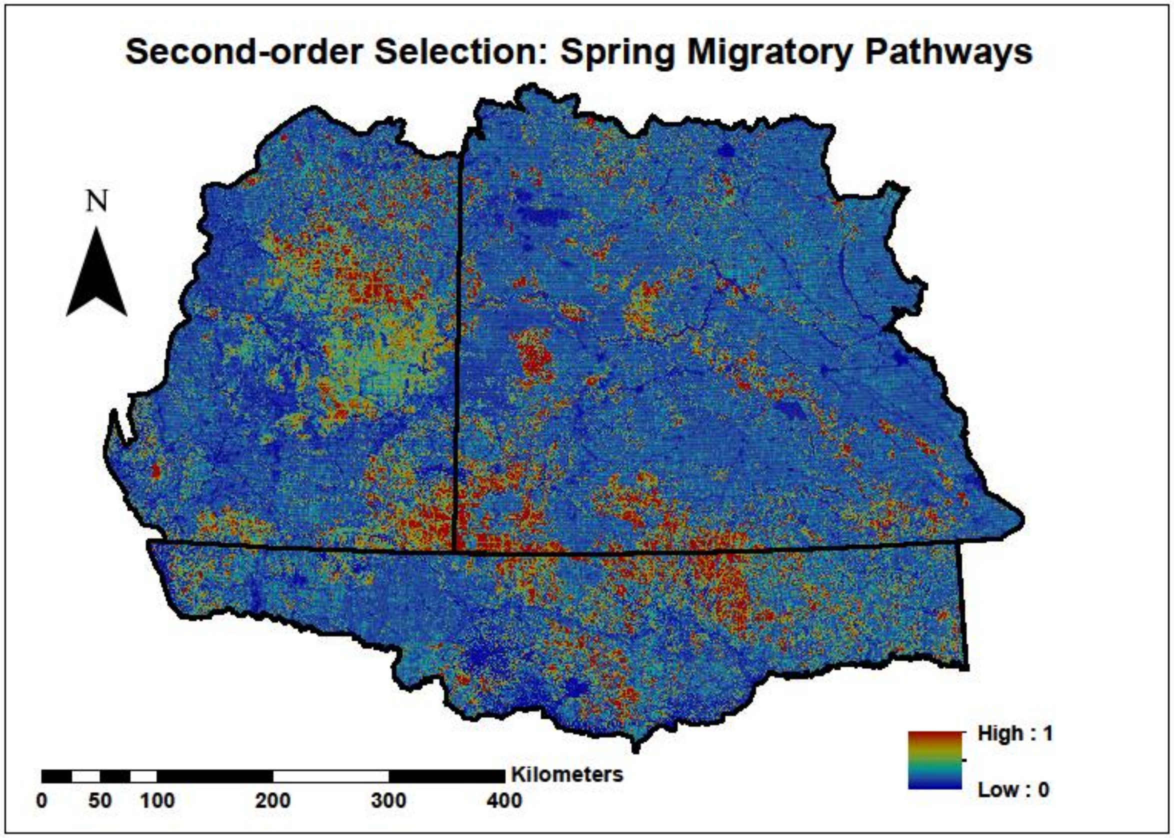
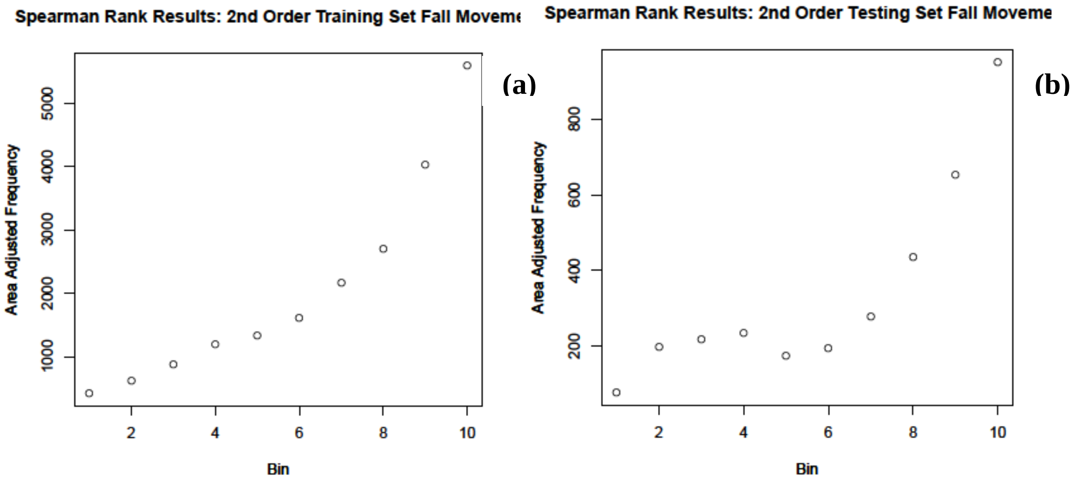


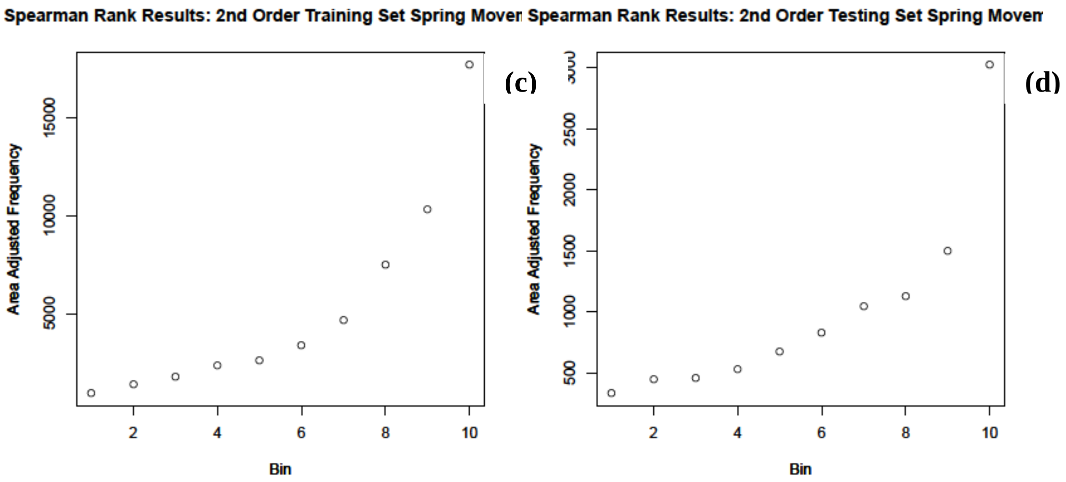
Figure 3.8 (a-b): Second-order fall and spring migratory pathway selection spatial predictions for pronghorn across the NSS from 2004-2010. Red pixels indicate high probability areas for seasonal migration pathway selection, while blue pixels indicate low probability areas.

(b)


Second-order Selection: Spring Migratory Pathways
N
High : 1
Low : 0
Kilometers
0
50
100
200
300
400



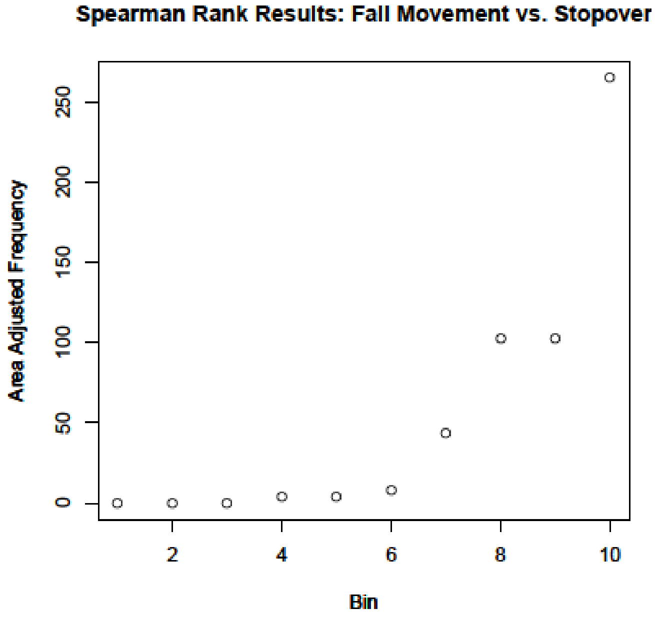
(a) Fall training data ρ = 1, *p* = 2.2E-16; (b) Fall testing data ρ = 0.818, *p* = 0.007



(c) Spring training data ρ = 1, *p* = 2.2E-16; (d) Spring testing data ρ = 1, *p* = 2.2E-16

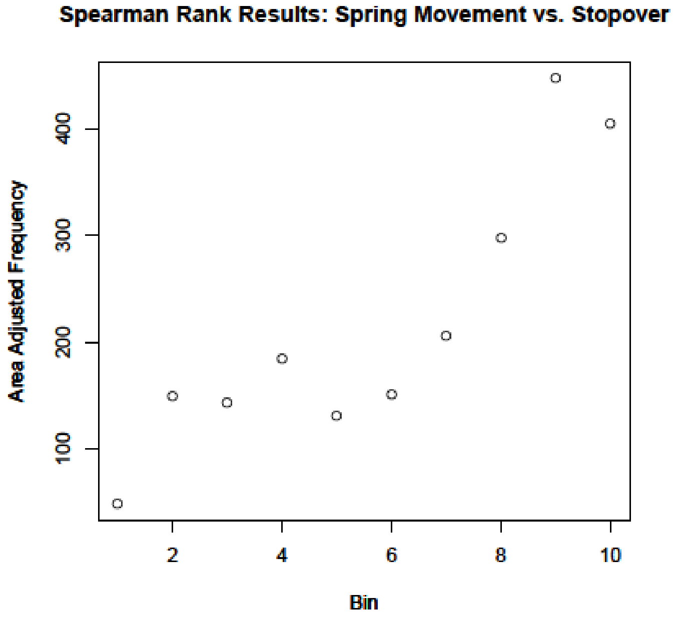
Figure 3.9: Spearman rank correlations for second-order fall and spring migratory pathway selection, using both training and testing data. Graphs (a) – (d) all indicate excellent performance in predicting pronghorn probability of migratory pathway selection at this across the NSS, using data from 2004-2010.

(a)



(a) Fall: ρ = 0.982, *p* = 4.85E-07

(b)



(b) Spring: ρ = 0.879, *p* = 0.002

Figure 3.10: Spearman rank correlations for fall and spring stopover site selection from migratory pathways. Graphs (a) – (b) indicate excellent performance in predicting pronghorn stopover sites from migratory pathways across the NSS, using data from 2004-2010.

(a)

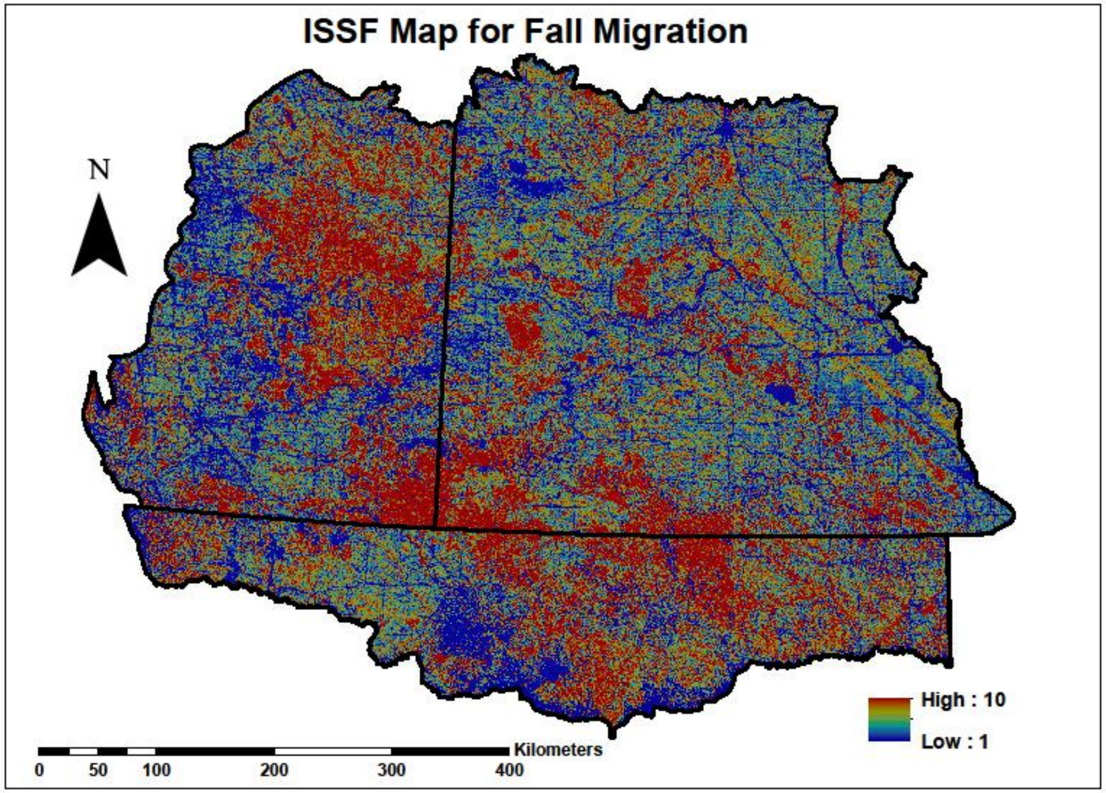
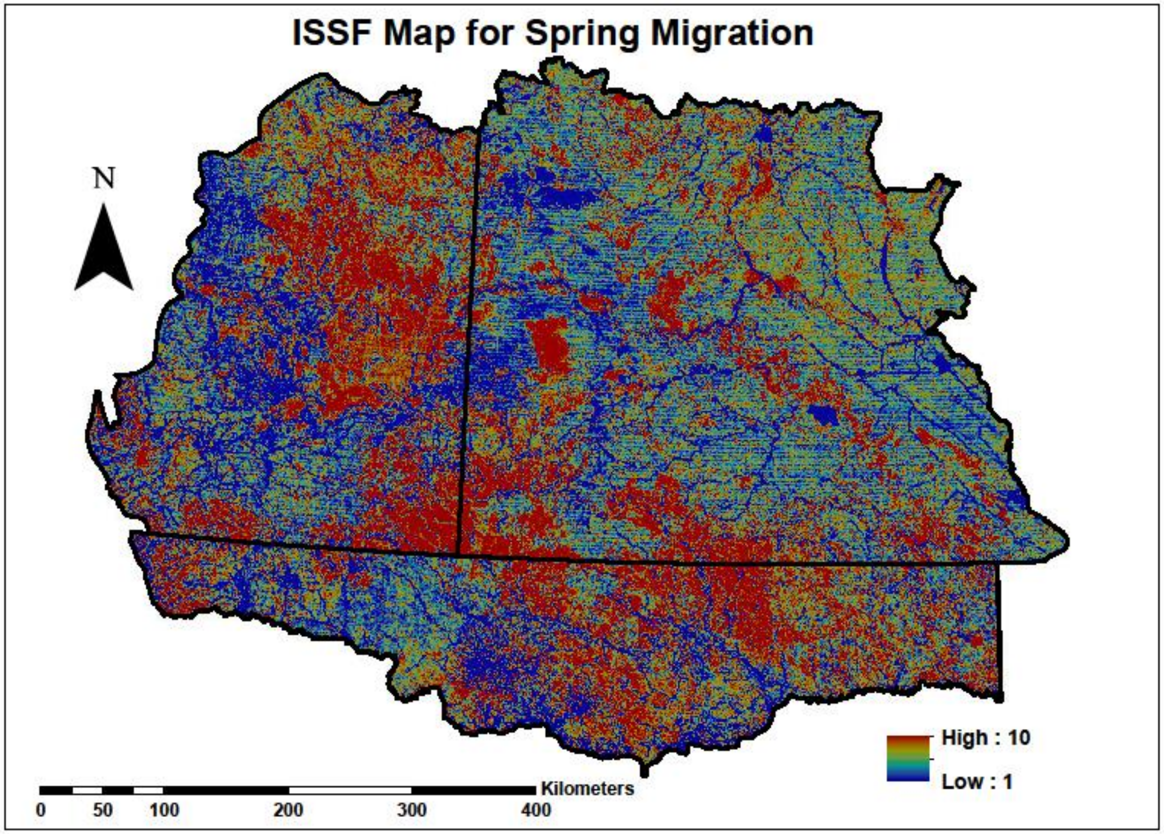
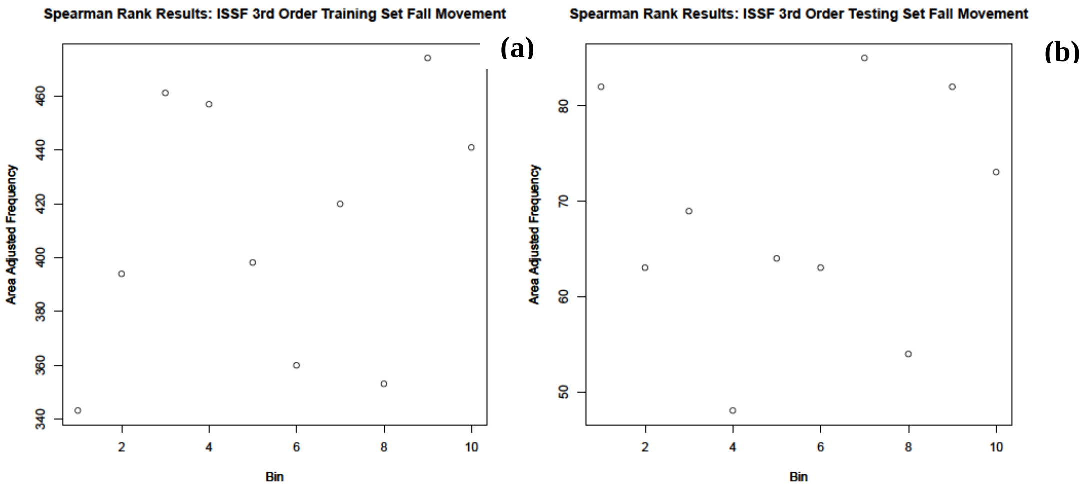


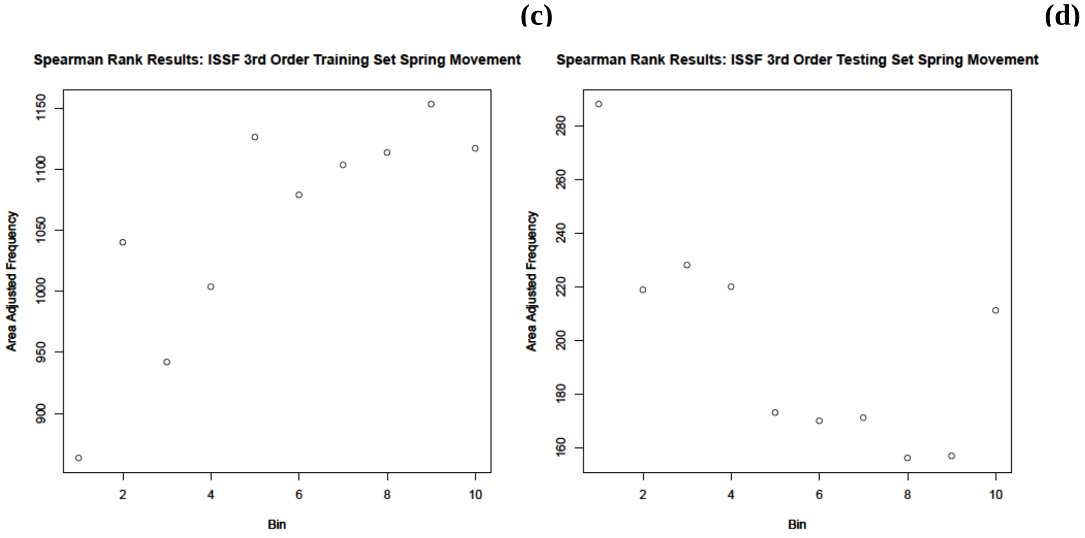
Figure 3.11 (a-b): Final scale-integrated step selection function (ISSF) map for fall (a) and spring (b) pronghorn migration across the NSS, using data from 2004-2010. The ISSF map integrated global third and second-order migration pathway selection models into one map output. Red pixels indicate high probability areas for seasonal migration pathway selection, while blue pixels indicate low probability areas.

(b)


ISSF Map for Spring Migration
N
High : 10
Low : 1
Kilometers
0
50
100
200
300
400

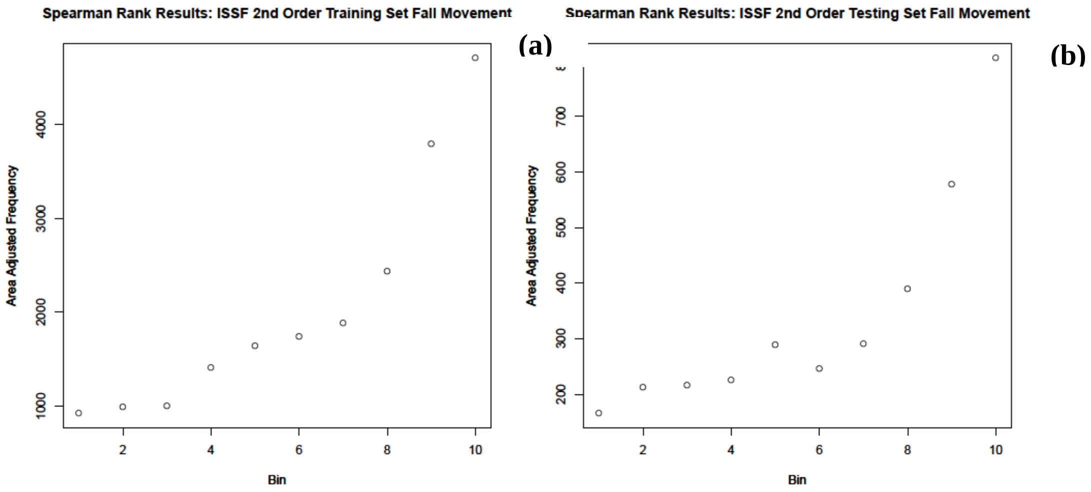


(a) Fall training data ρ = 0.321, *p* = 0.368; (b) Fall testing data ρ = 0.165 *p* = 0.65

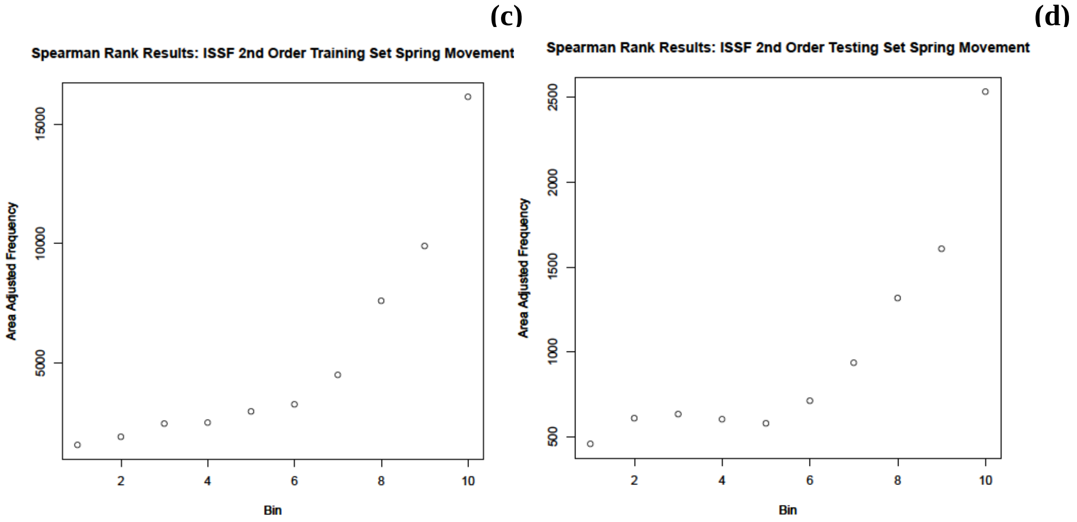


(c) Spring training data ρ = 0.818, *p* = 0.007; (d) Spring testing data ρ = -0.758, *p* = 0.016

Figure 3.12: Spearman rank correlations for third-order fall migratory pathway selection using ISSF maps, for both training and testing data. Graphs (a), (b), (c) indicate poor performance while graph (d) indicates good performance in predicting pronghorn probability of migratory pathway selection at this across the NSS, using data from 2004-2010.



(a) Fall training data ρ = 1, *p* = 2.20E-16; (b) Fall testing data ρ = 0.988 *p* = 2.20E-16



(c) Spring training data ρ = 1, *p* = 2.20E-16; (d) Spring testing data ρ = 0.891, *p* = 0.001

Figure 3:13: Spearman rank correlations for second-order fall migratory pathway selection using ISSF maps, for both training and testing data**.** Graphs (a) – (d) indicate excellent performance in predicting pronghorn probability of migratory pathway selection at this scale across the NSS, using data from 2004-2010.

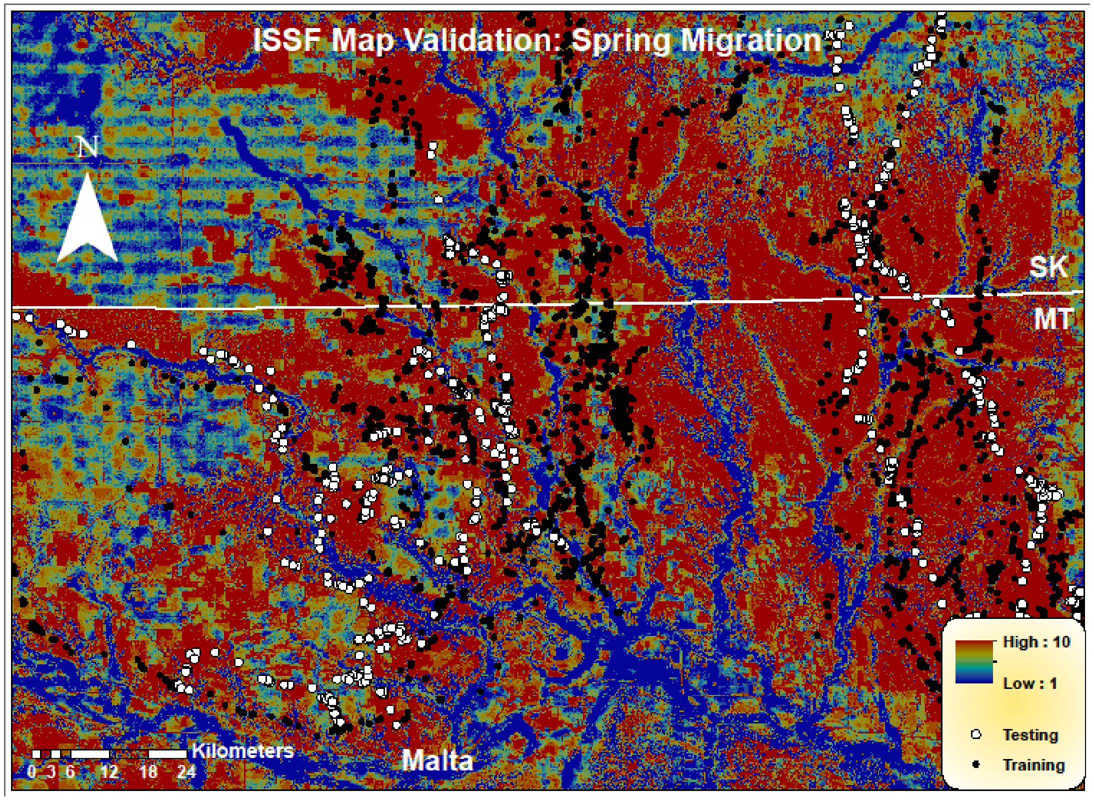


Figure 3.14: A close-up of spring migration pathway selection ISSF map using training and testing data for validation across the NSS, using data from 2004-2010.. Here, third and second-order models were built using training data ($\rho = 1$, $p = <0.01$) and validated using testing data ($\rho = 0.89$, $p = 0.001$). Both training and testing data fit the ISSF map output well, indicating a robust output for predicting spring migration pathways.

CHAPTER 4: CONNECTIVITY OF THE NORTHERN SAGEBRUSH STEPPE FOR PRONGHORN MIGRATION

INTRODUCTION

Recently, there has been increased interest in quantifying species movement among a variety of taxa (Bowlin et al. 2010, Bunnefeld et al. 2011, Hanks et al. 2011). To maintain healthy wildlife populations, species require suitable resources and the ability to move within and between suitable habitats or to completely new habitats (Hobbs 2002, Dingle and Drake 2007, Lowe 2009). Animal movement provides connections between suitable habitats across many spatiotemporal scales, such as daily foraging among patches, annual migrations between seasonal ranges, or dispersal events connecting populations. Migration is one movement type defined as repeated annual movements between discrete areas used at different times of the year (Berger 2004). Because it is a repeated phenomenon, migration can be a useful focus for identifying and maintaining landscape connectivity to sustain healthy wildlife populations. Population dynamics of organisms theoretically depend on the interactions between them and seasonal gradients and events during the annual cycle (Fretwell 1972). Migration allows animals to access critical resources and mitigate unfavorable abiotic and biotic conditions and, so is an important strategy for population persistence (Fryxell and Sinclair 1988, Bolger et al. 2007, Avgar et al. 2014).

Quantitative methods that predict animal migration across large landscapes could be used to identify landscape connectivity patterns for a region. Landscape connectivity is an important ecological process that encompasses structural and functional components (Taylor et al. 2006). Structural connectivity describes the physical relationships among habitat patches, while functional connectivity describes the degree to which landscapes increase movement of genetic, organism or population flows throughout the landscape within a mosaic of habitat types and uses (Chetkiewicz et al. 2006, Hilty et al. 2006, Walpole et al. 2012). The term “migratory connectivity” is a subset of functional connectivity. This term is unique because the spatial scale is typically large and the temporal scale is cross-seasonal, whereas functional connectivity generally occurs at any spatiotemporal scale to promote species-specific propagation (Webster et al. 2002).

One tool used to promote migratory connectivity is to identify corridors, defined as swaths of land supporting passage by wildlife species between two or more areas (Beier et al. 2008). Although debatable, corridors generally provide benefits to ecosystem processes and animals across anthropogenic-affected landscapes, and corridor effectiveness is dependent on width, length, location in the landscape, and prioritization for conservation planning (Beier and Noss 1998, Burgman et al. 2005, Hilty et al. 2006). Falcy and Estades (2007), for example, found that when seasonal patch size was small, corridors increased average population size more than patch enlargement. They reasoned that without opportunities to move between suitable patches, already limited populations will continue to decline over time from hampered gene flow.

Landscape ecology concepts provide a foundation for understanding habitat availability and use during animal migration. Large herbivore populations, for instance, require an abundance of quality forage to satisfy annual life-history requirements (Fryxell and Sinclair 1988, Hebblewhite et al. 2008, Mueller et al. 2011). Nutritional values of plants are spatiotemporally variable, dependent on changing climatic conditions, latitude and altitude (Van Soest 1994), and therefore, large herbivores must have adequate opportunity to move across the landscape to obtain these resources.

Foreman (1995) offered three attributes that make up a given landscape: the patch or node of suitable habitat, the corridor that connects patches, and the background matrix of remaining habitat. A fourth attribute, buffers that surround patches/nodes, provides habitat of decreased wildlife value that afford a gradual transition from patch to matrix (Hobbs 2002). Absent from Foreman’s landscape representation is the acknowledgement that the background matrix is not completely unsuitable as habitat or for movement of wildlife (Hilty et al. 2006). Organisms may perceive the landscape in terms of gradients of differential quality or risks with respect to ecological requirements, allowing for the consideration of use throughout the landscape in terms of resistance to movement (Hebblewhite and Merrill 2007, Cushman et al. 2009). Background matrix habitat may offer some available resources for use and may be permeable to wildlife movement (Hobbs 2002, Taylor et al. 2006).

Large vagile species such as ungulates are able to traverse a continuum of background matrix habitat varying in quality (Laszczak et al. 2010). Connectivity is paramount for ungulates so that they can track spatiotemporal shifts in habitat, adapt to anthropogenic influences and persist in altered landscapes that may become more suitable for colonization over time (Hilty et al. 2006). Subsequently, these species may need corridors crossing human-made barriers or filters to sustain connectivity across fragmented landscapes (Beier and Noss 1998, Hilty et al. 2006). In general, natural landscapes are more connected than landscapes with anthropogenic development in place. Providing corridors that circumnavigate or traverse through developments is one strategy to mitigate reduced connectivity (Noss 1987).

Regions and landscapes found within regions are human-defined terms that consider wildlife use at different operating scales for conservation opportunities (Foreman 1995). Wildlife scales of selection can be defined by elements that influence resources spatiotemporally, namely biotic (flora, fauna), abiotic (climate, soil) and human (cultural, economic) factors. Species select resource and movement attributes differently at various scales, making it difficult to determine which scales are best for wildlife management across a system (Burgman et al. 2005). However, broad-scale processes affect local-scale phenomena expressed in hierarchically nested selection (Hilty et al. 2006, Meyer and Thuiller 2006, DeCesare et al. 2012). Therefore, functionally meaningful corridors that provide continued animal movements must first be addressed at broad scales. Accordingly, managing for corridors at broad scales can incorporate influences of multiple ecological and anthropogenic factors on movement pathway selection (Webster et al. 2002, Hilty et al. 2006, Cushman et al. 2009).

Cost-selection modeling methods such as least-cost pathways (LCP) analysis and circuit theory are commonly used for calculating and mapping wildlife connectivity across broad scales (Beier et al. 2008, McRae et al. 2008*a*, Laszczak et al. 2010, Poor et al. 2012, Thurfjell et al. 2014). The cost distance between a source and a destination (both are required inputs) is defined as the accumulated cost of traveling the simplest path between the two locations and can be calculated in geographical information system (GIS) packages (Richard and Armstrong 2010). Cost distance however, should be measured not only between source and destination habitats but also within large areas of source or destination habitat to further define connectivity (Beier et al. 2011). Cost distance is a more realistic measure than Euclidean distance because it additively weighs each pixel on a background cost surface based on its predicted movement resistance. Conceptually, cost distance discriminates between areas that are more or less difficult to move through based on movement modeling results for a species (Richard and Armstrong 2010). Combining resource selection function (RSF) model outputs and step-selection function (SSF) model outputs into connectivity cost surfaces provides a quantifiable and repeatable method to apply cost distance analysis towards the identification of corridors for conservation (Beier et al. 2008, Chetkiewicz and Boyce 2009, Squires et al. 2013, Thurfjell et al. 2014). A further improvement on this approach would acknowledge and account for the multi-scale nature of animal-habitat relationships, particularly with regards to animal movement. Recently, the program "Linkage Mapper" (McRae and Kavanagh 2011) has been used to identify connectivity throughout regional networks (Carroll et al. 2012). This program includes several toolsets, one of which called "Pinchpoint Mapper" (McRae 2012*a*) hybridizes identified LCPs with circuit theory, using the program Circuitscape (McRae et al. 2008*a*) to prioritize corridors in an effort to maintain connectivity throughout the network. These corridors may not be topographically evident areas or natural passageways; instead, they may occur where land-use changes funnel individuals into a specific area (Taylor et al. 2006). Here, I combine newly developed methods merging cost distance analysis and circuit theory (McRae et al. 2008*b*) with multi-scale, movement-based cost surfaces (Chapter 3) to study connectivity and prioritize corridors for pronghorn in a region of conservation concern. This approach is founded in the application of multi-scale modeling of migration movements for understanding and mapping broad-scale patterns of functional connectivity.

Individuals may select for high-quality microhabitats that appear less suitable using coarse grain map outputs (Sawyer et al. 2011). Inversely, individuals often avoid low quality habitat within largely suitable areas. I attempt to account for scale discrepancies such as these by using integrated mapping techniques, outlined in Chapter 3. The resulting maps considered multi-scalar selection and were used as the background cost surface to account for migratory pathway selection variability between scales.

Human activities and their footprints have expanded worldwide over the past two centuries, and their impacts on wildlife have been well noted (Johnson et al. 2005, Sawyer et al. 2006, Copeland et al. 2009, Dunkin et al. 2009). These footprints increase to keep pace with human demands for economic and social stability and growth (Handley et al. 1998, Polasky et al. 2005). Policies to moderate human-based cumulative effects have been formulated in various regions with varying degrees of success (Duinker and Greig 2006, Kiesecker et al. 2010). Naturally, resources utilized by wildlife may be heterogeneously distributed throughout a region (Owen-Smith 2004). In landscapes dominated by human development (i.e. agricultural landscapes), in contrast, wildlife-dependent resources are more patchily distributed (Opdam et al. 2003, Brennan and Kuvelsky 2005, Polasky et al. 2005, Samways et al. 2010). Human cultures recognize that conservation of wildlife, particularly large mammals, is important for regional identity, economic benefits and food subsistence (Handley et al. 1998). Yet humans may be the primary cause for the many hardships that wildlife face regionally (Hobbs et al. 2008). Efforts to provide regional designs can mutually benefit wildlife and humans (Opdam et al. 2003). Regional planners must first demonstrate that approaches based on ecological principles will additionally provide benefits to humans before policy decisions and on-the-ground implementation can begin.

Here I use landscape ecology principles and hierarchical theory to create cost-modeling connectivity outputs intended for use in a regional network design across the NSS for pronghorn (*Antilocapra americana*), North America's only extant endemic ungulate (White et al. 2007). Landscape planning initiatives should account for multi-species use at multiple scales and so identifying surrogate species that most accurately represent various scales of wildlife selection is a crucial first step towards conservation planning (Cabeza 2003, Hilty et al. 2006). Pronghorn interact with environmental gradients and anthropogenic influences at multiple scales and could serve as a surrogate for the requirements of other species across the NSS.

In this chapter, I considered migratory connectivity as a focus for regional corridor management. I selected pronghorn, a large, common and mobile species that may offer insights to regional connectivity needs (Lambeck 1997, Gaston and Fuller 2008), and then evaluated migration requirements at multiple scales to prioritize corridors that address functional connectivity (Chetkiewicz et al. 2006). Two scales of migratory pathway selection (second and third order), were used to define a connectivity network across a region and resulting maps can be used to support planning to sustain healthy regional populations (Beier et al. 2011). Using the multi-scale migratory pathway selection results from Chapter 3 to identify broad-scale connectivity compared migration requirements effectively, and further distinguished these from habitat requirements to address wildlife's universal movement demands. The pronghorn was a useful species for identifying connectivity through the Northern Sagebrush Steppe (NSS), which is the northern extent of the species' range. Wildlife populations at the periphery of their range may be more isolated and sporadically distributed, and consequently, can be supported through conserving functional connectivity (Walpole et al. 2012). In Chapters 2 and 3, I reported that pronghorn are fairly ubiquitous across the NSS, populations are partially migratory and they respond to environmental and anthropogenic factors differently at various spatiotemporal scales.

In this chapter, my objectives were to apply Chapter 2 and 3 multi-scalar results to synthesize a pronghorn connectivity network for use in regional planning. I first identified and validated LCPs within and between pronghorn habitat patches for seasonal migratory periods, using a novel approach. I then identified appropriate seasonal corridor widths by prioritizing efficient geographical areas that retain high proportions of pronghorn migration point locations. Next, I prioritized corridors within and between habitat patches that are most likely to maintain functional connectivity (Beier et al. 2008, Beier et al. 2011). I propose how results of this chapter serve as a pronghorn connectivity network and how other species may benefit from a design based on migration connectivity. Finally, I discuss how the methods presented here provide a repeatable method for modeling hierarchically nested scales of movement selection.

METHODS

Least-cost Pathway Analysis

The study area, capture, and data collection methods were described previously in chapter 2. I used multiple layers created in ArcMap 10.1 (ESRI 2012) to analyze LCPs for pronghorn connectivity. The NSS is the northern extent of grasslands of the Northern Great Plains and encompasses 315,876 km^2 of prairie/sagebrush steppe in Alberta, Saskatchewan and Northern Montana (Figure 4.1). There are a number of methods available to researchers to address regional connectivity (http://www.conservationcorridor.org/). I selected the Linkage Mapper toolkit because it integrates LCP and Circuitscape tools for use in ArcMap 10.1 toolboxes and allows flexibility in selecting appropriate corridor widths and prioritizes connections for defining a network (McRae and Kavanagh 2011, McRae 2012*a*).

To design pronghorn connectivity networks, I first created a background cost surface based on a number of factors considered relevant to connectivity for this species. Previous studies have used predictive maps based on seasonal habitat selection models as background cost surfaces (Chetkiewicz and Boyce 2009). Instead, I used multi-scale migratory pathway modeling to predict cost-surfaces most relevant for characterizing region-level connectivity. In previous work, I first categorized migration data into fall (*n*=70) and spring (*n*=94) migration movements (see Chapter 2 for an overview), and then reclassified multi-scale integrated step-selection function (ISSF) map outputs for seasonal migratory pathways across the NSS (Chapter 3). I reclassified ISSF maps into cost surfaces by inversing the rankings of equal area prediction categories (1-10) such that the highest migratory prediction category would have the lowest resistance and vice versa (Figure 4.2 a-b). Importantly, this approach nests multi-scale migration requirements to assess broad-scaled connectivity. This ensures that the broad-scale ecological process behind the phenomenon of connectivity is used to predict underlying landscape resistance.

I next defined habitat patches for connectivity evaluation. Both LCP and Circuitscape programs require beginning and end terminals to evaluate cost distance. Because suitable habitat patches that varied in size were distributed across the landscape, an objective method was required to evaluate broad-scale connectivity between patches. Thus, I evaluated LCPs between and within suitable habitat patches because of abundance and large size of potential patches. Assessing connectivity within habitat patches is important, especially when mapping at broad scales (Beier et al. 2011). In addition, thoughtful consideration of connectivity within suitable patches reduces bias from computer programs arbitrarily selecting solitary beginning and end terminals either along or within the boundaries of habitat patches (Parks et al. 2013, Squires et al. 2013). Using the NSS 30 m^2 landcover map, I reclassified landcover types into either a non-native/forested habitat category or native grassland/shrubland category. Across the NSS, pronghorn most strongly select for grasslands during seasonal migration at broad scales (Chapter 3). I then used mean annual home range size (summer and winter ranges), that was calculated by Suitor (2011) for pronghorn in Alberta and Saskatchewan, to serve as a proxy for mean annual home range size across the NSS. Suitor (2011) calculated mean summer range area for pronghorn as 58.4 km^2 and mean winter range as 137.3 km^2, for a total of 195.7 km^2. I used this mean annual home range size as a cutoff area where any native habitat patch ≥ 195.7 km^2 met the minimum size criterion to be considered suitable habitat for subsequent analysis. I found the area of each native habitat patch using Spatial Statistic Tools in ArcMap 10.1. This resulted in 47 polygons (or habitat patches) totaling 62,437 km^2 of native grassland/shrubland habitat. I then created 1000 randomly distributed points within native habitat patches to provide ample coverage throughout polygons and to serve as beginning and end terminals (used as "core areas" in Linkage Mapper literature) for LCP analysis within and between habitat patches (Figure 4.3).

Next, I used tools provided within the Linkage Mapper toolkit (McRae and Kavanagh 2011) to build networks, map and prioritize LCPs throughout the NSS. The Linkage Mapper toolkit provides researchers a suite of options to specify desired outputs. In the Linkage Mapper toolkit, the main tool inputs include "core areas" and "resistance raster." The ISSF raster output for either fall or spring migratory pathways was used as the resistance raster, and core areas were represented by the 1000 random points created within native grassland/shrubland habitat patches. Next in the command window are a series of five processing steps for consideration, which I selected all of except for Step 4 "Prune network." Finally, I did not select any of the additional options available. During processing, adjacent core areas are identified, networks between adjacent core areas are built and Euclidean distances measured. The program then calculates cost-weighted distances and LCPs for each connection between core areas. Finally, it calculates and aggregates LCPs into a single connectivity raster across the NSS for both fall and spring migratory periods.

Least-cost Pathway Validation

I used methods outlined in Driezen et al. (2007) to validate LCPs with actual telemetry data. Results of this approach indicate whether individuals select better routes, measured by resistance cost, than expected by chance alone. Driezen et al. (2007) used straight-line distances between the starting telemetry point and each subsequent telemetry point of hedgehog (*Erinaceus europaeus*) dispersal movements to create corresponding buffers, using each distance as the subsequent buffer's radius. However, because pronghorn are such a vagile species and the size of the area in my project was considerable, I utilized each individual's maximum step length to create corresponding buffers using this length as the subsequent buffer's radius. Each seasonal period, either spring or fall, was considered a separate "population." Then, the mean connectivity predicted value and standard deviation for each buffer was calculated using the "isectpolyrast" command in Geospatial Modelling Environment (GME) (Beyer www.spatialecology.com/gme). I intersected all pronghorn GPS locations for an individual with the connectivity raster using the "isectpntrast" command in GME to obtain a connectivity value for each point.

The normalized z-score was calculated for each case point by taking the resistance cost per point, subtracting it from the mean resistance cost of the corresponding buffer and dividing this result by the standard deviation of the resistance cost of the corresponding buffer. A negative z-score indicates that a pronghorn GPS location is at a lower resistance cost than the corresponding buffer. A negative z-score indicates the pronghorn GPS location is located on a better than random location in terms of cost value, where a positive value describes the opposite. I estimated the population average z-score using an intercept-only mixed-effects regression model of the pooled set of all z-scores and random intercepts for each individual. The overall fixed intercept of this model represented the population-level average z-score while accounting for variable sample sizes among individuals. I set profile confidence intervals at 95% to assure the two-tailed 2.5% lower and upper confidence intervals were negative. If z-score confidence intervals were different from zero and negative, I could infer that across the NSS, individuals selected better routes for each seasonal resistance cost layer than expected by chance alone (Driezen et al. 2007).

Corridor Width Selection

Once seasonal connectivity rasters were validated, I designated an appropriate corridor width for each migration season. To define seasonal corridor widths, I first created a minimum convex polygon (MCP) encompassing the population's overall movements during both migratory periods. Compared to the entire NSS area of 315,876 km^2, the MCP total area was 178,438 km^2. I used the MCP area instead of the NSS area because it provided a more accurate account of marked pronghorn use across the region. Following the techniques of Poor et al. (2012), I truncated seasonal connectivity rasters to create 16 corridor widths using utilities tools in Linkage Mapper Toolkit (McRae and Kavanagh 2011). The corridor widths included: the full NSS, 200 km, 100 km, 50 km, 25 km, 20 km, 15 km, 10 km, 5 km, 3 km, 2 km, 1 km, 500 m, 300 m, 200 m, and 100 m. Next, I calculated the percent area of each corridor width related to the width across the entire MCP, using tools in ArcMap. I then intersected each migratory season's case points to each corridor width using the "isectpntrast" command in GME. The number of case points was totaled for each truncated corridor raster to calculate the percentage of case points within each corridor truncation compared to each original seasonal connectivity raster. For each truncation, I found the percent difference between corridor area and migratory use (measured by location points) during fall and spring. The corridor truncation with the greatest difference was defined to be the optimal corridor width to design a connectivity network because it accounts for the greatest percentage of pronghorn locations within the smallest area possible.

Prioritizing Corridors

To prioritize seasonal connectivity across the NSS, I used the Pinchpoint Mapper tool in Linkage Mapper Toolkit, using previously identified LCP corridors at the appropriate width (McRae 2012*a*). The Pinchpoint Mapper tool hybridizes least-cost corridor with circuit theory, using Circuitscape (McRae et al. 2008*a*). As a result, the tool identifies the most efficient LCPs and critical pinch points (i.e. corridors between suitable habitats) by constraining current flow to the identified best corridors. The Pinchpoint Mapper tool has command-window-based options from which the user can select. Required inputs into the command window include core areas (i.e. 1000 random points), resistance raster (seasonal ISSF raster), and a cost-weighted corridor width (optimal seasonal corridor widths). I squared values from the original resistance raster to provide increased differentiation of results because values were categorized from 1-10. I set the "Calculate raster centrality using Circuitscape" option using the "All-to-one" mode. The result depicts current running through all core areas as a network from an identified central core area. This is an appropriate approach because the resulting layer displays areas that have high current flow centrality, indicating their importance in keeping the entire network connected (McRae et al. 2008*b*, Carroll et al. 2012).

RESULTS

Least-cost Pathway Analysis

Approximately 25% of identified grassland/shrubland habitat patches were in areas where no marked pronghorn locations were recorded. In addition, two of the identified suitable habitat patches (one in the most western area of the NSS in AB and the other in the most northeastern area of the NSS in SK) were in areas where pronghorn no longer occur or have yet to be observed, presumably because these patches are isolated by large parcels of matrix habitat. I estimated LCPs between each pair of random points. For spring, results identified 3,419 adjacent pairs, and after censoring procedures, 3,365 corridor linkages across the NSS were discerned (Figure 4.4a). For fall, 3,401 adjacent pairs were identified, and after censoring, 3,354 corridor linkages were processed (Figure 4.4b). Overall inspection of fall and spring general LCP map outputs at this broad scale were difficult to interpret and imply that the majority of the NSS is relatively similar with respect to a lack of migration resistance.

Least-cost Pathway Validation

Seventy individual migrations were analyzed separately during fall using a total of 4,965 pronghorn GPS locations (Figure 4.5a). Ninety-four individual migrations were analyzed separately during spring using 12,581 pronghorn GPS locations (Figure 4.5b). In the fall, individual z-scores ranged from -1.712 to 4.560 where 62% of the case points had negative values. In the spring, individual z-scores ranged from -1.68 to 6.31, where 70% of case points had negative values. Using mixed-effect regression to account for repeated measures per pronghorn, the estimated population-level mean z-score and 95% profile confidence were -0.084 (-0.013 and -0.155) during fall migration. During spring, the estimated population-level mean z-score and 95% profile confidence interval were -0.153 (-0.243 and -0.126). These results support the inference that during fall and spring migration, pronghorn moved through significantly lower resistance areas as predicted by the multi-scale, migration-based cost surface.

Selecting Corridor Widths

I identified the most appropriate corridor width for pronghorn seasonal migration using a series of corridor truncations. For fall and spring migrations, I found 10 km and 5 km as the appropriate corridor widths, respectively (Figure 4.6 a-b). The next appropriate corridor width during fall was the 5 km truncation with a percent difference of 0.303, while during spring the 3 km truncation was the next plausible corridor width with a percent difference of 0.345. I then truncated both general LCP map outputs by the identified corridor width for fall and spring migration (Appendix 4.1 a-b).

During fall, truncated LCPs appeared to generally follow linear routes between large habitat patches. Although routes appeared to traverse small patches (i.e. ≤ 195.7 km^2) of native habitat, routes largely tended to follow intermediate to large hydrologic features such as streams, creeks and rivers. For example, 10 km LCPs were identified along the Milk River, Sage Creek and Willow Creek in northern Montana during fall. During spring, truncated LCPs appeared either to follow routes where small patches of native habitat occurred between beginning and end terminals, or they followed secondary roads (paved or gravel with low to intermediate traffic volume). These examples were most evident in southern Saskatchewan. Across large native habitat patches in Montana, there were multiple yet isolated 5 km LCPs identified, as exemplified near the towns of Chinook, Harlem, Malta, Saco and Glasgow. The main bisecting feature between large native patches was U.S. Highway 2. Similarly, in southern Alberta two large habitat patches near the town of Medicine Hat were also bisected by a major highway - The Trans-Canada Highway. Here, too, multiple yet isolated 5 km LCPs were identified as connecting the two large habitat patches.

Corridor Prioritization

I prioritized and mapped corridors during both fall and spring between and within native grassland/shrubland habitat patches (Figure 4.7 a-b). The priority corridors between habitat patches for both seasons identified significant connectivity between southeastern AB and the large habitat patch associated with CFB Suffield. These patches are bisected by the Trans-Canada Highway, associated fencing and subdivisions near Medicine Hat, AB. I found that pronghorn avoided urban development during migration (Chapter 3). Similarly while assessing connectivity, I found that priority corridors circumnavigated large urban development. Priority corridors were also identified between the southeast AB native habitat patch to patches in western AB, and southwestern SK, especially corridors to the Great Sand Hills region of SK. In SK, a high priority corridor occurred between native habitat patches from the international border near Montana/North Dakota up through the province to northern habitat patches in AB. Finally in Montana, high priority corridors occurred north of Harlem, MT, between all three jurisdictions, as well as multiple, isolated priority corridors that connected the large habitat patches bisected by the transportation complex of U.S. Highway 2, railroad and fencing. During fall migration only, more importance was given to corridors between habitat patches that followed intermediate to large streams and river valleys.

Determining connectivity pathways within habitat patches during both seasons provided additional insights about pronghorn movement. Independent of migratory season, I found that the southeast AB/southwest SK grassland/shrubland complex was the broadest and most important area for the entire regional pronghorn connectivity network in the NSS. Results of this study identified a major almost linear connection from areas north of Malta and Harlem, MT, to CFB Suffield, north of Medicine Hat, AB. Other priority corridors within large habitat patches occurred in north-central MT, within and surrounding the Great Sand Hills region of SK, and within CFB Suffield in AB. Within CFB Suffield, priority corridors running north-south were identified most notably in less dense well areas, including the wildlife refuge in the southeastern corner of the base. Specifically during fall migration, a more dispersed corridor occurs throughout the NSS. In addition, linear connections that follow hydrologic systems within large habitat patches were evidently priority corridors, including Porcupine Creek, Poplar Creek and Beaver Creek in north-central MT. During spring, pronghorn utilize roadside right-of-ways (ROWs), i.e. areas owned by jurisdictional transportation departments that bisect roads/highways from neighboring landowners, much more frequently than during fall migration, especially in Alberta and Saskatchewan.

Corridors important for pronghorn migration were clearly evident in the connectivity maps. I provided an example to demonstrate the effectiveness of connectivity maps (Figure 4.8). Here, three individuals migrated across the Trans-Canada Highway near the city of Medicine Hat, AB. They were captured in southeastern AB and subsequently undertook spring migration heading north, following corridors within the grassland/shrubland habitat patches illustrated in Figure 4.8. These corridors funneled individuals to adjacent locations along the southern edge of the Trans-Canada Highway where migration was delayed, seemingly by the complex of linear anthropogenic features. All three individuals then selected corridors connecting habitat patches to continue spring migration. Once they crossed the Trans-Canada Highway, they continued migration following high priority corridors within the next northerly habitat patch.

DISCUSSION

Analytical Approaches

Ungulates on seasonal range gain energy by consuming high quantities of vegetation while making small, discrete movements (Parker et al. 2009). Conversely, ungulates moving off seasonal range through dispersal or migration expend considerable energy by continually travelling long distances over extended periods (Fryxell and Sinclair 1988). Consequently, ungulates may select for varying resources at different degrees during specific periods of the annual cycle (i.e. fall migration, spring migration, etc.). I used seasonal multi-scalar integrated resistance layers as the background cost surface for connectivity assessment. Species may select resources at varying magnitudes based on the scale of selection. As others have shown, selection is a hierarchically nested process where an individual’s finer-scale selections are based upon selections at a broader scale (Rettie and Messier 2000, DeCesare et al. 2012). The use of integrated multi-scalar cost surfaces enabled scale-dependent selections to be accounted for in regional connectivity analysis.

Overall, Linkage Mapper proved to be a valuable tool (McRae and Kavanagh 2011, McRae 2012*a*) to identify and prioritize corridors that could sustain connectivity throughout the NSS. The toolset provided the means to hybridize useful components of least-cost modeling and circuit theory to reveal important conservation insights. Additionally, I identified pronghorn connectivity across the NSS using a number of techniques that offer utility for other studies. First, I used migratory pathway selection results to construct connectivity outputs, which effectively allows similar phenomena, i.e. movement, to dictate species connectivity (Squires et al. 2013). As increasing detailed movement data is collected, it may become apparent that species select for varying resources during movement bouts (i.e. migration, dispersal, etc.) versus while on seasonal range.

I chose quantitative methods considering pronghorn movement requirements to identify connectivity within and between habitat patches. Generally, pronghorn selected for native (grasslands, sagebrush) habitats while migrating across the NSS (Chapter 3). I concluded that these habitat types serve as both connectivity and seasonal range habitat (Dirschl 1963, Bayless 1969, Schwartz et al. 1977), and hence have lower resistance to movement than other landcover types. Identifying suitable patches to assess regional connectivity can prove challenging as researchers must prioritize suitable areas to analyze across a matrix of landcover types. I selected mean annual home range size for pronghorn from the region as an objective measure. Often, connectivity modeling efforts identify beginning and terminal patches, dependent in part, on those patches that provide high-levels of management or protection (Beier et al. 2008, Poor et al. 2012). In contrast, using the mean annual home range to quantify suitable habitat patches for modeling considers pronghorn ecological requirements to identify inter-patch connectivity. Consequently, this approach not only indicates areas between well-managed or protected lands as important to maintain connectivity but also indicates areas that are predominantly privately-owned (Parks et al. 2013). In many cost-modeling efforts, connectivity is identified between habitat patches only, while not addressing intra-patch connectivity (Poor et al. 2012, Squires et al. 2013). Intra-patch connectivity is important in spatially large habitat patches because resources within habitat patches that a species selects for or against may channel connections to specific locations along the habitat patch edge (Beier et al. 2011, Parks et al. 2013). Across the NSS, pronghorn habitat patches were large, and thus, I generated a large number of random points within patches to saturate the area and calculate connectivity within and between habitat patches. As a result, connectivity was measured across the NSS using a comprehensive and repeatable approach that is consistent with a species' requirements.

Recently, greater attention has been placed on validating LCP map outputs. In one study, authors inspected a number of LCP studies and found that a minimum of these used validation approaches to finalize map outputs (Sawyer et al. 2011). However, in another study researchers used uncertainty analysis to ascertain model output changes in response to input parameters as an effective validation procedure (Beier et al. 2009). In my research I refined an approach used by Driezen et al. (2007), using maximum step-length distances, to validate LCP outputs using pronghorn telemetry data. Pronghorn are a highly vagile ungulate species which annually ranges over great distances. I therefore used maximum step-length distances to generate pertinent z-scores for each individual which was successful in differentiating use versus available migration steps. There are ample research opportunities, as addressed here, to progress scale appropriate validation procedures that consider the ecology of the species of interest.

Each species has ecological requirements that dictate an optimal corridor width that promotes functional connectivity for the given species. This is a major consideration when constructing landscape connectivity designs (Hilty et al. 2006, Beier et al. 2008). From a management perspective, identifying a corridor width that accounts for the highest percentage of migration relocations within the smallest area possible provides managers and conservationists with a strategy for selecting an ideal corridor width, while allowing flexibility in indicating the appropriate corridor width over time (Poor et al. 2012). Using this approach, I determined the ideal corridor width for each season by creating a series of corridor truncations from the LCP map output and finding the percent difference between percent area and the percent of pronghorn relocations found within that area. Interestingly, three truncations during both fall and spring migrations were identified with a <0.05 difference from an optimum width (Tables 4.1-4.2). In other words, managers do have viable options in selecting the appropriate width per area of interest, based on conservation and management objectives for a given state or province. For example, if natural gas exploration increased, it may require the widening of corridors through management, to safeguard species movement requirements.

Connectivity across the NSS

At a regional scale (i.e. the NSS), I found similar priority corridors between and within habitat patches for fall and spring migrations. I observed that shorter, priority corridors typically occurred where high densities of anthropogenic disturbances bisected habitat patches. For example, for decades wildlife officials have observed pronghorn concentrated in areas surrounding Medicine Hat, AB, during seasonal migrations or during extreme winter conditions (D. Eslinger – personal communication) (Figure 4.8). Results of this study were consistent with this being an important area for sustaining connectivity between large native grassland patches. A conservation planning need is evident in this priority corridor. Potential tools include conservation easements, fence modifications, over-pass structures, or discrete temporal management measures that could mitigate potential barriers to migration (Beckmann et al. 2012, Seidler et al. 2014).

By using randomly placed beginning and end terminals in habitat patches, I was able to identify priority corridors within patches. For example, the area north of Medicine Hat, AB, is the largest un-fragmented tract of grassland in the province, yet holds one of the highest densities of oil and gas wells and pipelines. Results of this study indicate that pronghorn migration is channeled within this large habitat patch in part because of these anthropogenic influences. I noted that at existing densities wells constrained connectivity to corridors with low anthropogenic development, as has been shown for greater sage-grouse, mule deer and pronghorn elsewhere (Aldridge and Boyce 2007, Sawyer et al. 2009, Beckmann et al. 2012).

In general, two main distinctions were evident between fall and spring migration corridor patterns. During fall, pronghorn tended to use corridors that followed large hydrologic systems much more than during spring, e.g. Battle Creek and Sage Creek north of Havre, MT (Figure 4.7a). During fall, pronghorn made rapid migratory movements to find suitable winter range (Chapter 2). Long and wide valleys offer forage communities associated with mesic soil conditions and swaths of sagebrush habitats (*Artemisia cana* north of the Milk River and *Artemisia tridentata* south of the Milk River; Forrest 2004) that are highly selected for as winter range (Dirschl 1963, Barrett 1982, Jacques et al. 2009). The valley slopes are wind-blown and relatively snow-free natural features that are used by pronghorn to sustain rapid movements in anticipation of or in response to winter storms and severe snow conditions.

During spring migration, pronghorn are driven to replenish depleted tissue reserves and support fetal growth demands by electing to forage on high-quality grasses and forbs (Wiseman et al. 2006, Tollefson et al. 2010). Many ROWs provide a concentrated source of high nutrient forage because they are depressions that retain moisture longer than adjacent sites. In Chapter 3, I found the most likely density that pronghorn respond to roads is at 100m, which is generally comparable with ROW widths. Pronghorn may follow ROWs to exploit dense, quality forage resources available there. Results of my research support the inference that alignment of movements with road features may be one reason that corridor widths were narrower during spring than during fall migration (Tables 4.1-4.2).

Identifying seasonal migration connectivity patterns across the NSS highlights important factors for conservation planning to sustain pronghorn migration. In the NSS, as elsewhere, migration connectivity is influenced by temporal changes to climatic conditions and phenology of forage (Hoskinson and

Tester 1980, Beckmann et al. 2012). In Chapter 3, I reported annual variation in snowcover and NDVI values and found that NDVI was a significant factor in explaining spring migration pathways, as well as determining stopover sites. Although migration initiation and timing of was annually variable, movement rates and displacement ratios were not annually influenced (Chapter 2) and so had little determination on the movement pathway itself. In addition, NDVI was one of many factors in modelling and illustrating migratory pathway selection across the NSS. Accordingly, stakeholders should feel confident in using spatial predictions provided here as they integrate a six year average of the overall variation in NDVI. In the NSS, migration connectivity is largely unconstrained by intermountain valleys or dense forests. In general, pronghorn migrate through large grassland complexes rather than agricultural croplands. Factors that likely contribute to this pattern include the nutrient quality of forage found in grasslands and that typically, grasslands are the landcover least fragmented from roads, fences and other anthropogenic features, which pronghorn have been shown to avoid during fall and spring migrations (Chapter 3). As the growing literature indicates, pronghorn migrations can be greatly altered by roads and high densities of anthropogenic use and should be managed to sustain migratory connectivity (Sheldon 2005, Suitor 2011, Beckmann et al. 2012, Seidler et al. 2014).

Based in circuit theory, the Pinchpoint Mapper toolkit calculates connections that are the most important for sustaining a connectivity "circuit" or network based on a central area approach (McRae et al. 2008*b*). Outputs from the central area analysis (measured as "Centrality") define corridors with high current flow, and suggest their importance for sustaining the functionality of a regional network (McRae 2012*a*). The southeast corner of Alberta and southwest corner of Saskatchewan are characterized by large tracts of native grasslands and are centrally important for sustaining connectivity in the NSS. High priority corridors were typically connected to this central area and other large native grassland habitat patches (Figures 4.4 a-b). These critical connections aligned with migration corridors in northern Montana, indicating the importance of transboundary conservation planning (Sodhi et al. 2011). I also identified weaker corridors connecting smaller, isolated satellite habitat patches that currently are not highly managed for in sustaining overall pronghorn population. These habitat patches have become isolated from habitat conversion and fragmentation. Isolated habitat patches decrease connectivity for wildlife and over time, lead to constricted population distributions which ultimately can lead to extirpation. Interestingly, these habitat patches currently hold low numbers of pronghorn (Mitchell 1980, Arsenault 2007). However, these satellite habitat patches provide options in the face of continued incremental anthropogenic development and shifting environmental factors from climate change. In the future, these patches could be crucial for sustaining populations in the region (Webster et al. 2002). If range shifts do occur from changing conditions, the results presented here could assist management efforts in sustaining populations by using present-day low priority corridors between suitable satellite habitat patches that may become highly suitable in the future (Hilty et al. 2006).

Regional Landscape Planning

Lambeck (1997) uses the term focal species to define a collection of species whose functional spatial needs would encompass the needs of other species at a particular scale. Caro and O'Doherty (1999) argued that the best surrogate species are those that can be easily monitored while Gaston and Fuller (2008) suggested that common species are disproportionately significant in determining broad-scale patterns. Because landscapes and regions should be managed using a multi-species approach (Cabeza 2003), the selection of focal species that most appropriately represent hierarchically nested scales and spatial needs of other species is an important early step in regional landscape planning (Opdam et al. 2003). Species movement measures, such as connectivity, can be used to address requirements for other species in regional landscape planning initiatives (Opdam et al. 2003, Hilty et al. 2006). Pronghorn are highly mobile and widely distributed across the NSS and thus represent attributes required of a broad-scale focal species. The pronghorn connectivity networks identified in my study could provide habitat required by other wildlife species. Using a similar hierarchically nested approach to predict other species movements at finer spatiotemporal scales could serve to construct an overarching multi-scale, multi-species NSS regional conservation network design, following suggestions by Opdam et al. (2003) and similar to Cushman et al. (2013) for prairie species.

The connectivity networks generated in this study for pronghorn have design implications for conserving wildlife diversity at the periphery of range for a suite of species. Typically, a species' overall range will expand or contract from the periphery of a contiguous range (Brown 1995). The NSS is the northern limit of the Great Plains region of North America and consequently is at the edge of many grassland/sagebrush species' ranges including pronghorn. In addition to anthropogenic influences and a suite of environmental factors, these animal populations are regulated by extreme climatic conditions (sub-zero temperatures, blowing wind and snow cover, sporadic drought). Pronghorn are highly mobile, and particularly at the periphery of their range long-distance movements are an important adaptation providing opportunities to mitigate extreme conditions. Pronghorn make similar movements at the southern periphery of their range in response to environmental extremes such as extreme heat, low rainfall, drought, etc. (Okenfels et al. 1994). In short, prioritized corridors are vital to species at the periphery of their range because they provide populations a means to cope with extreme and fluctuating conditions (Walpole et al. 2012).

The population at the northern periphery of pronghorn range crosses the international boundary between Canada and the United States. Coordination and cooperation among federal and state/provincial agencies, NGOs, local communities, industry, etc. entities is vitally important for functional landscape connectivity and wildlife populations (Sodhi et al. 2011). Transboundary conservation and management efforts can use connectivity network maps to address conservation and development planning needs of the region (Kiesecker et al. 2010). Pronghorn relocations and explanatory variable data were gathered from both countries, while interested personnel across the region have been kept informed and are engaged, which provides regional buy-in. In this way, similar NSS connectivity efforts for greater sage-grouse (*Centrocercus urophasianus*) could occur. The greater sage-grouse population in the NSS is at the northern periphery of their range, engages in long-distance movements and is susceptible to ongoing anthropogenic development (Aldridge and Boyce 2007, Smith 2013). From a transboundary perspective, interested personnel can initiate conservation and management actions for landscape level planning using one map, potentially for multiple species (Opdam et al. 2003, Johnson et al. 2004, DeCesare et al. 2012). As a result, decision makers may consider focusing efforts on protecting and mitigating movement barriers in priority corridors during seasonal migration (Cushman et al. 2009).

Hierarchically Nested Migratory Pathway Selection

I used a sequential approach to analyze pronghorn migration pathway selection and connectivity across scales. This approach was founded on the concept that selection is hierarchically nested and provides a suitable analytical method for movement modeling (Rettie and Messier 2000, DeCesare et al. 2012). I first modelled fine-scale pronghorn migratory pathway selection using SSFs (Fortin et al. 2005, Forrester et al. 2009). I then modelled broader-scale pronghorn migratory pathway selection by considering the control points at the third-order scale as second-order case points and modelled these against randomly distributed control points across the NSS (DeCesare et al. 2012, Chapter 3). I multiplied map outputs together to create an integrated multi-scalar resistance layer as my background cost surface in modeling migratory connectivity. The resulting connectivity network can be applied at the broadest-scale possible (regional and transboundary) for conservation planning for pronghorn. Effectively, I demonstrated that, as with habitat selection, species select resources during migration at varying magnitudes based on the scale of use (Chetkiewicz and Boyce 2009, Thurfjell et al. 2014). Although this multi-scalar process does not fit as precisely as "orders of scale" used in habitat selection analysis, it provides an approach for considering multi-scalar movements (Johnson 1980, Meyer and Thuiller 2006). Connectivity results can be displayed as one map output, which is important for prioritizing management and conservation opportunities at broad scales (Johnson et al. 2004, DeCesare et al. 2012

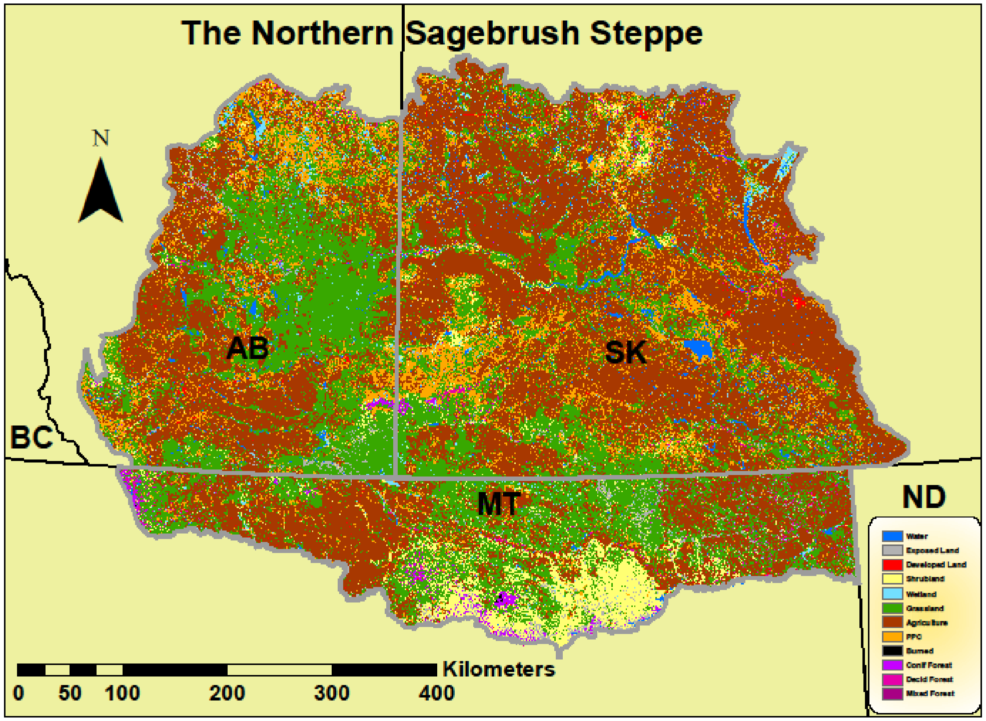


Figure 4.1: The Northern Sagebrush Steppe (NSS) depicting various landcover types. This is the northern extent of contiguous grasslands in the Northern Great Plains Region and coincides with the most northerly distribution of pronghorn in North America where study was conducted using data from 2004-2010.

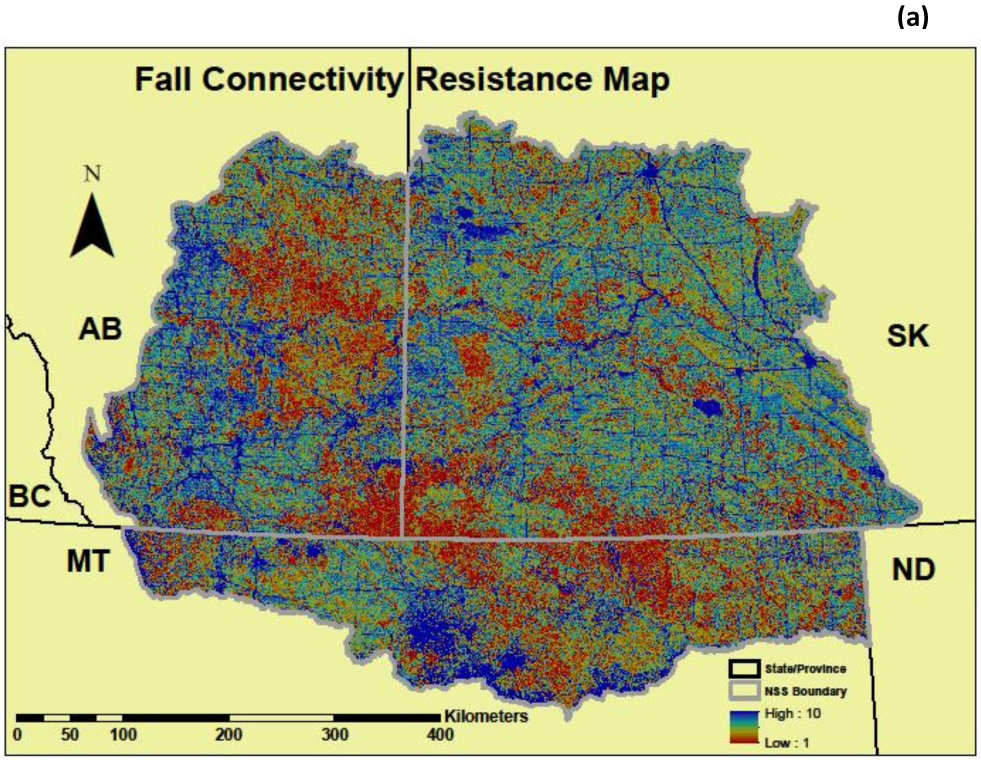
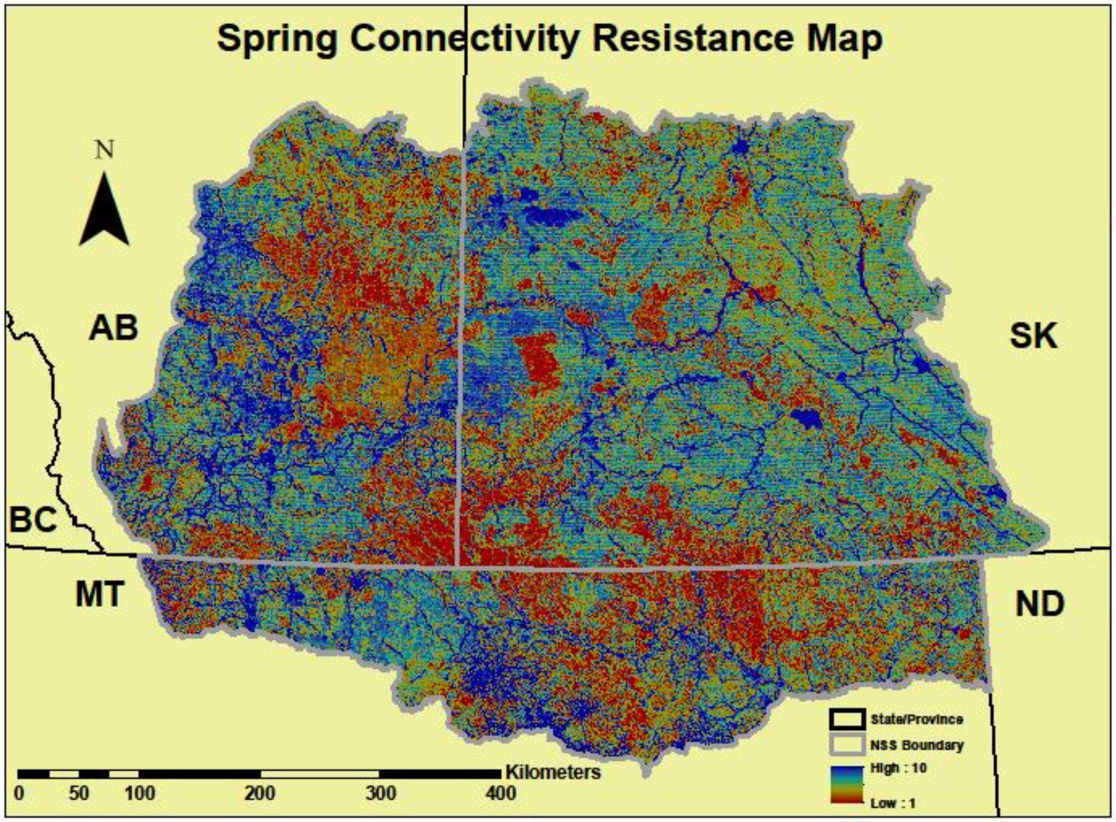


Figure 4.2 (a-b): Northern Sagebrush Steppe fall (a) and spring (b) resistance maps used for modeling pronghorn connectivity across the NSS, using data from 2004-2010. Red pixels indicate low movement resistance (typically native grassland and shrubland) while dark blue pixels indicate high movement resistance. Large rivers, creeks and streams provide less resistance during fall more so than during spring.

(b)


Spring Connectivity Resistance Map
N
AB
SK
BC
MT
ND
State/Province
NSS Boundary
High : 10
Low : 1
0
50
100
200
300
400
Kilometers

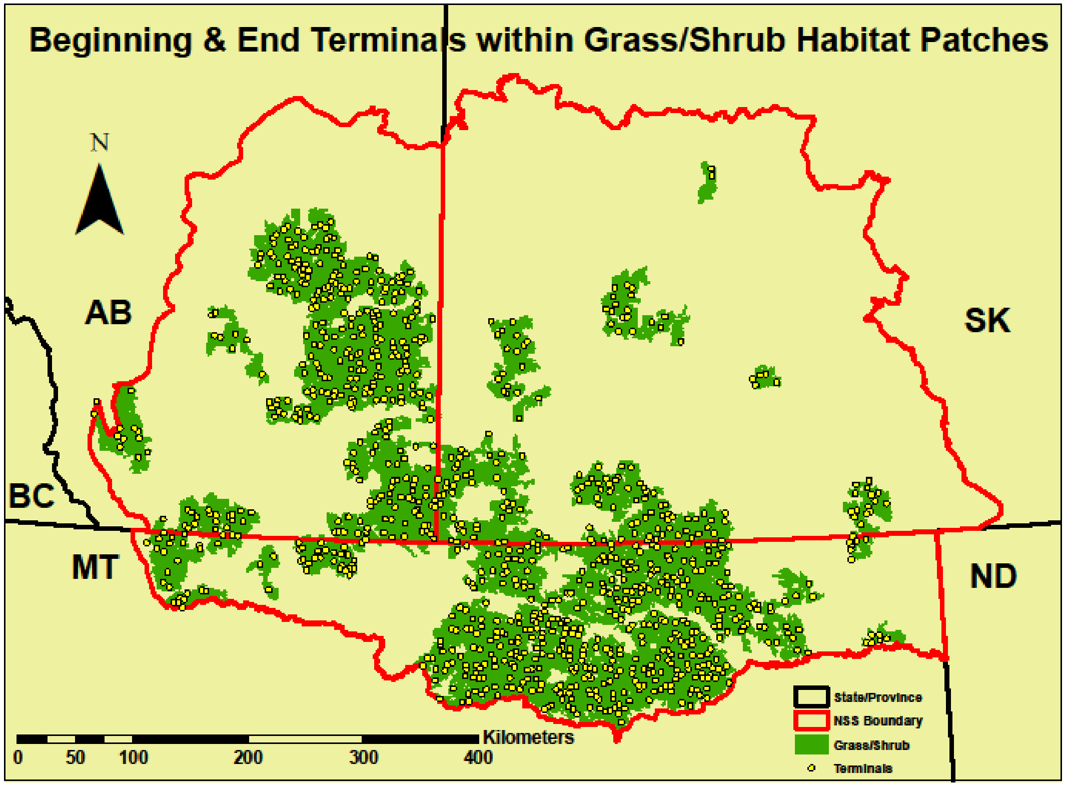


Figure 4.3: Beginning and end terminals (*n* = 1000) used to construct pronghorn least-cost pathways within and between grassland and shrubland habitat patches across the NSS, using data from 2004-2010.

(a)

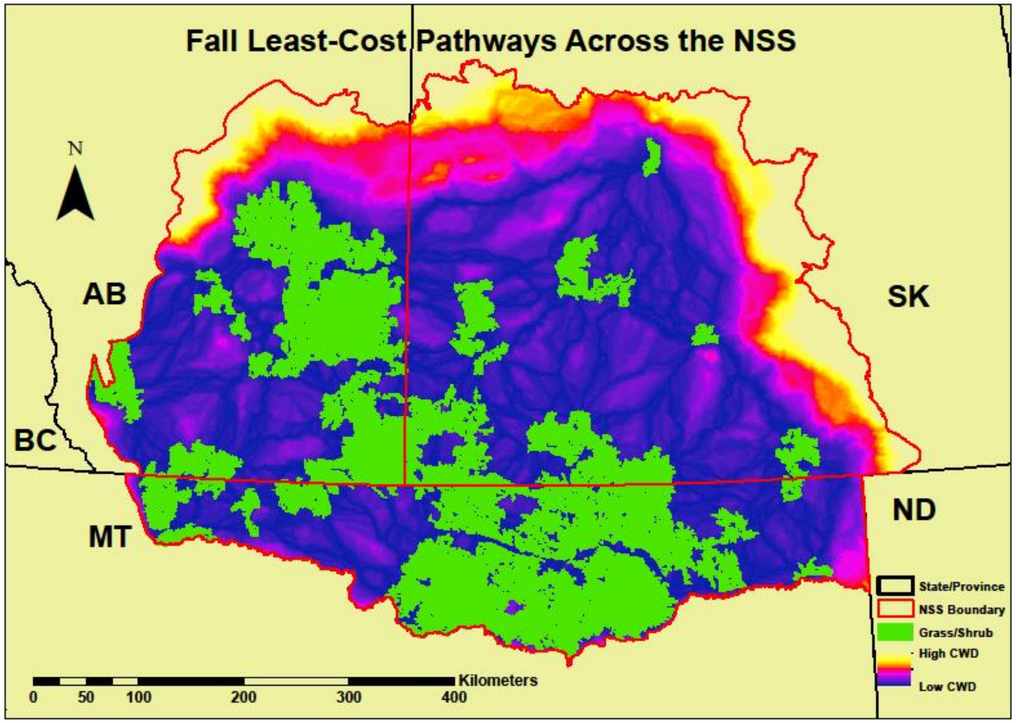
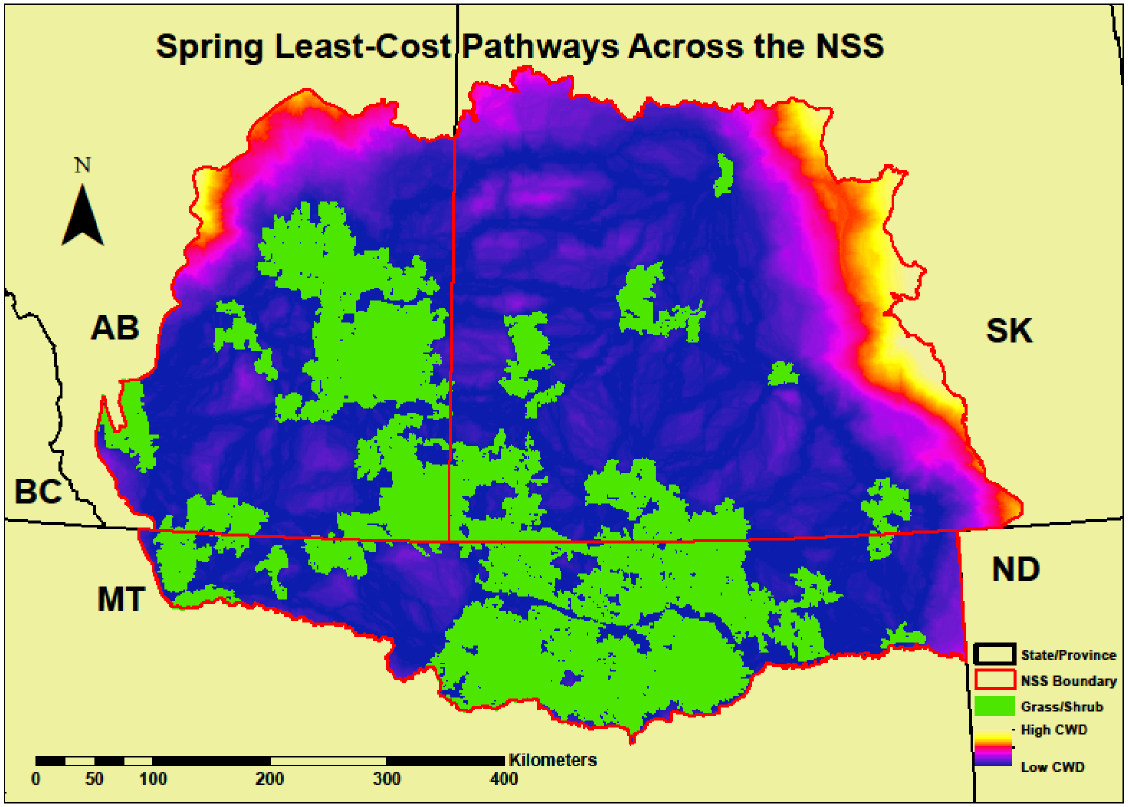


Figure 4.4 (a-b): Fall (a) and spring (b) pronghorn least-cost pathway results across the NSS, using data from 2004-2010. Dark purple indicates pathways with lowest cost-weight distance. Spring least-cost pathways are more regionally dispersed, in particular at the northern boundary of the region.

(b)


Spring Least-Cost Pathways Across the NSS
N
AB
BC
SK
MT
ND
State/Province
NSS Boundary
Grass/Shrub
High CWD
Low CWD
Kilometers
0
50
100
200
300
400

(a)

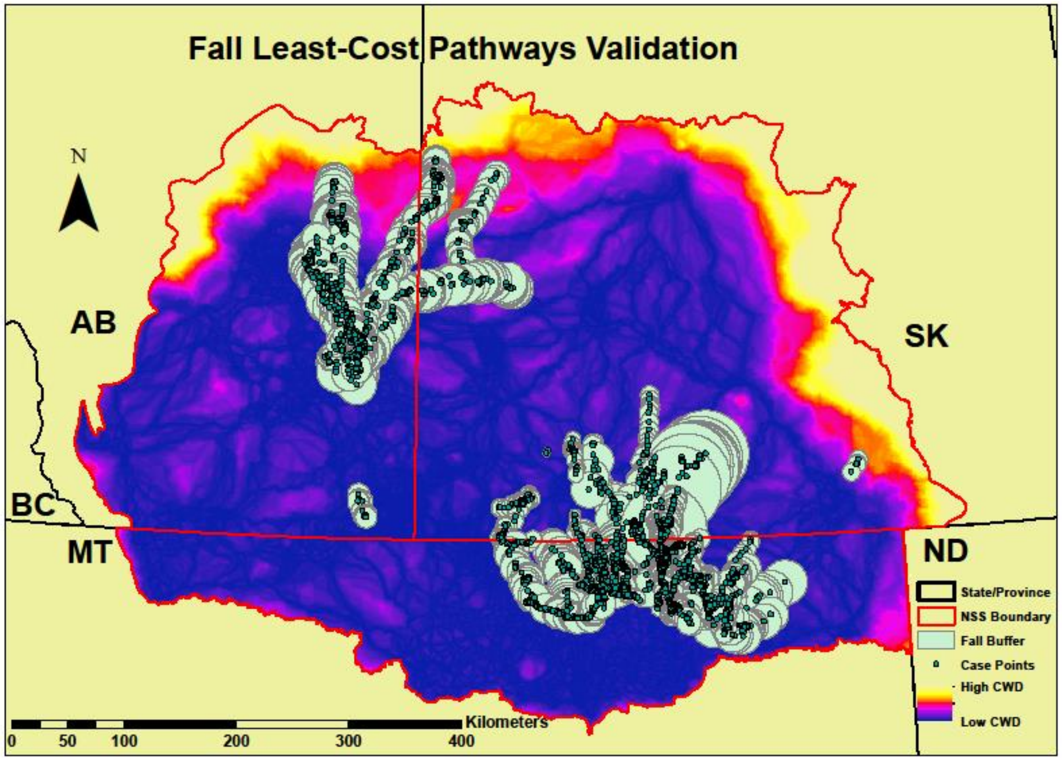
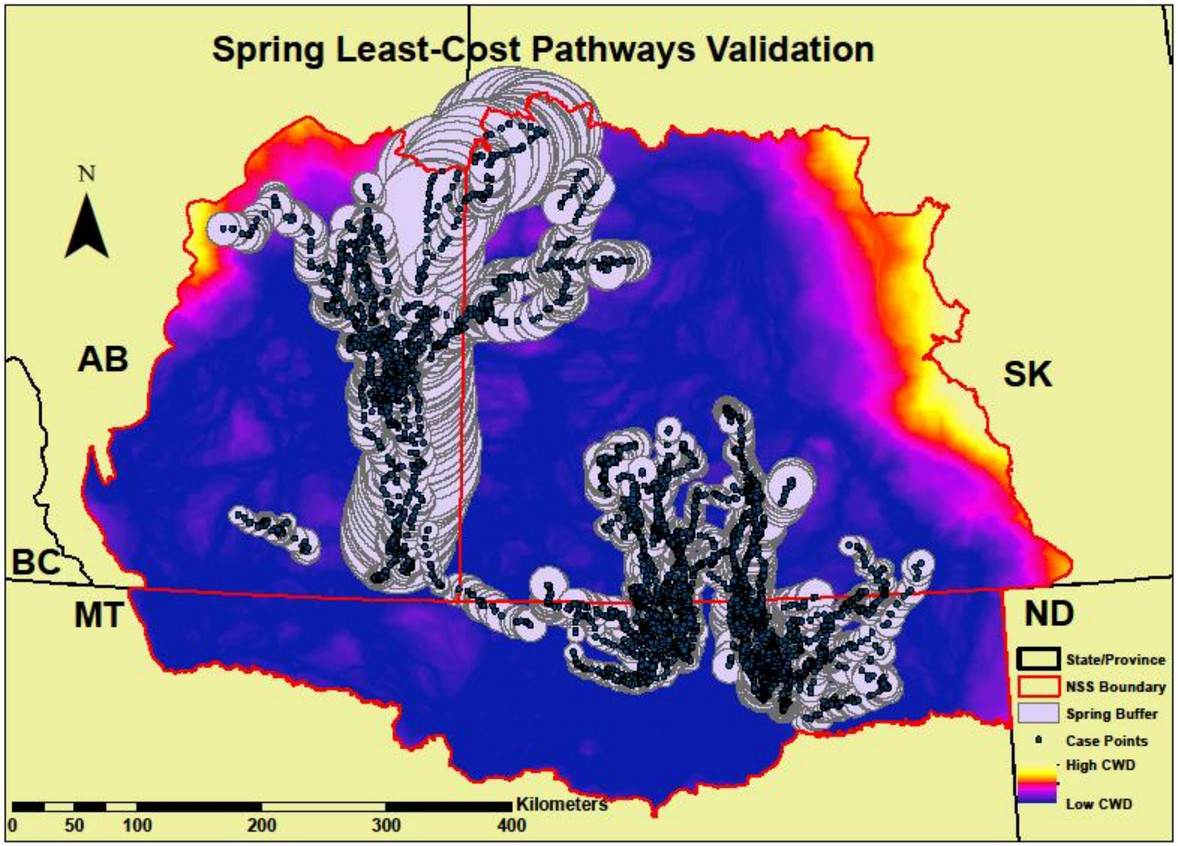


Figure 4.5 (a-b): Fall *n*= 70 (a) and spring *n* = 94 (b) least-cost pathways validation procedures for pronghorn across the NSS, using data from 2004-2010. Each buffer radius is the seasonal maximum step length for each individual. Resistance costs were calculated and compared between pronghorn GPS locations and each corresponding buffer. A negative z-score for the population indicates migratory routes were selected more often than by chance alone.

(b)


Spring Least-Cost Pathways Validation
N
AB
SK
BC
MT
ND
State/Province
NSS Boundary
Spring Buffer
Case Points
High CWD
Low CWD
0
50
100
200
300
400
Kilometers

(a)

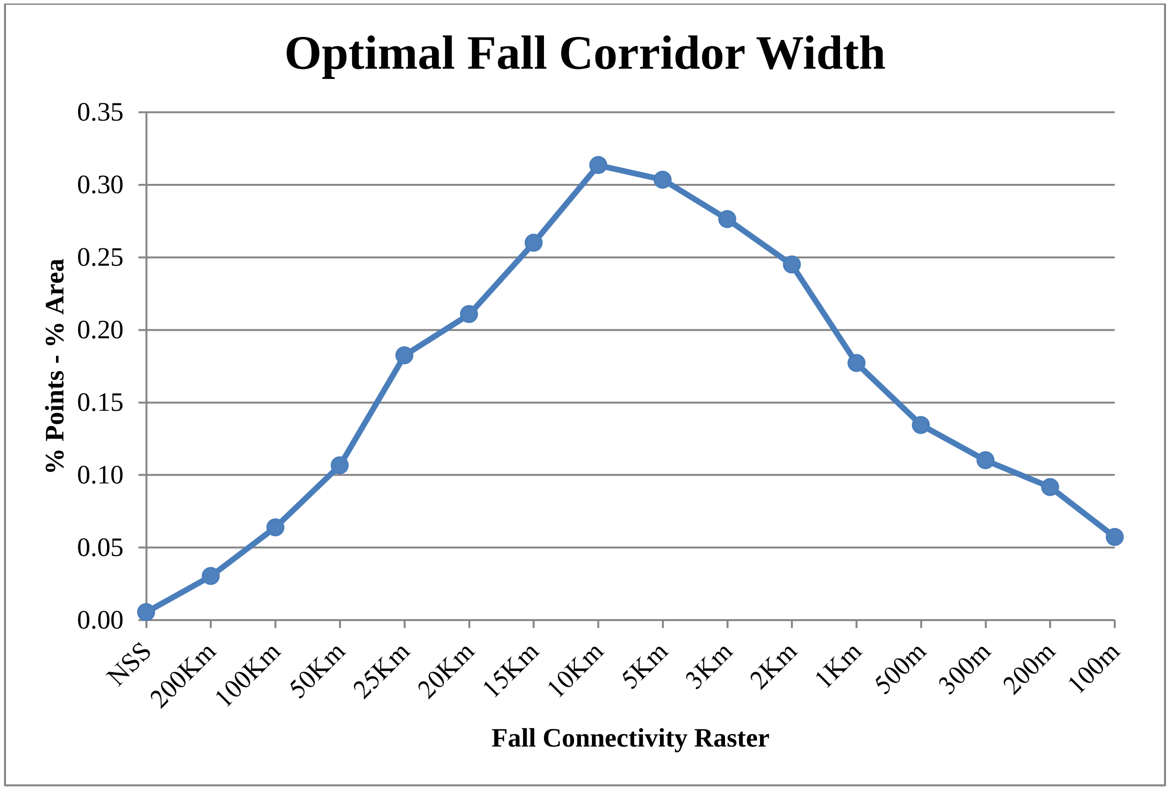
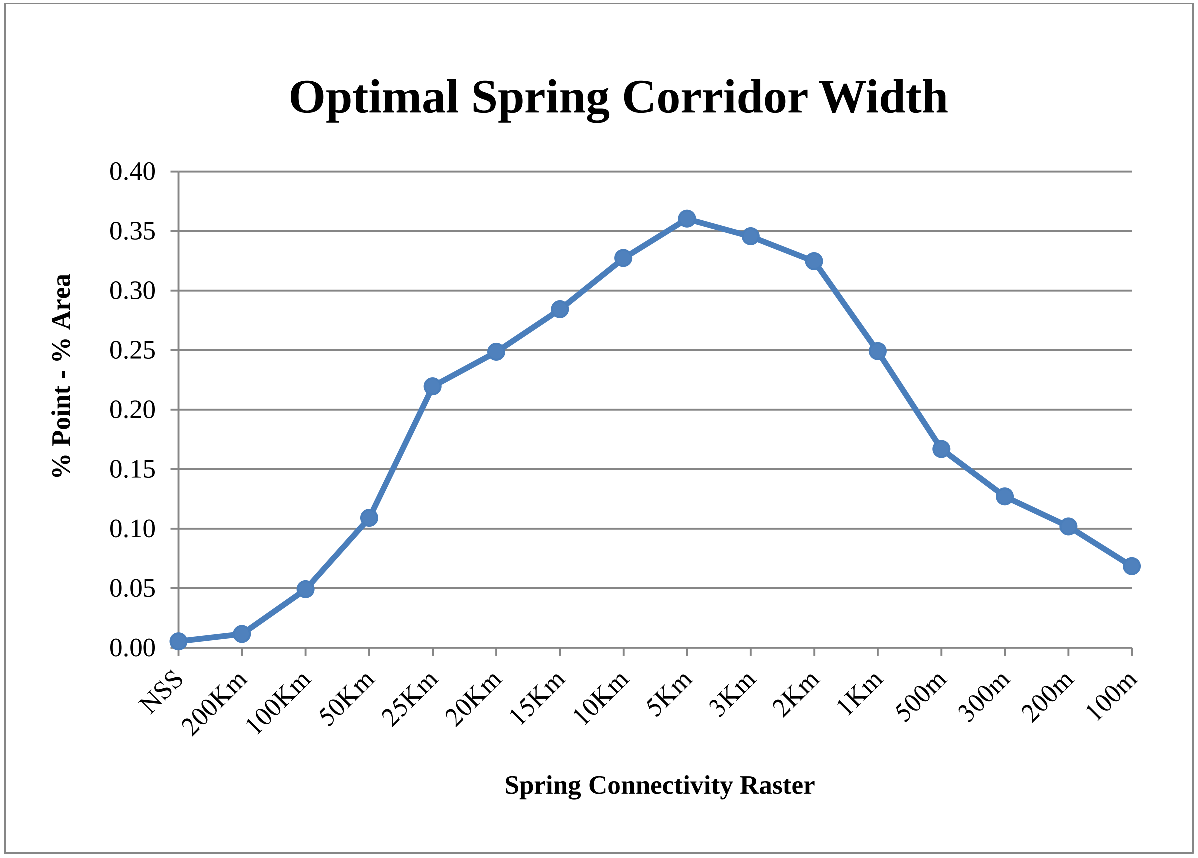


Figure 4.6 a-b: Pronghorn corridor width identification during fall (a) and spring (b) migration calculated from pronghorn GPS locations across the NSS from 2004-2010. The highest difference between percent of GPS locations from percent area indicates the prioritized corridor width. Dependent on jurisdictional requirements, corridor widths are flexible and adaptable for management purposes.

(b)


Optimal Spring Corridor Width
% Point - % Area
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
NSS
200Km
100Km
50Km
25Km
20Km
15Km
10Km
5Km
3Km
2Km
1Km
500m
300m
200m
100m
Spring Connectivity Raster

(a)

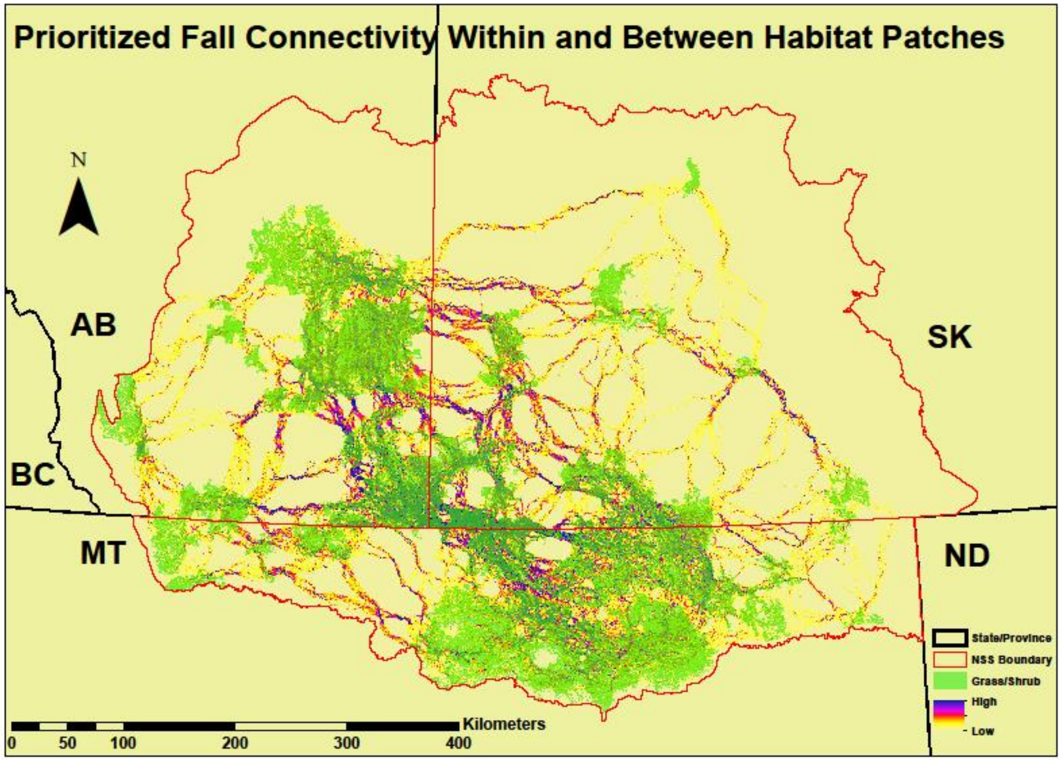
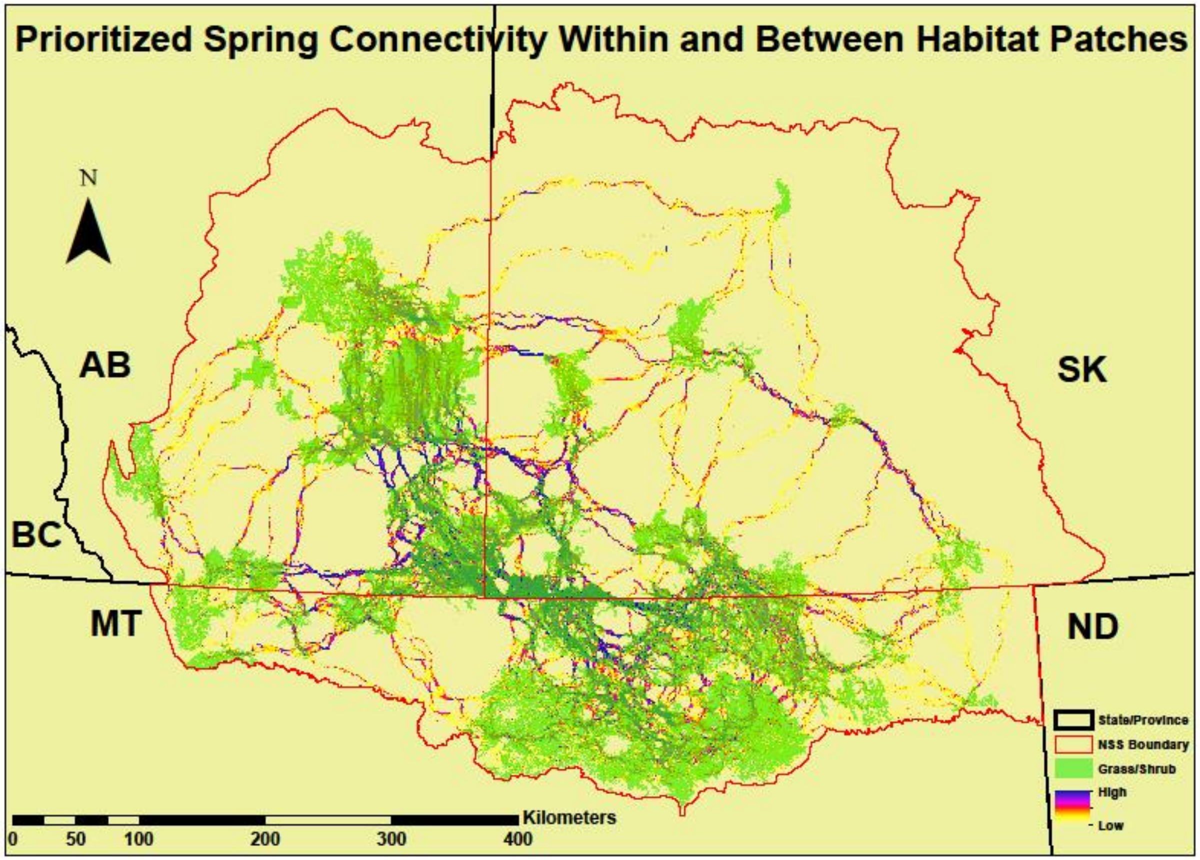


Figure 4.7 (a-b): Prioritized 10 km-wide fall (a) and 5 km-wide spring (b) pronghorn connectivity networks within and between native grassland and shrubland habitat patches, indicated in green across the NSS, using data from 2004-2010. Dark purple connections are priority corridors between patches while dark green areas are priority corridors within patches. The most important area for connectivity was identified as the corner of SE Alberta – SW Saskatchewan.

(b)


Prioritized Spring Connectivity Within and Between Habitat Patches
N
AB
SK
BC
MT
ND
State/Province
NSS Boundary
Grass/Shrub
High
Low
Kilometers
0
50
100
200
300
400

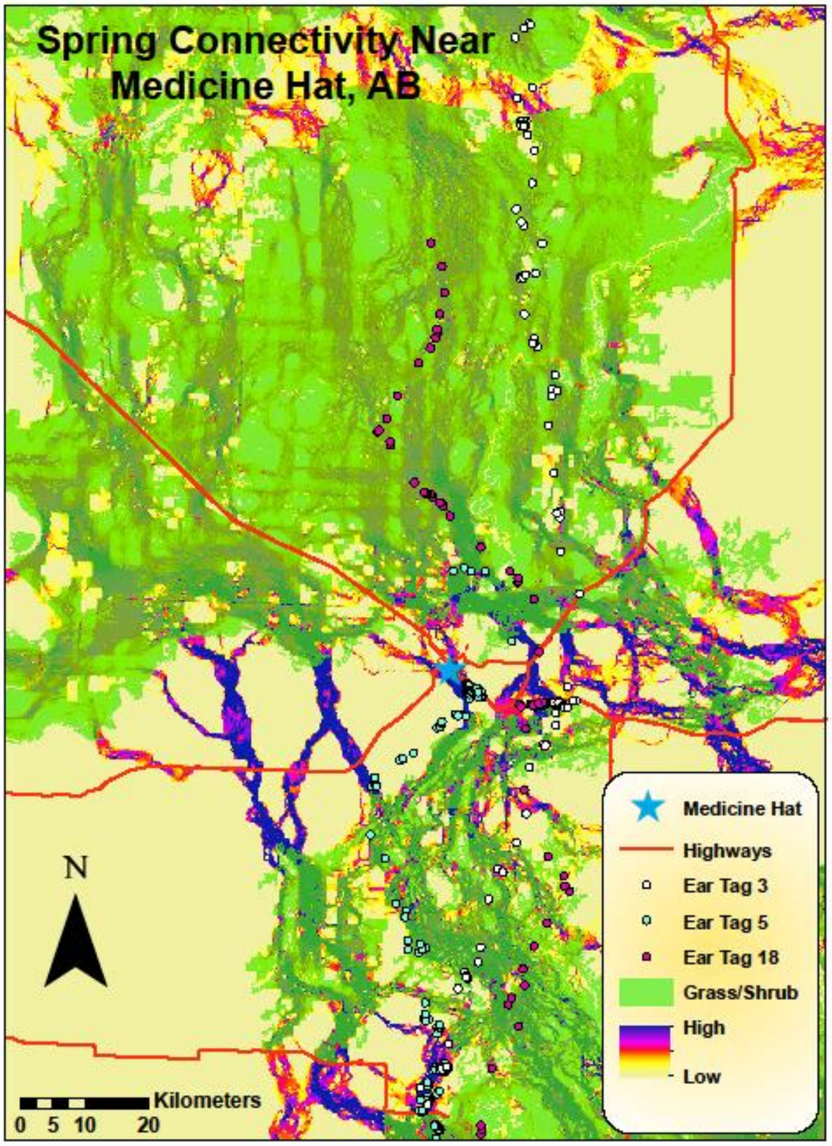


Figure 4.8: Close-up example of spring pronghorn connectivity results against spring migratory locations of three individuals from across the NSS, using data from 2004-2010. The corridor between large grassland and shrubland habitat patches is located east of Medicine Hat, AB.

CHAPTER 5: IMPLICATIONS TO MANAGEMENT

Metrics for long-distance movements and migratory components for pronghorn are lacking in the literature on this species. Additionally, multi-scalar migratory pathway selection in response to environmental and anthropogenic influences for pronghorn and its utility in developing connectivity networks deserve attention.

The purpose of my work was to develop a multi-scalar hierarchically nested modeling approach to predict pronghorn migrations for use in designing a connectivity network at the northern edge of pronghorn range, thus providing a foundation for a species diversity regional network by propagating hierarchically nested scales of movement selection for conservation.

The objectives of my dissertation research were to: 1) Assimilate regional data into spatiotemporal layers; 2) Classify and determine metrics for various movement behaviors and states within individuals; 3) Predict multi-scalar seasonal pronghorn migrations across the NSS and integrate scales into one map output for conservation planning; 4) Create pronghorn connectivity network maps across the NSS and; 5) Provide objective methods for defining and analyzing hierarchically nested migratory pathway selection

I found that across the Northern Sagebrush Steppe pronghorn populations partially engage in long-distance movements and seasonal migrations to complete annual life-history requirements. In my study, 55% of individuals migrated while 45% remained resident based on responses to spatiotemporal variation in resources, responses to environmental gradients, density-dependent fluctuations in population densities and demographic rates, or age and body condition. In addition, strategies could be based on genetic factors, social learning and spatial recognition. More so, more evidence indicates individuals have the ability to switch migratory strategies (Chapman et al. 2011, Gaillard 2013). I conclude that a population's ability to continue to undertake long-distance movements and migrations is particularly important at the periphery of a species' range and should be conserved and managed for. In addition while migrating, pronghorn select for and against various environmental and anthropogenic features at different magnitudes and different scales, consistent with hierarchically nested selection concepts (Rettie and

Messier 2000, Thullier and Meyer 2006). Wildlife and resource managers must continue to be attuned to the spatiotemporal requirements during seasonal migrations to allow for continued healthy pronghorn populations. I examined movement metrics and behaviors of migrating pronghorn and subsequently modelled multi-scalar migratory pathway selection across the NSS. I also investigated specific influences of migrating pronghorn in selecting stopover sites and multi-scalar impacts of anthropogenic features on migration. I created multi-scalar map outputs which allowed me to construct a pronghorn connectivity networks across the NSS. This network may be useful to other prairie species at the northern edge of their range.

Initiating large-scale, transboundary conservation work is important both ecologically and economically to a given region (Polasky et al. 2005, Samways et al. 2010). Successful interjurisdictional conservation work actively seeks out and integrates all stakeholder viewpoints and is proficient in formulating polices to moderate human-based effects to the landscape for planning adaptive initiatives (Kiesecker et al. 2010). Globally, advances have occurred in managing transboundary terrestrial species (Gates et al. 2005, Plumptre et al. 2007). Here I provide key findings for each analytical chapter and contribute transboundary management recommendations and actions that could be undertaken to mitigate effects on sagebrush steppe systems and assist in continued conservation of the Northern sagebrush steppe. In addition, I point out opportunities for future research to continue conservation and management for pronghorn and other species found within the NSS and other similar ecological systems.

KEY FINDINGS

Key findings for pronghorn movements across the NSS include:

Movement metrics

- The population exhibited partial migratory traits in that over half (55%) the captured animals undertook seasonal migrations. Similar patterns are found in other large herbivores, including elk, and may be an important adaptive behavioral pattern in response to environmental conditions, population densities, predation, anthropogenic influences, or age and sex of the individual. Fall migrations lasted on average 11 days from October 31 – November 10 while spring migrations lasted on average 20 days from March 22 – April 10.

- Stopovers sites were used during both fall and spring, however spring migrations accounted for 75% of migrations where stopovers are identified. I inferred that the use of stopover sites allows individuals to match migration to increasing forage quality across the landscape and to sustain nutritional requirements for maintenance and reproduction.
- Eleven fawning-associated movements were identified and could be an important survival strategy for mothers and accompanying fawns at heel to decrease predation risk by aggregating individuals into small groups, providing increased safety.
- Driven movements were identified in both migrant and resident individuals (*n*=53) and I suggest they are a significant survival strategy for pronghorn facing extreme environmental conditions during the winter. In these instances, pronghorn apply their ability to move rapidly over great distances to acquire improved conditions.
- Fall migration, fawning-associated movements and driven movements (both migratory and resident individuals) had similar movement metrics; they were linear and rapid, which can be inferred as movements utilized for increasing survival in response to varying ecological factors. In contrast, spring migrations were more sinuous and greater in duration and distance, which can be inferred as movements for meeting nutritional demands for reproduction under spatially variable ecological conditions. Fall and spring stopover movement metrics were similar between the two seasons. In general, stopover site behavior is a mechanism for maintaining body condition for an individual and/or in preparation for fawning during late spring.
- Three individuals with multi-year collars switched movement strategies from mixed-migratory to resident, suggesting that movement strategies were flexible. Switching strategies may be based on behavioral and social factors such as following the behavior of a group or kin. Switching may vary with the age and sex of the individual. Finally, switching may occur in response to variability in

ecological gradients such as forage quality, snow accumulation, population densities, etc.

Multi-scale migration modeling

- At third-order scales, pronghorn responded to road density most strongly at 100m, to well densities at 1000m and to large hydrologic systems at 750m. Results define the appropriate distances for prescribed pronghorn management for these parameters. At this scale during fall, roads had the greatest influence on selection, followed by large hydrologic systems and then well densities. During spring, large hydrologic systems had the greatest influence on movement selection, followed by roads and then well densities.
- At second-order scales, pronghorn selected for grassland, intermediate slopes, south-facing aspects and against high road and well densities during fall and spring migrations. Specifically during fall, pronghorn selected in order of decreasing strength for grasslands, intermediate slopes, south-facing aspects and against all roads, and paved roads specifically. During spring they selected in order of decreasing strength for grasslands, against all roads, for areas with higher forage productivity, intermediate slopes, against large hydrologic systems and, against increased well densities. In relation to anthropogenic influences, increased road densities had a strong negative influence on migratory pathway selection by pronghorn.
- Pronghorn selected stopover sites that had higher forage productivity and were on north-facing slopes more frequently than migratory pathways. In addition, pronghorn selected stopover sites in areas that had lower well densities and with less grassland and shrubland landcover types, compared to migratory pathways. Pronghorn opportunistically identified high quality forage areas (using NDVI values as a broad-scale proxy) to feed and rest. Landcover type was not a critical factor determining stopover site location. North-facing slopes hold moisture earlier into fall and longer into spring, allowing for delayed forage senescence and earlier forb germination. Areas with increased well densities accompanied by indirect influences (traffic, noise, etc.) may disturb weary individuals and thus are avoided as stopover sites along a migratory pathway.

- At third-order scales, anthropogenic factors (roads and wells) marginally influenced pronghorn migratory pathway selection. However at second-order scales, these factors were highly influential. Results demonstrated that migratory pathway selection was hierarchically nested consistent with previous multiple resource selection studies. Overall selection was based first by broader scale conditions that determined selection at finer scales. Here, pronghorn avoided high well densities over large landscapes at the second-order scale. Once broader scaled selections were made however, pronghorn migrating through areas that contained well sites (i.e. at the third-order scale) were less affected by these specific features.
- Seasonal scale-integrated step selection function (ISSF) maps were combined with multi-scalar models into one product. Third-order models performed poorly using both third-order and ISSF maps to validate results using both testing and training data sets. However, second-order models performed well using both second-order and ISSF maps to validate maps from both data sets. ISSF maps validated second-order models just as well or better than second-order map outputs, justifying their use as regional seasonal migration conservation planning tools.

Pronghorn connectivity network

- Innovative approaches to map and prioritize corridors were used to define a connectivity networks for pronghorn that involved using seasonal multi-scalar cost surfaces, investigating corridors within and between habitat patches, validating results against pronghorn data, and identifying appropriate seasonal corridors widths to prioritize corridors using relocation data.
- Fall and spring migration connectivity networks were similar. However during fall, corridors were influenced more by large hydrologic systems as individuals followed these linear features to decrease transit time required to reach winter destinations. During spring, corridors were influenced more by roads as these features either slowed already sinuous migratory movements thus creating mismatches with temporally increasing forage quality or in contrast, individuals

followed roads to feed on high quality forage found along roadside right-of-ways (ROWs).

- I concluded that the pronghorn is a useful broad-scale focal species for designing multi-species regional networks and in particular across the NSS. Species such as elk, moose, mule deer, greater sage-grouse, sharp-tailed grouse, coyote, swift fox, multiple grassland bird species, and multiple bat species may all benefit from corridor conservation planning for pronghorn. Mule deer and greater sage-grouse would most likely benefit from the connectivity network produced in my study because along with pronghorn, these species migrate and have large spatiotemporal needs for completing annual life-history requirements.
- Using movement metrics is a good approach for designing regional initiatives, because migratory movement is an essential ecological process responding to variable environmental conditions particularly at the edge of a species range.

MANAGEMENT RECOMMENDATIONS

The following recommendations and actions could be undertaken:

Recommendation 1: Wildlife and land managers could consider actively managing regional landscapes for long-distance movements during fall and spring migrations and movements driven by extreme winter conditions.

Long-distance movements (LDM's) are identified in Chapter 2. Seasonal migrations and fawning-associated movements occurred at specific times of the year. Driven movements occurred in response to extreme environmental conditions, specifically harsh winter storm events. Over half the pronghorn collared during this study undertook seasonal migration and other LDM's. As a priority, identified seasonal migration periods could be actively managed for by opening gates, modifying fences, establishing road signs, etc during these discrete time periods. In addition, extreme winter weather events could be actively monitored for and as events arise, respond appropriately (e.g. modify fencing, open gates, establish road signs) to allow for continued LDM's across the NSS. LDM's are adaptive strategies that sustain a healthy population at the northern periphery of pronghorn range. Management tools (identified in

Recommendation 5) that promote continued LDM's could be used to maintain connectivity during these specific time periods.

Recommendation 2: Land and wildlife managers may consider working closer with industry companies and other agencies to continue to inject wildlife management objectives into guidelines.

Continued research demonstrates the effects of anthropogenic features on wildlife in sagebrush systems (Aldridge and Boyce 2007, Sawyer et al. 2006, Hebblewhite 2011, Seidler et al. 2014). Federal, state and provincial agencies are tasked with managing lands from a multi-use perspective for resource extraction and wildlife/habitat management. I found pronghorn were sensitive to high road and well densities during migration (Chapter 3). In particular, pronghorn avoided spring stopover sites with increased well densities while they avoided fall migration pathways with increased road densities (Chapter 3).

CFB Suffield is a large government agency owned grassland complex north of Medicine Hat, AB that is important for sustaining pronghorn migration. I identified priority corridors through CFB Suffield, despite a high density of oil/natural gas extraction by various industrial companies located on site (Chapter 4). Innovative infrastructure at CFB Suffield keeps most of the oil/natural gas operations underground and close to the limited number of roads on base. More underground infrastructure, in addition to remote monitoring techniques, could be used throughout the NSS to achieve both resource development and wildlife needs. Additionally, the ideal time period for drilling and maintaining wells is during summer months when forage availability is at a peak and widespread across large spatial areas. Increased communication between industry, land agencies and wildlife agencies could occur to promote innovative approaches for managing landscapes for sustaining pronghorn. In addition to oil/natural gas industries, wind industry and road industries and/or agencies could be approached and kept involved in long-term planning initiatives to promote resource development balanced with wildlife conservation needs.

Recommendation 3: All stakeholders, including land and wildlife agencies, NGO's, landowners and industry could incorporate information from this study in discussions regarding the importance of transboundary movements and stopover ecology for various planning efforts.

I documented stopover sites used by pronghorn during fall and spring migration (Chapter 2). Stopover sites are used by numerous migrating species and stopover sites have been identified in other ungulate populations to take advantage of high quality patches of forage (Sawyer and Kauffman 2011, Seidler et al. 2014). I found that pronghorn avoided stopover sites in areas with high anthropogenic feature densities (Chapter 3). I also found that compared to migratory pathways and relative to agricultural areas, pronghorn avoided grassland and shrubland landcover types. I do not suggest that overall pronghorn avoid grassland stopover sites, but more accurately, pronghorn select stopover sites with high forage productivity. These areas may occur in agricultural areas, including tame pastures or irrigated perennial crops. Stopover sites are a major migration component, required for resource replenishment and rest and should be conserved appropriately (Calvert et al. 2009, Sawyer and Kauffman 2011). Presently, there is much to learn and bring awareness to others about stopover site ecology as research continues to provide insights into migration ecology. My project is one of the first to analyze stopover site data and interpret stopover site metrics and seasonal selection requirement results for an ungulate species. As a result, efforts by land and wildlife agencies, researchers and non-profit organizations to work with the ranching and farming community could continue so that stopover sites are included in connectivity planning. One mechanism of communicating this to multiple entities is used by the Montana Chapter of The Nature Conservancy. The Conservancy holds an annual "biosymposium" to serve as a forum for researchers, agencies, non-profit organizations, ranchers, landowners, and industry personnel to come together, share ideas and learn from one another.

Recommendation 4: Land and Wildlife Managers may consider using seasonal pronghorn connectivity network maps for transboundary pronghorn population management.

Results uphold earlier studies (Martinka 1966) confirming that pronghorn traverse the Canadian-U.S. boarder to complete annual life-cycle requirements. Additionally, my results provide details about timing, metrics and selection requirements for pronghorn seasonal migrations and LDM's (Chapter 2,3). Given the transboundary nature of pronghorn populations in the NSS, population management and seasonal habitat and connectivity needs can be addressed from a regional transboundary perspective using pronghorn connectivity network map products resulting from my project. Currently, state and provincial wildlife agencies participate in the Northern Sagebrush Steppe Initiative (NSSI), for which one objective is to share data and build regional spatial layers. I recommend that in addition to these entities, federal agencies, non-profit organizations (NGOs), universities and industry personnel could be invited to address management and conservation needs across the system. In addition, a regional NSS coordinator could be established to manage efforts. The NSS coordinator would be tasked, among other needs, to:

- Work with spatial analysts to create more seamless, finer resolution spatial layers. Specific layers include a more seamless landcover layer, soil layer, wind farm layer and fence layer (both location and structure type).
- In addition, the NSS coordinator would explore temporal data sets to create higher resolution snow cover or snow depth layers, drought and temperature layers, as well as traffic volume layers.
- Coordinate research projects and interests and develop a region wide symposium to share research with other collaborators and the public.
- Research, apply for and manage available funding for research and management projects.
- Work with policy makers in state, provincial and federal agencies to inform complementary land-use and conservation policies across the NSS.

- Develop a multi-jurisdictional management strategy for pronghorn across the NSS by incorporating previous literature and research from agency and university personnel with current research results and strategies.

The pronghorn connectivity network maps (Chapter 4) would provide a NSS coordinator a starting point for informing multi-jurisdictional management efforts. A successful strategy at the northern periphery of pronghorn range begins with managing for larger parcels of open, contiguous grassland habitats, used in migratory pathway selection (Chapter 3). Currently, hunting districts (wildlife management units) are managed by each state/province when they could be managed regionally, to account for the timing of migration and migration corridors. For example, fall quota numbers could account for linear north-south migrations and resulting fluctuations in pronghorn numbers within hunting districts at different times during fall hunting season. Finally, prioritized corridors could be managed for chiefly between principle core habitat patches but also between satellite grassland habitat patches (Chapter 4). Satellite habitat patches may be important as climatic conditions shift or future augmentation efforts are required.

Recommendation 5: Using a suite of tools, habitat and wildlife management and conservation organizations could focus management actions within priority corridors identified in the pronghorn connectivity networks. Specifically, these organizations may initiate the use of management tools within three particular corridors where regular crossings occur during long-distance movements.

Priority corridors for conservation were identified using pronghorn migratory pathways analysis. A number of management tools can be used to sustain connectivity. These tools can be especially useful for corridors between large grassland habitat patches; areas determined as essential during fall and spring migrations. In particular, three corridors were identified to be significant contributors to regional landscape connectivity including: 1) The area just east of Medicine Hat, AB along TransCanada HWY 1; 2) The area just east of Malta, MT along the western edge of Bowdoin National Wildlife Refuge; 3) The area just west of Glasgow, MT along the southern boundary of Faraasen Recreational Park. Government agencies, non-profit organizations and landowners can use various management tools within these and other discrete areas that are important for continuing connectivity. Depending on landownership and ecological requirements of each land parcel, tools to implement could include:

- Conservation easements between private landowners and interested agencies/non-profit organizations.
- Fence modification/removal to facilitate continued wildlife movement. Landowners could prioritize fence modifications and removals in both highly used pronghorn migration corridors and to fences that are woven-wire or multi-stranded (i.e. four-strand barbed wire or more).
- Flagging fences to avoid run-ins by pronghorn and other wildlife.
- Landowners opening gates during seasonal migrations and harsh winter events.
- Department of transportation agencies fashioning traffic signs to be displayed within corridors at specific times of the year.
- Railroad modifications by railroad companies to allow for pronghorn movement off of railroads, particularly during major snow events. These could include crossing structures within the rail ties to allow pronghorn to move across railroads perpendicularly, adding fencing directly along historic railroad crossing sites so pronghorn cannot get onto railroads at these locations, installing ramps at historic railroad crossing sites to allow pronghorn to escape being struck by trains and/or becoming stranded in adjacent ditches during major snow events.
- Department of transportation agencies constructing wildlife overpasses over roads through prioritized corridors.
- Agencies, non-profit organizations, universities and private landowners educating communities across the NSS regarding pronghorn migration.

FUTURE RESEARCH

Recommendation 1: Continue multi-scalar pronghorn modeling efforts on habitats and movements to investigate various sampling and validation procedures.

I developed selection models and associated maps that predicted migratory pathways across scales for use in designing connectivity networks (Chapter 3 and 4). In my study, I used GPS collar locations and available random points to model pronghorn movements. As an alternative to my sampling design, vectors that either connect relocations or were assigned to available points could be used to model movements. Comparing overall model accuracies between case points versus vectors in modeling migratory pathways would be an intriguing technical exercise to examine which method is more useful. Similar design and modeling efforts could be tested to predict fawning-associated movements and driven movements across the NSS. In addition, multi-scalar habitat models could be developed using pronghorn data from all three jurisdictions for seasonal ranges (i.e. winter, fawning, summer). Efforts underway have modelled seasonal ranges in Alberta only (Jones et al. 2015). Mapping model outputs provides a useful guide towards managing wildlife regionally. More research could address the use and validity of multi-scale integrated maps. Similarly, research options could use genetic markers from blood and hair samples collected from harvested pronghorn to validate prioritized corridors presented here. Finally, models should use region-wide spatiotemporal layers to better hone in on movement and habitat selection drivers. Integrating other anthropogenic features and environmental conditions such as fences (locations and structure type), wind farms and, snow depth into models would provide a more accurate assessment. In addition, using the FRAGSTATS program to analyze and identify effects of fragmentation, resource patchiness, or effects from adjacent landcover types on multi-scalar pronghorn movement and habitat selection may provide additional insights.

Recommendation 2: Investigate the effects of various barriers on pronghorn multi-scalar movement.

Pronghorn have difficulty negotiating linear barriers (i.e. roads, railroads, fences) during various times of their annual cycle (Harrington and Conover 2006, Suitor 2011, Sawyer et al. 2013, Jones 2014, Poor et al. 2014, Siedler et al. 2014, Chapter 3). In my study I found that roads had a significant effect on pronghorn migratory pathway selection. Recently, the “Barrier Mapper” toolkit has been used to identify barriers that affect the quality and/or location of a corridor (McRae 2012*b*). This toolkit could address seasonal habitats and movements at a large spatial scale to further identify key linkage areas within priority corridors by integrating results produced from the suite of “Linkage Mapper” tools (McRae and Kavanagh 2011, McRae 2012*a*,*b*). In my study I noted stopover sites that likely occurred due to semi-permeable barriers (roads, fences, railroads), similar to Siedler et al. (2014). More research could investigate the impacts of anthropogenic features on stopover site selection.

From GPS relocation data, I observed multiple unnatural linear movements, which under further on-site investigation were responses to fencing. As a consequence, further research is needed to further quantify impacts of fencing on seasonal movements. Although anecdotal information and expert opinion have addressed the use of various fencing modifications to promote daily and seasonal pronghorn movements, critical analysis is needed to identify the most suitable fence modification types to sustain pronghorn movements. In addition during field work, pronghorn carcasses were observed either adjacent to or on fencing itself. Recently, a golden eagle attempted to prey on a pronghorn directly alongside a fence (Jones et al. 2015). Additional research could focus on fence effects on predation on pronghorn and other wildlife.

Recommendation 3: Assess pronghorn responses to various oil/gas and wind industry practices.

Along with other sagebrush steppe ungulates, pronghorn have been shown to avoid increasing oil/gas well density (Sawyer et al. 2006, Sawyer et al. 2009*b*, Beckmann et al. 2012, Chapter 3). Some natural gas and oil industry innovations have allowed for higher resource yields while simultaneously generating fewer impacts on surface resources, including wildlife. However, a spectrum of structures and infrastructure remains across the landscape. In addition, drilling and maintenance practices occur at different times of the year in gas/oil fields of varying densities. I accounted as much as possible for temporal variation in well drilling across the NSS. However, it was difficult to assess the variation in maintenance practices and the spectrum of oil/natural gas structures along with accompanying infrastructure. Detailed information regarding these variations in oil/natural gas resource extraction should be recorded for modeling purposes. From this, large-scale analysis can be conducted specifically on pronghorn movement responses to these variable structures/infrastructure, timing and densities. Results can then be used to decipher threshold responses to varying structure types and densities to make spatiotemporal recommendations. In addition, although wind farm densities are increasing across the NSS, little research has been placed on pronghorn responses to these structures. The Northern Sagebrush Steppe's regional industries can take guidance from industries in Wyoming, U.S. There, industry partners have funded research to find balanced solutions and best management practices for wildlife selecting habitat and movement requirements in resource extraction areas (Beckmann et al. 2012).

Recommendation 4: Identify and model other focal species to establish a multi-scalar, multi-species NSS conservation network.

At the northern edge of the North American Great Plains, multiple species respond to fluctuating environmental conditions. Focal species are defined as a set of species that use a landscape at various scales (Lambeck 1997). I have proposed that pronghorn serve as an appropriate broad-scale focal species for the NSS (Chapter 4). Future efforts could identify smaller scale focal species to model their directed movement (i.e. migration, dispersal) requirements which could include greater sage-grouse and swift fox at medium spatiotemporal scales and prairie rattlesnakes at small spatiotemporal scales. GPS data for these species already exists for species identified above for use in multi-scalar modeling (Ausband and Moehrenschlager 2008, Jorgensen 2009, Smith 2013). Results ultimately can lead towards designing a multi-scalar, multi-species biological diversity connectivity network across the NSS with efforts focusing on identifying where priority corridors for individual species overlap with one another (Opdam et al. 2003).

Recommendation 5: Investigate fawn recruitment and population re-establishment across the NSS.

Fawn recruitment is an important consideration for population management across the NSS especially due to severe winters and in particular, during the winters from 2009-2011. Reduced population counts, specifically fawn numbers, across Northern Montana and Southern Saskatchewan in 2011 caused wildlife agencies to drastically reduce hunting district quotas or to place a moratorium on pronghorn hunting all together. More research is needed regionally on fawning success, fawning-associated movements and their predictors, and factors that influence where and when pronghorn re-establish across the region. Questions to consider include what is the duration for the NSS population, through recruitment success, to reach numbers that were recorded before the consecutive severe winters of 2009-2011? Another could be are pronghorn re-establishing themselves in the same general areas as before or are there other habitats and migratory corridors that become used over time as a result to continued anthropogenic development and potential effects from climate change? Research involving field monitoring of fawns, spatial modeling and population modeling could address these and other population questions.

Recommendation 6: Further explore pronghorn switching of movement strategies.

I found that pronghorn can annually change movement strategies (either resident or migratory) (Chapter 2). Future research could test potential mechanisms that lead to switching strategies by collecting multi-year data on collared individuals. Switching mechanisms may be based on endogenous control factors (i.e. age, sex, social processes such as culturally transmitted information or conspecific attraction), exogenous control factors (i.e. ecological requirements, environmental cues, or anthropogenic variability), or both (Bauer et al. 2011, Hebblewhite and Merrill 2011, Gaillard 2013).

REFERENCES

Alberta Environment. 2007. Southern Alberta landscapes, meeting the challenges ahead, state of the landscape report. Information Centre, Alberta Environment, Main Floor, Oxbridge Place 9820-106 Street, Edmonton, Alberta T5K 2J6.

Aldridge, C., M.S. Boyce. 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered greater sage-grouse. Ecological Applications, 17: 508–526.

Alerstam, T., A. Hedenstrom, S. Akesson. 2003. Long-distance migration: evolution and determinants. Oikos, 103(2):247-260.

Apps, C.D., B.N McLellan, J.G. Woods., M.F. Proctor. 2004. Estimating grizzly bear distribution and abundance relative to habitat and human influence. Journal of Wildlife Management, 68(1):138-152.

Arsenault, A.A. 2007. Management strategy for pronghorn (*Antilocapra americana*) in Saskatchewan. Fish and Wildlife Technical Report 2008-01. S.M.o. Environment, Saskatchewan Ministry of Environment**,** 34 pp.

Ausband, D., Moehrenschlager, A. 2008. Long-range juvenile dispersal and its implication for conservation of reintroduced swift fox *Vulpes velox* populations in the USA and Canada. Oryx, 43(1): 73-77.

Avgar, T., G. Street, J.M. Fryxell. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology, 92:481-490.

Baker, R.J. 1978. The evolutionary ecology of animal migration. Hoddes and Sloughton, Seven Oaks, United Kingdom.

Ball, J. P., C. Nordengren, K. Wallin. 2001. Partial migration by large ungulates: characteristics of seasonal moose *Alces alces* ranges in northern Sweden. Wildlife Biology, 7:39-47.

Barnowe-Meyer, K.K., P.J. White, L.P. Waits, J.A. Byers. 2013. Social and genetic structure associated with migration in pronghorn. Biological Conservation, 168: 108-115.

Barrett, M.W. 1982. Distribution, behavior, and mortality of pronghorns during a severe winter in Alberta. Journal of Wildlife Management, 46(4):991-1002.

Barrett, M.W., J. Nolan, L. Roy. 1982. Evaluation of hand held net-gun to capture large mammals. Wildlife Society Bulletin 10:108-114.

Barrett, M.W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. Journal of Wildlife Management, 48(2):542-550.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London.

Bauer, S., B.A. Nolet, J. Giske, J.W. Chapman, S. Akesson, A. Hedenstrom, J.M. Fryxell. 2011. Cues and decision rules in animal migration *In* Animal migration: a synthesis. Milner-Gulland, E.J., J.M. Fryxell, A.R.E. Sinclair, editors. Oxford University Press, Oxford. 68-87 pp.

Bayless, S.R. 1969. Winter food habits, range use, and home range of antelope in Montana. Journal of Wildlife Management, 33(3):538-551.

Beckmann, J.P., K. Murray, R.G. Seidler, J. Berger. 2012. Human-mediated shifts in animal habitat use: sequential changes in pronghorn use of a natural gas filed in Greater Yellowstone. Biological Conservation, 147:222-233.

Beier, P., R. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology, 12(6):1241-1252.

Beier, P., D.R. Majka, W.D. Spencer. 2008. Forks in the Road: Choices in procedures for designing wildland linkages. Conservation Biology, 22(4):836-851.

Beier, P., D.R. Majka, S.L. Newell. 2009. Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecological Applications, 19(8):067-2077.

Beier, P., W. Spencer, R.F. Baldwin, B.H. McRae. 2011. Toward best practices for developing regional connectivity maps. Conservation Biology, 25(5):879-892.

Bekenov, A.B., Grahev Iu, A., Milner-Gulland, E.J. 1998. The ecology and management of the saiga antelope in Kazakhstan. Mammal Review, 28: 1-52.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fract dimension? Journal of Theoretical Biology, 229:209-220.

Berger, J. 2004. The last mile: how to sustain long-distance migrations in mammals. Conservation Biology, 18(2):320-331.

Berger, J., J.K.Young, K.M. Berger. 2008. Protecting migration corridors: challenges and optimism for Mongolian saiga. PLOS Biology, 6(7):1365-1367.

Beyer, H. 2013. Geospatial Modelling Environment (GME). Available at: www.spatialecology.com/gme.

Bolger, D.T., W.D. Newmark, T.A. Morrison, D.F. Doak. 2007. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters, 10:1-15.

Bowlin, M.S., I-A. Bisson, J. Shamoun-Baranes, J.D. Reichard, N. Sapir, P.P. Marra, T.H. Kunz, D.S. Wilcove, A. Hedenstrom, C.G. Guglielmo, S. Akesson, M. Ramenofsky, M. Wikelski. 2010. Grand challenges in migration biology. Integrative and Comparative Biology, 50(3):261–279.

Bowyer, R.T., J.G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions, 12:244-257.

Boyce, M.S., P.R. Vernier, S.E. Nielsen, F.K.A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling, 157:281–300.

Boyce, M.S. 2006. Scale for resource selection functions. Diversity and Distributions, 12:269–276.

Brennan, L.A., W.P. Kuvlesky Jr. 2005. North American grassland birds: an unfolding conservation crisis? Journal of Wildlife Management, 69(1):1-13.

Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.

Bruns, E.H. 1977. Winter behavior of pronghorns in relation to habitat. Journal of Wildlife Management, 41(3):560-571.

Bunnefeld, N., L. Borger, B. Van Moorter, C.M. Rolandsen, H. Dettki, E.J. Solberg, G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology, 80:466-476.

Burgman, M.A., D.B. Lindenmayer, J. Elith. 2005. Managing landscapes for conservation under uncertainty. Ecology, 86(8):2007-2017.

Burnham, K. P., D. R. Anderson. 2002. Model selection and inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Byers, J.A. 1997. Chapter 10: The mating system: conflict and cooperation between the sexes *In* American pronghorn: social adaptations and the ghosts of predators past. University Chicago Press, Chicago, Illinois, USA. pp 206-233.

Cabeza, M. 2003. Habitat loss and connectivity of reserve networks in probability approaches to reserve design. Ecology Letters, 6:665-672.

Cagnacci, F., S. Focardi, M. Heurich, A. Stache, A.J.M. Hewison, N. Morellet, P. Kjellander, J.D.C. Linnell, A. Mysterud, M. Neteler, L. Delucchi, F. Ossi, F. Urbando. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioral gradient determined by ecological factors. Oikos, 120: 1790-1802.

Calenge, C. 2011. Analysis of animal movements in R: the adehabitatLT package. Office national de la chasse et de la faune sauvage, Saint Benoist, France. 85 pp.

Calvert, A.M., S.J. Walde, P.D. Taylor. 2009. Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. Avian Conservation and Ecology, 4(2):5.

Caro, T.M., G. O'Doherty. 1999. On the use of surrogate species in conservation biology. Conservation Biology, 13:805-814.

Carroll, C., B.H. McRae, A. Brookes. 2012. Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conservation Biology, 26(1):78-87.

Chape, S., S. Blyth, L. Fish, P. Fax, M. Spalding. 2003. 2003 United Nations List of Protected Areas. IUCN, Gland, Switzerland and Cambridge, UK and UNEO-WCMC, Cambridge, UK. 44 pp.

Chapman, B.B., K. Hulthen, D.R. Blomqvist, L-R. Hansson, J-A. Nilsson, J. Brodersen, P.A. Nilsson, C. Skov, C. Bronmark. 2011. To boldly go: individual differences in boldness influence migratory tendency. Ecology Letters, 14:871-876.

Chetkiewicz, C-L.B., C. C. St. Claire, M.S. Boyce. 2006. Corridors for conservation: integrating pattern and process. Annual Review of Ecology, Evolution and Systematics, 37:317-342.

Chetkiewicz, C-L.B., M.S. Boyce. 2009. Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology, 46:1036-1047.

Clancey, E., Dunn, S.J., Beyers, J.A. 2012. Do single point condition measurements predict fitness in female pronghorn (*Antilocapra americana*)? Canadian Journal of Zoology, 90: 729-735.

Compton, B.W., J.M. Rhymer, M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology, 83(3): 833-843.

Copeland, H.E, K.E. Doherty, D.E. Naugle, A. Pocewicz, J.M. Kiesecker. 2009. Mapping oil and gas development potential in the US intermountain west and estimating impacts to species. PLoS ONE 4(10):1-7.

Coupland, R. F. 1961. A reconsideration of grassland classification in the northern great plains of North America. Journal of Ecology, 49(1):135-167.

Cushman, S.A., K.S. McKelvey, M.K. Schwartz. 2009. Use of empirically derived source-destination models to map regional conservation corridors. Conservation Biology, 23(2):368-376.

Cushman, S.A., E.L. Landguth, C.H. Flather. 2013. Evaluating population connectivity for species of conservation concern in the American great plains. USDA Forest Service / UNL Faculty Publications. Paper 244. Available at: http://digitalcommons.unl.edu/usdafsfacpub/244.

Dalton, K. 2009. Pronghorn: migration triggers and resource selection in southeastern Oregon. Masters of Science Thesis. Department of Natural Resource Sciences. Washington State University. Pullman, WA. 73 pp.

DeCesare, N. J., D.H. Pletscher. 2006. Movements, connectivity, and resource selection of rocky mountain bighorn sheep. Journal of Mammalogy, 87:531-538.

DeCesare, N.J., M. Hebblewhite, F. Schmiegelow, D. Hervieux, G.J. McDermid, L. Neufeld, M. Bradley, J. Whittington, K.G. Smith, L.E. Morgantini, M. Wheatley, M. Musiani. 2012. Transcending scale-dependence in identifying habitat with resource selection functions. Ecological Applications, 22(4):1068-1083.

Dingle, H., V.A. Drake. 2007. What is migration? Bioscience, 57(2):113-121.

Dirschl, H.J. 1963. Food habits of the pronghorn in Saskatchewan. Journal of Wildlife Management, 27(1):81-93.

Dray, S., A-B. Dufour, T. Jombart, S. Pavoine, J. Thioulouse. 2014. Multivariate analysis of ecological data with ade4. Springer eds. 193 pp.

Driezen, K., F. Adriaensen, C. Rondinini, C.P. Doncaster, E. Matthysen. 2007. Evaluating least-cost model predictions with empirical dispersal data: a case-study using radiotracking data of hedgehogs (*Erinaceus europaeus*). Ecological Modelling, 209:314-322.

Duinker, P.N., L.A. Greig. 2006. The impotence of cumulative effects assessment in Canada: ailments and ideas for redeployment. Environmental Management, 37(2): 153-161.

Dunkin, S.W., F.S. Guthery, S.J. Demaso, A.D. Peoples, E.S. Parry. 2009. Influence of anthropogenic structures on northern bobwhite space use in western Oklahoma. Journal of Wildlife_Management, 73(2):253-259.

Dussault, C., V. Pinard, J-P. Ouellet, R. Courois, D. Fortin. 2012. Avoidance of roads and selection for recent cutovers by threatened caribou: fitness-rewarding or maladaptive behavior? Proceedings of the Royal Society B., 279:4481-4488 doi:10.1098/rspb.2012.1700.

Eberhardt, L.L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology, 83:2841–2854.

Eggeman, S. 2012. Migratory behavior and survival of adult female elk in a partially migratory population. Masters of Science Thesis. College of Forestry and Conservation, University of Montana. Missoula, MT. 96 pp.

Environment Canada. 2010. Yearly and long-term (1981-2010) climatic conditions. Available at: http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html. Last accessed February 27, 2015.

Environmental Law Institute. 2003. Conservation thresholds for land use planners. Environmental Law Institute, Washington, D.C. Available at: www.elistore.org.

Eslinger, D. 2010. Personal communication in February 2010. Alberta Sustainable Resource and Development, Medicine Hat, AB.

ESRI. 2012. ArcGIS Desktop: Release 10.1. Redlands, CA: Environmental Systems Research Institute.

Fahrig, L. 2003. Effect of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics. 34:487-515.

Falcy, M.R., C.F. Estades. 2007. Effectiveness of corridors relative to enlargement of habitat patches. Conservation Biology, 21(5):1341-1346.

Fancey, S.G., Pank, L.F., Whitten, K.R., Regelin, W.L. 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. Canadian Journal of Zoology, 67:644-650.

Ferrier, S., G. Watson, J. Pearce, M. Drielsma. 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodiversity and Conservation, 11:2275-2307.

Fieberg, J., D.W. Kuehn, G.D. DelGiudice. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. Journal of Mammology, 89(6):1529-1539.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M.S. Boyce, J.L. Frair. 2010. Correlation and studies of habitat selection: problem, red herring or opportunity? Philosophical Transactions of the Royal Society B, 365:2233–2244.

Fielding, A.H., J.F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24:38–49.

Fischhoff, I.R.,S.R. Sundaresan, J. Cordingley, H.M. Larkin, M. Sellier, D.I. Rubenstein. 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. Animal Behaviour, 73:825-831.

Foreman, R. T. 1995. Chapter 1: Foundations *In* Land mosaics: the ecology of landscapes and regions. Cambridge: Cambridge University Press. 3-37 pp.

Forrest, S.C., H. Strand, W.H. Haskins, C. Freese, J. Proctor, E. Dinerstein. 2004. Ocean of grass: a conservation assessment for the northern great plains. Northern plains conservation network and northern great plains ecoregion, WWF-US, Bozeman, MT, USA.

Forrester, J.D., H.K. Im, P.J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. Ecology. 90(12):3554-3565.

Fortin, D., H.L. Beyer, M.S. Boyce, D.W. Smith, T. Duchesne, J.S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology, 86(5):1320-1330.

Fretwell, S.D. 1972. Populations in a seasonal environment: monographs in population biology 5. Princeton University Press.

Friar, J.L., J. Fieberg, M. Hebblewhite, F. Cagnacci, N.J. DeCesare, L. Pedrotti. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society B, 365:2187-2200.

Fryxell, J.M., A.R.E. Sinclair. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology and Evolution, 3:237-241.

Gaillard, J-M. 2013. Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. Ecology, 94(6):1261-1264.

Gaston, K.J. 2008. Geographic range limits: achieving synthesis. Philosophical Transactions of the Royal Society B, 276:1395-1406. doi:10.1098/rspb.2008.1480

Gaston, K. J., R.A. Fuller. 2008. Commonness, population depletion and conservation biology. Trends in Ecology and Evolution, 23(1):14-19.

Gates, C. C., Stelfox, B., Muhly, T., Chowns, T., Hudson, R.J. 2005. The Ecology of Bison Movements and Distribution in and Beyond Yellowstone National Park University of Calgary: 329 pp.

Gaudry, W., S. Said, J.M. Gaillard, T. Chevrier, A. Loison, D. Maillard, C. Bonenfant. 2015. Partial migration or just habitat selection? A case study of roe deer (Capreolus capreolus) seasonal movements in an Alpine population. Journal of Mammalogy *In Press*.

Gavin, S.D., P.E. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? Canadian Journal of Zoology, 84:1775-1780.

Gregg, M.A., M. Bray, K.M. Kilbride, M.R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. Journal of Wildlife Management, 65(1):19-24.

Gueguen, L. 2001. Segmentation by maximal predictive partitioning according to composition biases *In* Computation Biology. Gascuel, O., M.F. Sagot, editors. LNCS, 2066. 32-44 pp.

Handley, J., R. Wood, S. Kidd. 1998. Defining coherence for landscape planning and management: A regional landscape strategy for northwest England. Landscape Research, 48:2.

Hanks, E.M., M.B. Hooten, D.S. Johnson, J.T. Sterling. 2011. Velocity-based movement modeling for individual and population level inference. PLoS ONE 6(8):e22795. doi:10.1371/journal.pone.0022795.

Hannah, L., J.L. Carr, A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodiversity and Conservation, 4:128-155.

Harrington, J.L., M.R. Conover. 2006. Characteristics of ungulate behavior and mortality associated with wire fences. Wildlife Society Bulletin, 34(5):1295-1305.

Harris, G., S. Thirgood, J.G.C. Hopcraft, J.P.G.M. Cromsight, J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research, 7:55-76.

Hebblewhite, M., E.H. Merrill, L.E. Morgantini, C.A. White, J.R. Allen, E. Bruns, L. Thurston, T.E. Hurd. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. Wildlife Society Bulletin, 34(5):1280-1294.

Hebblewhite, M., E.H. Merrill. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia, 152:377–387.

Hebblewhite, M., E.H. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology, 45:834-844.

Hebblewhite, M., E.H. Merrill, G. McDermid. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs, 78(2):141-166.

Hebblewhite, M., E.H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs. Oikos, 120:1860-1870.

Hebblewhite, M. 2011. Effects of energy development on ungulates *In* Energy development and wildlife conservation in western North America. Naugle, D.E. editor. Island Press, Washington, DC. 71-94 pp.

Henwood, W.D. 2006. Linking the World's Grasslands: Enhancing International Cooperation for the Protection and Conservation of the World's Temperate Grasslands. Grasslands Protected Areas Task Force - A proposal submitted to the J.M. Kaplan Fund. 32 pp.

Hilty, J. A., W.Z. Lidicker Jr., A.M. Merenlender. 2006. Corridor ecology: the science and practice of linking landscapes for biodiversity conservation, Island Press. 323 pp.

Hobbs, N. T., K.A. Galvin, C.J. Stokes, J.M. Lackett, A.J. Ash, R.B. Boone, R.S. Reid, P.K. Thornton. 2008. Fragmentation of rangelands: implications for humans, animals, and landscapes. Global Environmental Change, 18:776-785.

Hobbs, R.J. 2002. Habitat networks and biological conservation *In* Applying landscape ecology in biological conservation. Gutzwiller, K.J. editor. New York: Springer-Verlag Press. 150-170 pp.

Hoekstra, J.M., T.M. Boucher, T.H. Ricketts, C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters, 8:23-29.

Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia, 78: 443-457.

Hoskinson, R.L., J.R. Tester. 1980. Migration behavior of pronghorn in southeastern Idaho. Journal of Wildlife Management, 44(1):132-144.

Hosmer, D.W, S. Lameshow. 2000. Chapter 4: Model-Building Strategies and Methods for Logistic Regression *In* Applied Logistic Regression Second Edition. John Wiley & Sons, Inc. 91-142 pp.

Ims, R. A. 1995. Movement patterns related to spatial structures *In* Mosaic Landscapes and Ecological Processes. Hansson L, L. Fahrig, G. Merriam editors. London: Chapman & Hall. 85-109 pp

Jacques, C., J.A. Jenks, R.W. Klaver. 2009. Seasonal movements and home-range use by female pronghorns in sagebrush-steppe communities of western South Dakota. Journal of Mammology, 90(2):433-441.

James, A.R.C., Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. The Journal of Wildlife Management, 64(1): 154-159.

Johnson, C.J., K.L. Parker, D.C. Heard, M.P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology, 71(2):225-235.

Johnson, C.J., D.R. Seip, M.S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology, 41:238-251.

Johnson, C.J., M.S. Boyce, R. Case, H. Cluff, R. Gau, A. Gunn, R. Mulders. 2005. Cumulative effects of human developments on arctic wildlife. Wildlife Monographs, 160(1):1-36.

Johnson, C.J., S.E. Nielsen, E.H. Merrill, T.L. McDonald, M.S. Boyce. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management, 70(2):347–357.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology, 61(1):65-71.

Jones, P.F., M. Grue, J. Landry-DeBoer, J. 2005. Resource selection by pronghorn antelope in the grassland natural region of Alberta: Progress report #1. Alberta Conservation Association, 2nd Floor YPM Place, 530 8th Street South, Lethbridge, Alberta, Canada T1J 2J8.

Jones, P.F. 2014. Scarred for life: the other side of the fence debate. Human-Wildlife Interactions, 8(1):150-154.

Jones, P.F., Seward, B., Baker, J.L., Downey, B.A. 2015. Predation attempt by a golden eagle (Aquila chrysaetos) on a pronghorn (Antilocapra americana) in Southeastern Alberta, Canada. Canadian Wildlife Biology & Management, 4(1): 66-71.

Jones, P.F., M. Grue, M. Suitor, C. Gates, D. Eslinger, J. Landry-DeBoer. 2015. Variability in the selection patterns of pronghorn: are they really native prairie obligates? *In Review.*

Jorgensen, D. 2009. Annual migrations of female prairie rattlesnakes, *Crotalus v. viridis*, in Alberta. Masters of Science Thesis. Faculty of Environmental Design, University of Calgary, Calgary, AB. 96 pp.

Kang, S., S.W. Running, M. Zhao, J.S. Kimball, J. Glassy. 2005. Improving continuity of MODIS terrestrial photosynthesis products using an interpolation scheme for cloudy pixels. International Journal of Remote Sensing. 26(8):1659-1676.

Kawamura, K., Akiyama, T., Yokota, H. 2005. Monitoring of forage conditions with MODIS imagery in the Xilingol steppe, Inner Mongolia. International Journal of Remote Sensing, 26: 1423-1436.

Kie, J.G., T. Bowyer, M.C. Nicholson, B.B. Boroski, E.R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology, 83(2):530-544.

Kiesecker, J.M., H. Copeland, A. Pocewicz, B. McKenney. 2010. Development by design: blending landscape level planning with the mitigation hierarchy. Frontiers in Ecology and the Environment, 8(5):261-266.

Kitchen, D.W. 1974. Social behavior and ecology of the pronghorn. Wildlife Monographs, 38(1):3-96.

Koening, S. 2010. Temporal nearest neighbor tool (version 1.0): user guide for calculating nearest neighbor distance within a temporal window.

Kolar, J.L., J.J. Millspaugh, B.A. Stillings. 2011. Migration patterns of pronghorn in southwestern North Dakota. Journal of Wildlife Management, 75(1):198-203.

Lack, D. 1968. Bird migration and natural selection. Oikos, 19:1-9.

Lambeck, R.J. 1997. Focal species: A multi-species umbrella for nature conservation. Conservation Biology, 11(4):849-856.

Laszczak E., K. Ostapowicz, T. Kuemmerle, J. Kozak, K. Perzanowski, V. Radeloff. 2010. Modeling of potential connectivity of European bison herd ranges in the Carpathian mountains using graph theory approach. International Forestry Review, 12(5):81.

Leblond, M., J. Frair, D. Fortin, C. Dussault, J-P. Ouellet, R. Courtois. 2011. Assessing the influence of resource covariates at multiple spatial scales: an application to forest-dwelling caribou faced with intensive human activity. Landscape Ecology, 26:1433-1446.

Lendrum, P.E., C.R. Anderson Jr., R.A. Long, J.G. Kie, R.T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. Ecosphere, 3:82.

Lendrum, P.E., C.R. Anderson Jr., K.L. Monteith, J.A. Jenks, R.T. Bowyer. 2013. Migrating mule deer: effects of anthropogenically altered landscapes. PLoS ONE, 8: doi:10.1371/journal.pone.0064548.

Lesica, P., F.W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology, 9(4):753–760.

Lowe, W.H. 2009. What drives long-distance dispersal? A test of theoretical predictions. Ecology, 90(6):1456-1462.

Luckas, P. 2012. Personal communication in June 2012. College of Forestry and Conservation, University of Montana, Missoula, MT.

Main, M.B., B.E. Coblentz. 1996. Sexual segregation among rocky mountain mule deer. Journal of Wildlife Management, 60:497-507.

Martinka, C. 1966. International antelope herd. Montana Wildlife, July: 4 pp.

McCune, B., J.B. Grace. 2002. Chapter 4: Ordination *In* Analysis of ecological communities. Gleneden Beach, OR: MjM Software Design. 102-142 pp.

McRae, B.H., V.B. Shah, T.K. Mohapatra. 2008*a*. Ciruitscape software. Available at: http://www.circuitscape.org/.

McRae, B.H., B.G. Dickson, T.H. Keitt, V.B. Shah. 2008*b*. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology, 10:2712-2724.

McRae, B.H., D.M. Kavanagh. 2011. Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle WA. Available at: http://www.circuitscape.org/linkagemapper.

McRae, B.H. 2012*a*. Pinchpoint mapper connectivity analysis software. The Nature Conservancy, Seattle WA. Available at: http://www.circuitscape.org/linkagemapper.

McRae, B.H. 2012*b*. Barrier Mapper Connectivity Analysis Software. The Nature Conservancy, Seattle WA. Available at: http://www.circuitscape.org/linkagemapper.

Meyer, C.B., W. Thuiller.2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions, 12:288-297.

Mitchell, G.J. 1980. The pronghorn antelope in Alberta. University of Regina, Regina, Saskatchewan. 165 pp.

Mueller, T., K.A. Olson, T.K. Fuller, G.B. Schaller, M.G. Murray, P. Leimgruber. 2008. In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. Journal of Applied Ecology, 45:649-658.

Mueller, T., K.A. Olson, G. Dressler, P. Leimgruber, T.K. Fuller, C. Nicolson, A.J. Novaro, M.J. Bolgeri, D. Wattles, S. DeStefano, J.M. Calabrese, W.F. Fagan. 2011. How landscape dynamics link individual to population-level movement patterns: a multispecies comparison of ungulate relocation data. Global Ecology and Biogeography, 12 pp.

Murtaugh, P.A. 2007. Simplicity and complexity in ecological data analysis. Ecology, 88:56-62.

Myneni, R.B., C.D. Keeling, C.J. Tucker, G. Asrar, R.R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. Nature, 386:698-702.

Mysterud, A., R.A. Ims. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. Ecology, 79:1435-1441.

Mysterud, A., R. Langvatn, N.G. Yoccoz, N.C. Stenseth. 2001. Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography. Journal of Animal Ecology, 70(6):915-923.

Mysterud, A., L.E. Loe, B. Zimmermann, R. Bischof, V. Veiberg, E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes - a role for density dependence? Oikos, 120:1817-1825.

Mysterud, A. 2013. Ungulate migration, plant phenology, and large carnivores: the times they are a-changin'. Ecology, 94(6):1257-1261.

Naidoo, R., M.J. Chase, P. Beytell, D. Preez, K. Landen, G. Stuart-Hill, R. Taylor. 2014. A newly discovered wildlife migration in Namibia and Botswana is the longest in Africa. Onyx, doi:10.1017/S0030605314000222.

National Snow and Ice Date Center (NSIDC). 2006. MODIS/Terra Snow Cover 8-Day L3 Global 500m Grid, Version 5. Boulder, Colorado. Available at: http://www.nsidc.org/data/docs/daac/modis_v5/mod10a2_modis_terra_snow_8-day_global_500m_grid.gd.html. Accessed November 20, 2011.

Nelson, M.E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology, 73:1069-1076.

Nelson, M.E. 1998. Development of migratory behavior in northern white-tailed deer. Canadian Journal of Zoology, 76:426-432.

Nicholson, M.C., R.T. Bowyer, J.G. Kie. 1997. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy, 78(2):483-504.

NOAA. 2014. National Climatic Data Center. Available at: http://www.ncdc.noaa.gov/. Accessed February 27, 2015.

Northrup, J.M., M.B. Hooten, C.R. Anderson, Jr., G. Wittemyer. 2013. Practical guidance on characterizing availability in resource selection functions under a use-availability design. Ecology, 94(7):1456-1463.

Noss, R.F., E.T. Laroe, J.M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. Report No. 0611- R-01 (MF). National Biological Service, Washington, D.C., USA.

Noss, R.F. 1987. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology, 1:159-164.

Odonkhuu, D., K.A. Olson, G.B. Schaller, J.R. Ginsberg, T.A. Fuller. 2009. Activity, movements, and sociality of newborn mongolian gazelle calves in the eastern steppe. Acta Theriologica, 54(4):357-362.

O'Gara, W.B., C.M. Janis. 2004. Chapter 1: Scientific classification *In* Pronghorn Ecology and Management. B.W. O'Gara, J.D. Yoakum editors. W. M. Institute, Boulder CO. University Press of Colorado. 3-25 pp.

O'Gara, W.B., R.E. McCabe. 2004. Chapter 3: From exploitation to conservation *In* Pronghorn Ecology and Management. B.W. O'Gara, J.D. Yoakum editors. W. M. Institute, Boulder CO. University Press of Colorado. 41-73 pp.

Ockenfels, R.A., A. Alexander, C.L.D. Ticer, W.K. Carrel. 1994. Home ranges, movement patterns, and habitat selection of pronghorn in central Arizona. Arizona Game and Fish Department Technical Report 13, Phoenix, Arizona. 80 pp.

Olson, K.A., T.K. Fuller, G.B. Schaller, B. Lhagvasuren, D. Odonkhuu. 2005. Reproduction, neonatal weights, and first-year survival of mongolian gazelles (*Procapra gutturosa*). Journal of Zoology, London 265:227–233.

Opdam, P., J. Verboom, R. Pouwels. 2003. Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. Landscape Ecology, 18:113-126.

Ortega, I.M., W.L. Franklin. 1995. Social organization, distribution and movements of a migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia Natural, 68:489-500.

Owen-Smith, N. 2004. Functional heterogeneity in resources within landscapes and herbivore population dynamics. Landscape Ecology, 19:761–771.

Owen-Smith, N., D.R. Mason, J.O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology, 74(4):774-788.

Owen-Smith, N., J.M. Fryxell, E.H. Merrill. 2010. Foraging theory upscaled: the behavioural ecology of herbivore movement. Philosophical Transactions of the Royal Society B, 365:2267-2278.

Parker, K.L., P.S. Barboza, M.P. Gillingham. 2009. Nutrition integrates environmental responses of ungulates. Functional Ecology, 23:57-69.

Parks, S.A., K.S. McKelvey, M.K. Schwartz. 2013. Effects of weighting schemes on the identification of wildlife corridors generated with least-cost methods. Conservation Biology, 27(1):145-154.

Pearce, J., S. Ferrier. 2000. An evaluation of alternative algorithms for fitting species distribution models using logistic regression. Ecological Modelling, 128(2):127-147.

Pennycuick, L. 1975. Movements of the migratory wildebeest population in the Serengeti areas between 1960 and 1973. East African Wildlife Journal, 13:65-87.

Perez-Tris, J., J.L. Telleria. 2002. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. Journal of Animal Ecology, 71:211-234.

Peterson, G., C.R. Allen, C.S. Holling. 1998. Ecological resilience, biodiversity, and scale. Ecosystems, 1:6-18.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C. 2005. Using satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology and Evolution, 20: 503-510.

Plumptre, A.J., Kujirakwinja, D., Treves, A., Owiunji, I., Rainef, H. 2007. Transboundary conservation in the Virunga landscape: its importance for landscape species. Biological Conservation, 34: 279-287.

Polasky, S., E. Nelson, E. Lonsdorf, P. Fackler, A. Starfield. 2005. Conserving species in a working landscape: land use with biological and economic objectives. Ecological Applications, 15(4):1387-1401.

Polfus, J.L., M. Hebblewhite, K. Heinemeyer. 2011. Identifying indirect habitat loss and avoidance of human infrastructure by northern mountain woodland caribou. Biological Conservation, 144:2637-2646.

Poor, E.E., C. Loucks, A. Jakes, D.L. Urban. 2012. Comparing habitat suitability and connectivity modeling methods for conserving pronghorn migrations. PLoS ONE 7(11):e49390. doi:10.1371/journal.pone.0049390.

Poor, E.E., A. Jakes, C. Loucks, M. Suitor. 2014. Modeling fence location and density at a regional scale for use in wildlife management. PLoS ONE 9(1):e83912. doi:10.1371/journal.pone.0083912.

Python Software Foundation. Python Language Reference, version 2.7. Available at: http://www.phython.org/. Accessed April 20, 2013.

R Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Rettie, W.J., F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography, 23:466-478.

Richard, Y., D.P. Armstrong. 2010. Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. Journal of Applied Ecology, 47:603-610.

Riley, J.L., S.E. Green, K.E. Brodribb. 2007. A conservation blueprint for Canada’s prairies and parklands. Nature Conservancy Canada, 115 pp.

Saher, D.J., F.K.A. Schmiegelow. 2005. Movement pathways and habitat selection by woodland caribou during spring migration. Rangifer, 16:143-154.

Samways, M.J., C.S. Bazelet, J.S. Pryke. 2010. Provision of ecosystem services by large scale corridors and ecological networks. Biodiversity Conservation, 19:2949-2962.

Sappington, J.M., K.M. Longshore, D.B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave desert. Journal of Wildlife Management, 71(5):1419-1426.

Saskatchewan Environment. 2005. Saskatchewan state of the environment report 2005. State of the environment reporting planning and evaluation branch Saskatchewan environment, 3211 Albert Street Regina, Saskatchewan S4S 5W6.

Saunders, L. 2007. Random point generator script. ESRI, Inc.

Sawyer, H., F. Lindzey, D. McWhirter. 2005. Mule deer and pronghorn migration in western Wyoming. Wildlife Society Bulletin, 33(4):1266-1273.

Sawyer, H., R.M. Nielson, F. Lindzey, L.L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management, 70(2):396-403.

Sawyer, H., M.J. Kauffman, R.M. Nielson, J.S. Horne. 2009*a*. Identifying and prioritizing ungulate migration routes for landscape level conservation. Ecological Applications, 19(8):2016-2025.

Sawyer, H., M.J. Kauffman, R.M. Nielson. 2009*b*. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management, 73(7):1052-1061.

Sawyer, H., M.J. Kauffman. 2011. Stopover ecology of a migrating ungulate. Journal of Animal Ecology, 80(5):1078-1087.

Sawyer, H., M.J. Kauffman, A.D. Middleton, T.A. Morrison, R.A. Nielson, T.B. Wyckoff. 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. Journal of Applied Ecology, 50:68-78.

Sawyer, S.C., C.W. Epps, J.S. Brashares. 2011. Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology, 48:668-678.

Schaefer, J.A., C.M. Bergman, S.N. Luttich. 2000. Site fidelity of female caribou at multiple spatial scales. Landscape Ecology, 15:731-739.

Schwartz, C.C., Nagy, J.G. 1976. Pronghorn diets relative to forage availability in Northeastern Colorado. Journal of Wildlife Management, 40(3): 469-478.

Schwartz, C.C., J.G. Nagy, R.W. Rice. 1977. Pronghorn dietary quality relative to forage availability and other ruminants in Colorado. Journal of Wildlife Management, 41(2):161-168.

Schwartz, C.C., Ellis, J.E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology, 18: 343-353.

Seidler, R.G., R.A. Long, J. Berger, S. Bergen, J.P. Beckmann. 2014. Identifying impediments to long-distance mammal migrations. Conservation Biology, 29:99-109.

Sheldon, D.P. 2005. Pronghorn movement and distribution patterns in relation to roads and fences in southwestern Wyoming. Masters of Science Thesis. Department of Zoology and Physiology, University of Wyoming, Laramie, WY. 126 pp.

Sheriff, K. A. 2006. Modeling temporal and spatial variation in pronghorn antelope population dynamics in Southern Alberta in relation to environmental gradients. Masters of Environmental Design Thesis. Faculty of Environmental Design. University of Calgary, Calgary AB. 195 pp.

Sinclair, A.R.E. 2003. Mammal population regulation, keystone processes and ecosystem dynamics. Philosophical Transactions of the Royal Society B, 358:1729-1740.

Singh, N.J., Grachev, I.A., Bekenov, A.B., Milner-Gulland, E.J. 2010. Tracking greenery across a latitudinal gradient in central Asia – the migration of the saiga antelope. Diversity and Distributions, 16: 663-675.

Singh, N.J., G. Ericsson. 2014. Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. Biology Letters, 10:20140379.

Sodhi, N.S., R. Butler, W.F. Laurance, L. Gibson. 2011. Conservation successes at micro-, meso- and macroscales. Trends in Ecology and Evolution, 26(11):585-594.

Smith, D.G., T.A. Hoppe. 2000. Prairie agricultural landscapes: a land resource review. Prairie Farm Rehabilitation Administration. Regina, SK. 196 pp.

Smith, R.E. 2013. Conserving Montana’s sagebrush highway: long distance migration in sage-grouse. Masters of Science Thesis. College of Forestry and Conservation, University of Montana, Missoula, MT. 55 pp.

Squires, J.R., N.J. DeCesare, L.E. Olson, J.A. Kolbe, M. Hebblewhite. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biological Conservation, 157:187-195.

Suitor, M.J. 2011. Factors affecting pronghorn movement ecology in Alberta. Masters of Science Thesis. Faculty of Environmental Design, University of Calgary, Calgary, AB. 153 pp.

Sweanor, P.Y., F. Sandegren. 1988. Migratory behavior of related moose. Holarctic Ecology, 11(3):190-193.

Sweeney, J.M., J.R. Sweeney. 1984. Snow depths influencing winter movements of elk. Journal of Mammology, 65:524-526.

Taylor, P.D., L. Fahrig, K.A. With. 2006. Landscape connectivity: A return to the basics *In* Connectivity Conservation. K.R. Crooks, M. Sanjayan editors. Cambridge University Press. 29-43 pp.

Telfer, E.S., J.P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. Ecology, 65:1828-1834.

Thirgood, S., A. Mosser, S. Tham, G. Hopcraft, E. Mwangomo, T. Mlengeya, M. Kilewo, J. Fryxell, A.R.E. Sinclair, M. Borner. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. Animal Conservation, 7:113-120.

Thurfjell, H., S. Ciuit, M.S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology, 2(4):1-12.

Tollefson, T.N., L.A. Shipley, W.L. Myers, D.H. Keisler, N. Dasgupta. 2010. Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. Journal of Wildlife Management, 74(5):974-986.

Trombulak, S., C. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology, 14(1):18-30.

Tucker, R., G.W. Garner. 1984. Home range and diel movements of pronghorn antelope fawns in Brewster County, Texas. Proceedings of Pronghorn Antelope Workshop, 11:71-89.

Turner, M.G., Y. Wu, L.L. Wallace, W.H. Romme, A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation and fire in northern Yellowstone park. Ecological Applications, 4:472-496.

Turner, M.G., V.H. Dale, R.H. Gardner. 1989. Predicting across scales: theory development and testing. Landscape Ecology, 3(4):245-252.

Vander Wal, E., A.R. Rodgers. 2009. Designating seasonality using rate of movement. Journal of Wildlife Management, 73(7):1189-1196.

Van Moorter, B.,D.R. Visscher, C.L. Jerde, J.L. Frair, E.H. Merrill. 2010. Identifying movement states from location data using cluster analysis. Journal of Wildlife Management, 74(3):588-594.

Van Soest, P.J. 1994. Chapter 2: Nutritional Requirements *In* Nutritional Ecology of the Ruminant, Ithaca: Cornell University Press. 7-21 pp.

Violette, A.G. 2011. Digital elevation model geoprocessing notes: northern sage steppe initiative. Alberta Sustainable Resource Development. Lethbridge, Alberta, Canada. 1-6 pp.

Walpole, A.A., J. Bowman, D.L. Murray, P.J. Wilson. 2012. Functional connectivity of lynx at their southern range periphery in Ontario, Canada. Landscape Ecology, 27:761-773.

Webster, M.S., P.P. Marra, S.M. Haig, S. Bensch, R.T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. Trends in Ecology and Evolution, 17(2):76-83.

Welch, I.D., A.R. Rodgers, R.S. McKinley. 2000 Timber harvest and calving site fidelity of moose in northwestern Ontario. Alces, 36:93-103.

Wheatley, M., C. Johnson. 2009. Factors limiting our understanding of ecological scale. Ecological Complexity, 6:150-159.

White, P.J., T.L. Davis, K.K. Barnowe-Meyer, R.L. Crabtree, R.A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation, 135:502-510.

White, P.J., K.M. Proffitt, L.D. Mech, S.B. Evans, J.A. Cunningham, K.L. Hamlin. 2010. Migration of northern Yellowstone elk: implications of spatial structuring. Journal of Mammalogy, 91(4):827-837.

White, R., M. Siobhan, M. Rohweder. 2000. Pilot Analysis of Global Ecosystems: Grassland Ecosystems. World Resources Institute, Washington, DC. 89 pp.

Whittington, J., M. Hebblewhite, N.J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. Journal of Applied Ecology, 48(6):1535-1542.

Wilmshurst, J.F., Fryxell, J.M., Farm, B.P., Sinclair, A.R.E., Henschel, C.P. 1999. Spatial distribution of Serengeti wildebeest in relation to resources. Canadian Journal of Zoology, 77: 1223-1232.

Wiseman, P.A., M.D. Carling, J.A. Byers. 2006. Frequency and correlates of birth-site fidelity in pronghorns (*Antilocapra americana*). Journal of Mammalogy, 87(2): 312-317.

Yoakum, J.D. 2004. Chapter 4: Distribution and abundance. *In* Pronghorn Ecology and Management. B.W. O'Gara, J.D. Yoakum editors. W. M. Institute, Boulder CO. University Press of Colorado. 75-105 pp.

Zar, J.H. Biostatistical Analysis. 1999. Prentice Hall, New Jersey. 663 pp.

Zimmer, K. 2012. Spatial-temporal Habitat Analysis Tools (STHAT) for analyzing wildlife habitat variables at multiple selection scales. Masters of Geographic Information Systems Final Project Report. Department of Geography, University of Calgary, Calgary, AB.

APPENDICES

CHAPTER 1 APPENDICES

Appendix 1.1: NSSI GIS Layer Creation

In conjunction with collaborators, I developed GIS layers across international boundaries by taking careful consideration in obtaining data and seamlessly constructing outputs. Policies, data collection methods and converting metrics were all considered while creating these broad-scaled, international GIS layers. In 2007, Northern Sagebrush Steppe Initiative (NSSI) cooperators, Montana Fish, Wildlife & Parks, Alberta Sustainable Resource and Development and Saskatchewan Ministry of Environment signed a Memorandum of Understanding (MOU). The main purpose of this document was to manage wildlife species from a holistic perspective, which included seasonal ranges and migrations that occur on both the U.S. and Canadian side of the boarder. One of the objectives in this MOU was to create seamless spatial layers for the NSS area for the following GIS layers.

Landcover Layer

The NSSI landcover layer was created by mosaicking datasets from the Land Cover for Agricultural Regions of Canada-circa 2000 (AAFC) and the Montana Land Cover Framework 2010, resulting in 12 categorical landcover types. The initial land cover were based on Canadian AAFC, and in 2013 the NSSI land cover layer was reclassified based on MT Natural Heritage Program expertise to align Montana land cover types more properly with the overarching 12 categories of the Canadian AAFC land cover layer. The resulting layer resolution is 30m x 30m.

Digital Elevation Model Layer

A NSSI digital elevation models (DEM) layer was created by Alberta Sustainable Resource Development personnel with various topographic products. For my needs, a 30m x 30m raster cell size continual decimal surface was utilized to create subsequent aspect, slope and vector ruggedness measure (VRM) NSS layers. Full documentation is provided in Violette (2011).

Natural Gas/Oil Well Layer

A NSSI natural gas/oil well layer was created by combining datasets acquired from both government and industry entities. Alberta well data was obtained from Alberta Sustainable Resource and Development through conditional access provided by IHS Energy (Canada) Ltd. (http://energy.ihs.com/Solutions/Regions/Canada/). Saskatchewan well data was obtained from Saskatchewan Energy and Resources. Montana well data was obtained from Montana Fish, Wildlife & Parks through the Montana Board of Oil and Gas. Montana drill date attributes were specifically obtained from Montana Fish, Wildlife & Parks through Montana Board of Oil and Gas – Live Data Website (http://www.bogc.dnrc.mt.gov/MBOGCdotNET/).

Road Layer

The NSSI roads dataset was created by mosaicking roads layers across the NSS area. Alberta datasets were obtained from Alberta Sustainable Resource and Development through a partnership with AltaLIS Ltd., as agent for Spatial Data Warehouse Ltd. (SDW) (www.altalis.com). Saskatchewan datasets were obtained from Saskatchewan Ministry of Environment - Information Services Corporation of Saskatchewan in partnership with NRCAN. Montana datasets were obtained from Montana Fish, Wildlife & Parks through the Montana Department of Transportation, Planning/Data & Statistics Bureau and Montana State Library, and U.S. Census Bureau/Geography Division.

Hydrography Layers

NSSI collaborators created two scales of hydrography layers to represent linear hydrology features (major rivers, streams, creeks, canals, etc.) across the NSS.

1:1,000,000 Scale

Data was downloaded from the Government of Canada – Natural Resources of Canada Website: http://www.geogratis.gc.ca/download/frameworkdata/hydrology/analytical/drainage_network/. The "Nelson" drainage file was used because it covered the entirety of the NSS region. Collaborators then clipped the file to the boundary of the NSS. Since the data was first downloaded, the drainage layers have been separated on the Government of

Canada website. Data can now be downloaded from the following websites and clipped to the NSS boundary:

1) Nelson Drainage
http://geogratis.gc.ca/api/en/nrcan-rncan/ess-sst/cff70bbc-977e-5a4d-8d5b-b5498b29ca08.html

2) Mississippi Drainage
http://geogratis.gc.ca/api/en/nrcan-rncan/ess-sst/af47d9da-e189-582a-a1e1-43c16ec29cf7.html

1:250,000 Scale

Hydrography layers at this finer scale were not complete across the entire NSS region (i.e. Canadian and American layers were found at different scales). As a result, data was downloaded from the following sources, edited and mosaicked together to represent linear hydrologic features at this scale. First, 1:250,000 scale linear hydrography maps (known as NTDB) were downloaded from the Government of Canada website that covered the Canadian portion of the NSS: http://geogratis.cgdi.gc.ca/geogratis/en/product/search.do?id=F3D83500-2564-D61E-4F37-FEF860E6DDC0. The documentation for the NTDB is in http://www.canadaNTDB_dataDictionary_3_1.pdf , http://www.NTDB_250k_appentd3_en.pdf and, http://www.ntdb_v3_shape_format_geogratis_en.pdf (this file contains attribute codes and definitions). For the U.S. side, NSSI collaborators downloaded 1:100,000 scale linear hydrography data from NHD http://nhd.usgs.gov/ and NHN http://www.geobase.ca/geobase/en/data/nhn/index.html;jsessionid=1CA5ECB447B642ED42C624912455AEAB websites covering the NSS region and clipped these layers to the Montana portion of the NSS. Collaborators then downloaded 1:250,000 Digital Raster Graphics (DRGs) obtained from USGS http://topomaps.usgs.gov/drg/ that covered the Montana portion of the NSS to manually delete linear hydrography data from the 1:100,000 layer that did not appear on the 1:250,000 DRGs. Specific edits included adding a “Hydro100k” field and attributing the field as “y” for those lines that did not appear on the 1:250,000 DRG’s. The result was an edited 1:250,000 linear hydrography layer for Montana’s portion of the NSS. This edited Montana layer was merged with the

Canadian 1:250,000 linear hydrography layer in ArcGIS and then clipped to the boundaries of the NSSI, resulting in a final 1:250,000 "NSSIWatercourse" layer. The "NSSIWatercourse" layer was comprised of selected line work from the edited 1:250,000 Montana layer (where "Hydro100k" field <> 'y') and all line work from the 1:250,000 Canadian layer.

CHAPTER 2 APPENDICES

Appendix 2.1: Refined movement classification script based on Bunnefeld et al. (2011) using pronghorn ET179 as an example and standardized rules for identifying start/stop relocations for pronghorn across the NSS from 2003-2011.

Script

```
ET179 = read.csv("C:/Users/ET179.csv",header=TRUE)
head(ET179)

diff.NSD = diff(ET179$NSD)
nrow(ET179)
diff.date = ET179$NUMDATE[1:length(diff.NSD)]
plot(diff.date,diff.NSD)
par(mfrow=c(2,1))
plot(ET179$NUMDATE,ET179$NSD)
plot(diff.date,diff.NSD)
hist(diff.NSD)

FAWN = 0 # #Enter 1 if discrete fawning range##
FACULTATIVE = 1 ## Enter 1 if facultative movement occurs##
nsdhist = hist(ET179$NSD,breaks=50)
avg.sum = median(nsdhist$mids[nsdhist$counts>5&nsdhist$mids>mean(ET179$NSD)])
max.sum = max(ET179$NSD)
sum.diff = ET179$NSD-avg.sum
max.diff = ET179$NSD-max.sum
diff.date[diff.NSD<wint.tol*avg.sum]
```

```
end.diff = ET179$NSD-ET179$NSD[length(ET179$NSD)]

plot(diff.date, diff.NSD)
points(diff.date[mig],diff.NSD[mig], col="red")

wint.tol = .01
sum.tol = .05
start.spring = diff.date[which(diff.NSD>wint.tol*avg.sum)[1]]
if (FAWN ==1){
        end.spring = ET179$NUMDATE[which(abs(max.diff)<sum.tol*max.sum)[1]+1]
        } else {
        end.spring = ET179$NUMDATE[which(abs(sum.diff)<sum.tol*avg.sum)[1]+1]
        }
rev.date = rev(diff.date)
rev.DATE = rev(ET179$NUMDATE)
rev.diff.NSD = rev(diff.NSD)
rev.sum.diff = rev(sum.diff)
#end.fall = rev.date[which(rev.diff.NSD>wint.tol*avg.sum)[1]]
start.fall = rev.DATE[which(abs(rev.sum.diff)<sum.tol*avg.sum)[1]+2]
end.NSD = diff.date[!(diff.date %in% diff.date[diff.NSD<wint.tol*avg.sum])& diff.date>start.fall]
end.diff = ET179$NSD- mean(end.NSD)
end.fall= diff.date[which(end.diff<wint.tol*avg.sum)[which(end.diff<wint.tol*avg.sum)>start.fall][1]+1]

if (FACULTATIVE == 1){
        start.fac=
sort(rev.DATE[which(diff(rev(ET179$NUMDATE[which(end.diff>wint.tol*ET179$NSD[length(ET179$NSD)])])))<(-1))])
        start.fac = start.fac[start.fac>end.fall][1]-1
        end.fac = ET179$NUMDATE[rev(which(abs(end.diff)<sum.tol*ET179$NSD[length(ET179$NSD)]))]
```

```
	end.fac = ifelse(any(end.fac>start.fac), (end.fac=end.fac[1]+1),NA)
	}

#start.fall = ET179$NUMDATE[which((-diff.NSD)>sum.tol*avg.sum)[(diff(which((-diff.NSD)>sum.tol*avg.sum),lag=2)<4)][1]-1]
#end.fall= diff.date[which(end.diff<wint.tol*avg.sum)[which(end.diff<wint.tol*avg.sum)>start.fall][1]]
mig = c(start.spring,end.spring,start.fall, end.fall,start.fac,end.fac)

plot(ET179$NUMDATE,ET179$NSD, type="b")
points(ET179$NUMDATE[mig],ET179$NSD[mig], col = "red")
```

Rules

Start Movement: Relocation must be within 24 hour time period of allocated start date identified by refined script. The first movement relocation is the last observation on seasonal range before linear movement occurs.

End Movement: Relocation must be within 24 hours of allocated end date identified by refined script. The last movement relocation is the last observation that is in the same trajectory (<90°) of previous relocations when reaching seasonal range destination. In the case of driven movements, the last relocation may follow this rule or it may be either the first mortality relocation or the first relocation where collar fell off.

Appendix 2.2: Complete ANOVA and analysis of deviance results to test for annual variation in each movement metric for each pronghorn movement classification across the NSS from 2003-2011.

Spring Migration

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	3156	631.2	3.391	0.00756
Residuals	88	16381	186.2		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	16382			
2	93	19537	-5	-3155.9	0.00459

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	3965	793.0	2.605	0.0303
Residuals	88	26784	304.4		

Analysis of Deviance

Resid.	Df	Resid.Dev	Df	Deviance	Pr(>Chi)
1	88	26784			
2	93	30749	-5	-3964.9	0.02313

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	1214	242.9	0.906	0.481
Residuals	88	23599	268.2		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	23599			
2	93	24814	-5	-1214.5	0.4761

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	32733	6547	2.346	0.0476
Residuals	88	245550	2790		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	245550			
2	93	278283	-5	-32733	0.03867

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	153235	30647	1.767	0.128
Residuals	88	1526433	17346		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	1526433			
2	93	1679668	-5	-153235	0.1159

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.104	0.02077	0.513	0.765
Residuals	88	3.559	0.04044		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	3.5591			
2	93	3.6629	-5	-0.10384	0.7663

Rate of Movement- Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.0392	0.007838	0.373	0.866
Residuals	88	1.8499	0.021022		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	1.8499			
2	93	1.8891	-5	-0.039191	0.8676

Rate of Movement- Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.050	0.01001	0.542	0.744
Residuals	88	1.624	0.01845		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	1.624			
2	93	1.674	-5	-0.050028	0.7445

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	20.3	4.068	0.598	0.701
Residuals	88	598.2	6.798		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	88	598.19			
2	93	618.53	-5	-20.34	0.7012

Fall Migration

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	19053	3811	3.968	0.00356
Residuals	60	57616	960		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	57616			
2	65	76669	-5	-19053	0.001338

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	11029	2205.9	2.625	0.0327
Residuals	60	50417	840.3		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	50417			
2	65	61446	-5	-11029	0.02223

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	1425	285.0	2.807	0.0241
Residuals	60	6091	101.5		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	6090.7			
2	65	7515.6	-5	-1424.9	0.01538

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	36730	7346	4.536	0.00142
Residuals	60	97177	1620		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	97177			
2	65	133907	-5	-36730	0.0003888

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	88504	17701	2.51	0.0396
Residuals	60	423166	7053		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	423166			
2	65	511670	-5	-88504	0.02799

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.0984	0.01969	0.544	0.742
Residuals	60	2.1704	0.03617		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	2.1704			
2	65	2.2688	-5	-0.098447	0.7428

Rate of Movement – Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.0611	0.01223	0.329	0.893
Residuals	60	2.2298	0.03716		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	2.2298			
2	65	2.2910	-5	-0.06115	0.8957

Rate of Movement – Measure Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	0.0672	0.01343	0.341	0.886
Residuals	60	2.3642	0.03940		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	2.3643			
2	65	2.4314	-5	-0.067164	0.8883

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	5	1.54	0.3074	0.428	0.827
Residuals	60	43.09	0.7182		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	60	43.092			
2	65	44.629	-5	-1.5369	0.8295

Fawning-associated Movements

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	2092.1	697.4	8.704	0.00924
Residuals	7	560.8	80.1		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	560.83			
2	10	2652.91	-3	-2092.1	9.036e-06

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	2679	893.0	22.17	0.000597
Residuals	7	282	40.3		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	282.0			
2	10	2960.9	-3	-2678.9	2.398e-14

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	51.83	17.28	0.504	0.692
Residuals	7	240.17	34.31		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	240.17			
2	10	292.00	-3	-51.833	0.6798

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	1169	389.5	1.595	0.275
Residuals	7	1710	244.3		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	1709.9			
2	10	2878.5	-3	-1168.6	0.1883

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	699	233	0.025	0.994
Residuals	7	66226	9461		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	66226			
2	10	66925	-3	-699.31	0.9948

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.1845	0.06149	0.632	0.618
Residuals	7	0.6814	0.09735		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	0.68142			
2	10	0.86589	-3	-0.18447	0.5945

Rate of Movement – Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.2923	0.09742	0.628	0.619
Residuals	7	1.0851	0.15502		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	1.0851			
2	10	1.3774	-3	-0.29226	0.5965

Rate of Movement – Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.2288	0.07628	0.786	0.538
Residuals	7	0.6789	0.09698		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	0.67889			
2	10	0.90772	-3	-0.22883	0.5012

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	18.745	6.248	13.52	0.00268
Residuals	7	3.235	0.462		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	3.2348			
2	10	21.9794	-3	-18.744	8.098e-09

Driven Movements

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	1847	615.7	1.405	0.252
Residuals	49	21469	438.1		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	21469			
2	52	23316	-3	-1847.1	0.2391

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	1177	392.2	0.655	0.584
Residuals	49	29333	598.6		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	29333			
2	52	30510	-3	-1176.7	0.5796

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	1259	419.5	3.802	0.0158
Residuals	49	5406	110.3		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	5406.3			
2	52	6664.8	-3	-1258.6	0.009716

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	14612	4871	4.677	0.00596
Residuals	49	51024	1041		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	51024			
2	52	65637	-3	-14612	0.002861

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	46019	15340	4.834	0.00502
Residuals	49	155478	3173		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	155478			
2	52	201497	-3	-46019	0.002294

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.261	0.08701	2.785	0.0505
Residuals	49	1.531	0.03124		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	1.5307			
2	52	1.7917	-3	-0.26102	0.03921

Rate of Movement – Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.1153	0.03844	1.589	0.204
Residuals	49	1.1851	0.02419		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	1.1851			
2	52	1.3005	-3	-0.11533	0.1896

Rate of Movement – Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.1795	0.05984	2.12	0.11
Residuals	49	1.3831	0.02823		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	1.3832			
2	52	1.5627	-3	-0.17951	0.09537

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	11.46	3.819	3.709	0.0175
Residuals	49	50.45	1.030		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	49	50.453			
2	52	61.909	-3	-11.456	0.01106

Spring Stopover

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	850	212.5	1.161	0.348
Residuals	29	5311	183.1		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	5310.6			
2	33	6160.7	-4	-850.13	0.326

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	1682	420.4	2.181	0.0961
Residuals	29	5590	192.8		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	5589.9			
2	33	7271.6	-4	-1681.7	0.06837

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	206.2	51.54	1.78	0.16
Residuals	29	839.6	28.95		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	839.58			
2	33	1045.76	-4	-206.18	0.1296

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	21.99	5.498	0.74	0.573
Residuals	29	215.59	7.434		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	215.59			
2	33	237.58	-4	-21.991	0.5648

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	7793	1948	1.618	0.196
Residuals	29	34911	1204		

Analysis of Deviance

Resid.	Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	34911			
2	33	42704	-4	-7792.6	0.1665

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	0.03898	0.009745	1.247	0.313
Residuals	29	0.22660	0.007814		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	0.22660			
2	33	0.26558	-4	-0.03898	0.2885

Rate of Movement – Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	0.000835	0.0002088	1.082	0.384
Residuals	29	0.005596	0.0001930		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	0.0055964			
2	33	0.0064318	-4	-0.00083535	0.3633

Rate of Movement – Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	0.01211	0.003028	0.661	0.624
Residuals	29	0.13287	0.004582		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	0.13287			
2	33	0.14498	-4	-0.012112	0.6191

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	4	47.48	11.87	2.924	0.038
Residuals	29	117.74	4.06		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	29	117.74			
2	33	165.22	-4	-47.482	0.01977

Fall Stopover

Start Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	1335.5	445.2	3.264	0.0894
Residuals	7	954.7	136.4		

Analysis of Deviance

Resid. Df		Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	954.67			
2	10	2290.18	-3	-1335.5	0.02041

Stop Date

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	842.2	280.7	1.67	0.259
Residuals	7	1176.7	168.1		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	1176.8			
2	10	2018.9	-3	-842.16	0.1711

Duration

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	205.1	68.38	1.665	0.26
Residuals	7	287.4	41.06		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	287.42			
2	10	492.55	-3	-205.13	0.1721

Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	15.77	5.257	1.437	0.311
Residuals	7	25.61	3.659		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	25.615			
2	10	41.388	-3	-15.772	0.2299

Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	5825	1942	1.8	0.235
Residuals	7	7549	1078		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	7549.4			
2	10	13374.1	-3	-5824.7	0.1447

Displacement Ratio

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.01705	0.005682	0.494	0.698
Residuals	7	0.08047	0.011496		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	0.080474			
2	10	0.097521	-3	-0.017046	0.6863

Rate of Movement – Euclidian Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.0000598	1.993e-05	0.181	0.906
Residuals	7	0.0007688	1.098e-04		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	0.00076875			
2	10	0.00082855	-3	-5.9795e-05	0.909

Rate of Movement – Measured Distance

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	0.02490	0.008300	3.233	0.091
Residuals	7	0.01797	0.002567		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	0.017972			
2	10	0.042873	-3	-0.0249	0.02131

Radians

ANOVA	Df	Sum Sq	Mean Sq	F value	Pr(>F)
data$year	3	2.509	0.8363	0.91	0.483
Residuals	7	6.433	0.9189		

Analysis of Deviance

	Resid. Df	Resid. Dev	Df	Deviance	Pr(>Chi)
1	7	6.4326			
2	10	8.9413	-3	-2.5088	0.4351

CHAPTER 3 APPENDICES

Appendix 3.1: Assessed approaches for matching control to case points across for third-order modeling of pronghorn migratory pathway selection across the NSS from 2004-2010.

Approach	Turn Angle Distribution	Step Length Distribution	Season
DefinedTurns2EmpiricalStep	Constrained to 180°	Empirical - Individual Level	Separate
DefinedTurnsEmpiricalSteps	Constrained to 90°	Empirical - Individual Level	Separate
EmpiracalOneAnimals	Empirical - Individual Level	Empirical - Individual Level	Separate
EmpiracalStdss	Standard Deviations - Population Level	Standard Deviations - Population Level	Separate
CauchyWeibull	Wrapped Cauchy - Population Level	Weibull - Population Level	Both

Appendix 3.2: Refined "Temporal Nearest Distance" Python 2.7 script based on Koenig (2010) that calculates the nearest neighbor distance between two points of consideration within a temporal window.

```
#   Purpose: This script finds the nearest feature in a feature class representing
#   an independent variable to every feature in a feature class representing a
#   dependent variable and then adds that value to a field in the dependent
#   feature class. The script conducts this work after limiting the features
#   in the independent feature class to a user defined temporal window around the
#   'datetime' for the feature in question in the dependent feature class.

#   Requirements: ArcGIS 10.1

#   Notes: This script assumes the dependent and independent feature classes are
#   in the same projection. The projection selected should be a distance
#   preserving one. Currently the script sets the distance to -1 if no
#   independent features are found within the temporal window for a given feature.
#-----------------------------------------------------------------------------

import arcpy

import datetime

import os

##This function accepts a single coordinate pair and a dictionary of coordinate##

##Pairs to check the distance to. It returns the minimum distance##
```

```
##Distances returned are virtually identical to those of the NEAR command in ArcMap##
#This function assumes the coordinates are in a projected (i.e. flat) coordinate system##
def findShortestDist(inCoord,testDict):
    import math
    x1 = inCoord[0][0]
    y1 = inCoord[0][1]
    distances = []
    for test in testDict:
        x2 = testDict[test][0][0]
        y2 = testDict[test][0][1]
        distance = math.sqrt(math.pow(x2-x1,2) + math.pow(y2-y1,2))
        """The next two lines, if uncommented, could set a 'null' value
        for wells over a certain distance if desired."""
        #if distance > 5000:
            #distance = -1
```

```
        distances.append(distance)
    #print "Min distance:",min(distances)
    return min(distances)

##Environment variables##
arcpy.env.overwriteOutput = True
##User input##
"""Need to change the paths below for depFc and indepFC to reflect your real inputs"""
"""depFc = antelope"""
"""indepFc = wells"""
depFc = r"C:\Users\ajakes9\Documents\GIS\StepSelectionFunctionAnalysis\Mock Database"
indepFc = r"F:\NSSLayers\NSSI_EnergyWells\toolData\wellData.gdb\nssiWells"
"""You might need to change the names of the date fields as well"""
depDate = "DATETIME_MASTER"
```

```
indepDate = "DRILL_DATE"
"""Set the temporal window using these values. Currently set to a 14 day window (7 days either side)."""
daysBefore = 8
daysAfter = 8
"""Might need to change the location of this folder, which is used as a location for the scratch.gdb"""
scratchFolder= r"C:\Temp\jakes\temporalDistance"
##Create a path for the scratch workspace##
scratchWs = scratchFolder + os.path.sep + "scratch.gdb"
##Create the scratch geodatabase##
if not arcpy.Exists(scratchWs):
    arcpy.CreateFileGDB_management(scratchFolder,"scratch.gdb")
##Loop through all the records in the dependent feature class (antelope) and store the observation##
##date to a list##
dateList = []
with arcpy.da.SearchCursor(depFc,depDate) as cursor:
```

```
    for row in cursor:
        rowDate = row[0]
        dateList.append(rowDate)
##Find the minimum and maximum date for the entire dependent dataset##
minDate = min(dateList)
maxDate = max(dateList)
##Add/subtract a certain number of days (specified above as input variables) to the minDate and maxDate##
newMinDate=minDate - datetime.timedelta(days=int(daysBefore))
newMaxDate=maxDate + datetime.timedelta(days=int(daysAfter))
print "dependant variable dates examined"
##Select the rows from the independent dataset (wells) that are between newMinDate and newMaxDate##
whereClause = '"' + str(indepDate) +'"' + " >= date '" + str(newMinDate.date()) + "'" + " AND " + '"' + str(indepDate) +'"' + " <= date '" + str(newMaxDate.date()) + "'"
arcpy.MakeFeatureLayer_management(indepFc,"indepFcLyr",whereClause)
##Copy these selected records to the scratch geodatabase for use in the next steps##
arcpy.CopyFeatures_management("indepFcLyr",scratchWs + os.path.sep + "indepVar")
```

```
##Make a feature layer from this new (temporaly narrowed) feature class##
arcpy.MakeFeatureLayer_management(scratchWs + os.path.sep + "indepVar","indepVarLyr")
##Now create a search cursor that loops through each animal location##
##Write these out to a dictionary for later use##
global obsWindowDict
obsWindowDict = {}

fields = ["OID@","SHAPE@XY",depDate]
with arcpy.da.SearchCursor(depFc,fields) as cursor:
    for row in cursor:
        obsDate = row[2].date()
        earlyWindowDate = obsDate - datetime.timedelta(days = daysBefore)
        lateWindowDate = obsDate + datetime.timedelta(days = daysAfter)
        obsWindowDict[row[0]] = [row[1],earlyWindowDate,lateWindowDate]
print "dependant data added to dictionary"
```

```
for obs in obsWindowDict:

    earlyWindowDate = obsWindowDict[obs][1]

    lateWindowDate = obsWindowDict[obs][2]

    ##Create a selection set on the independent feature class that falls in the temporal window for the current observation##

    whereClause = '"' + str(indepDate) +'"' + " >= date '" + str(earlyWindowDate) + "'" + " AND " + '"' + str(indepDate) + '"' + " <= date
'" + str(lateWindowDate) + "'"


    arcpy.SelectLayerByAttribute_management("indepVarLyr","NEW_SELECTION",whereClause)

    result = int(arcpy.GetCount_management("indepVarLyr").getOutput(0))

    global wellsDict

    wellsDict = {}

    ## Check to make sure there are some wells within the given temporal window before attempting to find the nearest one##

    if result > 0:

        fields = ["OID@","SHAPE@XY",indepDate]

        with arcpy.da.SearchCursor("indepVarLyr",fields,whereClause) as cursor:

            for row in cursor:
```

```
                wellsDict[row[0]]=[row[1]]

        ##Run to find shortest distance function defined at top of script##
        nearDist = findShortestDist(obsWindowDict[obs],wellsDict)
    else:
        """If there are no wells to check distance to....then set the distance equal to -1"""
        """You might want to change this value."""
        nearDist = -1
    print obs, whereClause, nearDist
    obsWindowDict[obs].append(nearDist)
##Adds a field to hold the distance to Nearest well##
arcpy.AddField_management(depFc,"nearestWel","DOUBLE")
##Adds the Nearest well distance to the dependent feature class##
with arcpy.da.UpdateCursor(depFc,["OID@","nearestWel"]) as cursor:
    for row in cursor:
```

```
row[1] = obsWindowDict[row[0]][3]
    cursor.updateRow(row)
```

Appendix 3.3: Third-order individual variable coefficients for pronghorn fall migratory pathway selection across the NSS from 2004-2010.*

Pronghorn	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	Near Well	Well Den.	Hydro. Den.
ET03	2870.0	-1043000.0	47.1	89.7	-0.000020	70830.0	485.3
ET26	-7773.0	726800.0	-234.0	81760.0	-0.000036	-251900.0	75.9
ET27	18980.0	-4224000.0	643.9	-100500.0	-0.000142	-347200.0	3183.0
ET28	101800.0	-104500000.0	-241.0	25760.0	-0.000007	-114700.0	268.0
ET30	NA	NA	1002.0	-232500.0	-0.000217	-51670.0	NA
ET31	-847.6	73060.0	-198.9	36610.0	-0.000008	-25550.0	-103900.0
ET39	-5922.0	538700.0	-283.6	8730.0	0.000037	113500.0	-187.9
ET41	193.3	NA	-130.0	13230.0	-0.000027	-54890.0	-41270.0
ET51	NA	NA	1243.0	-210400.0	0.000050	-253100.0	-995.3
ET62	-8764.0	559000.0	-188.1	15450.0	0.000033	-97810.0	-2158.0
ET63	7772.0	-2411000.0	221.7	-80870.0	0.000003	-160200.0	NA
ET73	NA	NA	129.0	-24320.0	0.000084	-88430.0	NA
ET113	NA	NA	-407.4	52650.0	0.000085	-2059000.0	-751.9
ET123	NA	NA	-295.1	39970.0	NA	-170600.0	-63.6
ET125	NA	NA	938.1	-162000.0	0.000231	1390000.0	1235.0
ET130	-11710.0	2630000.0	309.2	-51500.0	0.000135	-27530.0	331.4
ET131	-10050.0	1354000.0	253.1	-25050.0	0.000084	-117300.0	-484.9
ET138	16960.0	-4231000.0	-347.2	45430.0	0.000147	-366300.0	-390.6
ET140	-9592.0	1139000.0	-46.2	11660.0	0.000680	-2166000.0	2799.0
ET141	-2738.0	NA	-2163.0	368600.0	0.000028	977700.0	2308.0
ET142	-9936.0	1255000.0	31.9	3174.0	0.000352	1424000.0	-120.0
ET145	12920.0	-1966000.0	-27730.0	3932000.0	0.000101	-295300.0	-98810.0

***Coefficients in RED indicate $p \leq 0.05$

Pronghorn	**NDVI**	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
ET03	5.6	596.2	0.303	-0.023	0.094	0.36	-18.1
ET26	-7.6	134.4	-0.324	0.015	-0.148	0.13	NA
ET27	3.3	3203.0	-0.418	-0.070	-0.496	-0.66	NA
ET28	4.1	-365.8	-0.137	0.000	-0.094	-0.34	0.1
ET30	-5.2	-72.8	0.065	-0.013	0.033	15.76	NA
ET31	-0.4	-302.4	0.323	-0.045	-0.238	0.28	1.6
ET39	0.4	-1050.0	0.470	-0.087	0.095	0.28	NA
ET41	-2.1	-954.5	0.573	-0.158	-0.367	1.08	NA
ET51	-5.2	-107.3	0.116	-0.019	-0.413	1.18	NA
ET62	-0.5	462.4	0.147	-0.032	-0.227	0.07	-16.1
ET63	-4.2	-1478.0	0.207	-0.022	-0.171	-0.55	-20.6
ET73	-14.4	346.2	0.604	-0.129	0.242	15.46	NA
ET113	-1.6	-131.2	-0.139	0.008	-0.247	-0.40	0.4
ET123	-0.5	-237.1	0.288	-0.019	-0.047	-0.79	-0.4
ET125	-14.5	-947.5	1.047	-0.096	0.240	19.58	20.4
ET130	-7.1	-237.1	0.271	-0.024	-0.691	0.89	0.8
ET131	-4.9	-184.8	0.326	-0.029	-0.595	1.35	NA
ET138	-6.8	-826.7	0.130	-0.007	-0.026	0.30	-1.0
ET140	-8.8	-206.1	-0.003	0.004	-0.625	1.42	0.4
ET141	-0.8	-73.0	0.036	-0.005	-0.050	-0.43	-17.8
ET142	-11.7	-80.4	-0.031	0.002	-0.424	0.78	1.0
ET145	4.2	-147.1	-0.603	0.076	-0.610	0.62	0.9

*****Coefficients in RED indicate $p \leq 0.05$

Pronghorn	**PPCROP**	**WETLAND**	**WATER**	**EXPOSED**	**DEVELOP**	**CONIF**	**DECID**
ET03	0.220	-17.820	-17.9	-18.3	0.2	-18.0	-18.0
ET26	-0.357	NA	NA	NA	NA	-18.4	NA
ET27	-18.920	-19.840	NA	NA	25.4	NA	NA
ET28	-0.056	-1.042	-19.3	NA	-18.4	NA	NA
ET30	NA	15.340	-1.3	NA	NA	NA	NA
ET31	0.890	0.677	0.1	44.9	NA	NA	-16.1
ET39	-17.210	0.467	-17.3	NA	NA	NA	NA
ET41	1.615	-18.520	-17.9	0.2	-19.3	NA	NA
ET51	-16.150	-15.590	-16.1	NA	NA	NA	-16.2
ET62	-0.374	0.631	-17.7	NA	15.6	-16.8	NA
ET63	-0.338	-20.520	-20.3	-20.6	-18.2	NA	-20.4
ET73	NA	NA	NA	NA	NA	NA	NA
ET113	-1.078	-0.005	NA	-15.4	NA	NA	NA
ET123	-1.082	-1.546	NA	-1.9	-16.5	NA	-16.7
ET125	1.003	-0.303	NA	21.0	NA	NA	NA
ET130	2.536	-17.790	NA	2.3	-48.6	NA	-17.2
ET131	-14.990	2.224	NA	3.3	-16.2	NA	-16.4
ET138	0.714	0.086	NA	0.5	1.0	NA	-16.7
ET140	0.885	-17.240	NA	0.9	-16.4	NA	-19.6
ET141	-2.018	NA	NA	NA	NA	NA	NA
ET142	0.231	-16.130	NA	0.3	-17.0	NA	-15.8
ET145	-0.340	NA	NA	NA	-51.5	NA	NA

*****Coefficients in RED indicate $p \leq 0.05$

Pronghorn	**Paved Rd.**	**Paved Rd.^{2}**	**All Road**	**All Road^2**	**Near Well**	**Well Den.**	**Hydro. Den.**
ET148	39510.0	-10670000.0	135.3	-67320.0	0.000226	180900.0	-417.3
ET150	NA	NA	-159.5	-14330.0	-0.000032	-1502000.0	119.9
ET154	NA	NA	-5862.0	441800.0	0.000116	-31220.0	-75.9
ET159	NA	NA	-12120.0	1476000.0	-0.000041	365000.0	-93.4
ET163	928.2	NA	-28960.0	4124000.0	0.000307	-535100.0	-692.3
ET165	312800.0	-49230000.0	-162700.0	25590000.0	-0.000422	NA	-742.6
ET166	-3578.0	NA	-1466.0	234100.0	-0.000082	706000.0	-920.3
ET167	NA	NA	1512.0	-268800.0	NA	1844000.0	-28000.0
ET168	NA	NA	-60.0	-25880.0	0.000118	3186000.0	-2493.0
ET169	NA	NA	-5982.0	414500.0	NA	-2948000.0	-129000.0
ET171	-60140.0	10430000.0	-176.4	19750.0	-0.000287	-6306000.0	-1066.0
ET174	NA	NA	197.1	-39960.0	NA	-350000.0	-27150.0
ET179	NA	NA	-533.1	76530.0	NA	411700.0	-95.5
ET185	115200.0	-18100000.0	-157.2	2950.0	NA	113600.0	-169.2
ET190	NA	NA	-135.0	5998.0	NA	-177300.0	660.7
ET191	NA	NA	262.0	-87230.0	NA	-102000.0	-223.2
ET192	-1621.0	453700.0	516.2	-204100.0	NA	-2066000.0	272.5
ET193	NA	NA	51.4	-19370.0	0.000286	128500.0	-94430.0
ET198	NA	NA	1037.0	-209000.0	NA	363400.0	-964.8
ET199	NA	NA	-203.4	31490.0	-0.000127	-45070000.0	NA
ET1944	-7177.0	699500.0	381.6	-58940.0	-0.000188	2005000.0	-4523.0

*****Coefficients in RED indicate $p \leq 0.05$

Pronghorn	NDVI	VRM	SLOPE	SLOPE^2	ASPECT	GRASS	SHRUB
ET148	6.3	33.3	-0.141	0.018	0.053	-0.81	-1.6
ET150	-6.8	-210.9	-0.121	0.005	-0.047	1.94	1.9
ET154	4.7	-562.1	-0.105	0.036	0.441	-0.32	-0.8
ET159	22.9	-103.5	-0.020	-0.007	-0.138	-0.78	-0.7
ET163	-7.4	-483.5	0.093	-0.004	-0.310	0.19	0.1
ET165	-2.5	-841.2	0.031	0.005	0.319	0.11	NA
ET166	1.8	984.8	0.303	-0.131	-0.078	-0.37	NA
ET167	-1.5	755.9	-0.360	-0.073	0.006	0.36	-18.0
ET168	0.7	-229.4	-0.037	-0.023	-0.127	-1.33	-17.2
ET169	5.3	-121.1	0.216	-0.039	-0.661	21.49	21.7
ET171	-2.6	97.6	-0.768	0.121	-1.146	0.66	NA
ET174	-2.8	-623.8	0.549	-0.120	-0.046	-0.95	-19.9
ET179	-4.3	-120.5	0.083	-0.009	-0.311	-0.26	-0.4
ET185	3.3	-205.8	-0.175	0.013	-0.068	0.97	1.0
ET190	8.4	-700.6	0.247	-0.015	-0.129	-0.16	-1.1
ET191	-1.5	-737.1	0.064	-0.021	-0.056	-0.41	-17.8
ET192	9.1	29.1	0.111	-0.004	-0.269	0.27	0.1
ET193	-1.8	-66.4	0.230	-0.021	-0.334	-0.55	-17.6
ET198	8.5	160.9	0.190	-0.032	-0.812	-0.16	-19.7
ET199	-0.6	-1787.0	0.602	-0.120	-0.186	1.01	NA
ET1944	-7.8	-1631.0	-0.533	0.077	-0.536	4.23	NA

*****Coefficients in RED indicate $p \leq 0.05$

Pronghorn	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
ET148	-0.609	NA	NA	-0.3	-14.9	NA	0.2
ET150	1.550	1.507	-13.2	2.1	NA	NA	NA
ET154	-20.990	NA	NA	0.4	NA	NA	NA
ET159	18.810	NA	NA	-17.1	NA	NA	-17.7
ET163	-18.570	NA	NA	-0.7	NA	NA	-18.9
ET165	-17.990	NA	NA	NA	NA	NA	NA
ET166	-18.580	-18.330	NA	NA	NA	NA	NA
ET167	-18.460	NA	NA	-16.8	NA	NA	NA
ET168	-1.249	NA	NA	0.4	-16.6	NA	NA
ET169	1.558	NA	NA	21.1	1.0	NA	23.2
ET171	0.867	NA	-17.6	NA	NA	NA	NA
ET174	-20.210	NA	NA	NA	NA	NA	-18.7
ET179	-0.225	1.699	-15.3	0.4	-15.5	NA	-0.1
ET185	1.472	-16.440	NA	-16.2	-15.7	NA	1.5
ET190	2.153	-18.670	NA	NA	NA	NA	-17.2
ET191	-0.957	-17.930	-18.1	-17.0	NA	NA	NA
ET192	-0.009	-17.910	-18.4	-18.6	-19.7	NA	-19.4
ET193	-0.050	-1.813	-18.1	20.9	NA	NA	NA
ET198	-19.660	NA	NA	NA	-18.7	NA	NA
ET199	0.965	NA	-15.0	NA	NA	NA	NA
ET1944	-0.315	NA	NA	NA	6.8	NA	NA

*****Coefficients in RED indicate $p \leq 0.05$

Appendix 3.4: Third-order individual variable coefficients for pronghorn spring migratory pathway selection across the NSS from 2004-2010.*

Pronghorn	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	Near Well	Well Den.	Hydro. Den.
ET02	821.0	-175400.0	-204.8	32480.0	0.00031	-785700.0	-20410.0
ET03	742.8	-136900.0	-107.9	11230.0	0.00007	-6520.0	-2602.0
ET05	40000.0	-22810000.0	-31.1	1631.0	0.00000	-29390.0	234.7
ET07	-15580.0	2095000.0	-323.9	12730.0	0.00012	84950.0	-246.2
ET18	629.1	-58230.0	-224.5	19840.0	-0.00004	-132200.0	-337.6
ET21	-9064.0	954800.0	61.9	-6501.0	-0.00023	626500.0	518.7
ET24	NA	NA	-8878.0	1440000.0	-0.00001	2227000.0	1457.0
ET26	-41870.0	6791000.0	370.4	-83640.0	0.00009	-25430.0	-2898.0
ET27	NA	NA	221.6	-18160.0	0.00004	-161000.0	-2597.0
ET29	-2957.0	NA	-772.5	115800.0	0.00023	-439000.0	-93450.0
ET30	NA	NA	-640.6	46720.0	-0.00003	-291800.0	NA
ET38	NA	NA	262.5	-37650.0	-0.00017	-49940.0	NA
ET41	574.5	-107000.0	-11.3	17880.0	0.00004	-20940.0	-65320.0
ET46	-6280.0	587100.0	-429.1	30420.0	0.00003	121200.0	-2879.0
ET59	106.0	-39070.0	572.8	-103600.0	-0.00003	-76620.0	-149.2
ET60	NA	NA	-21470.0	2936000.0	-0.00032	-7388.0	NA
ET62	NA	NA	-772.1	122000.0	-0.00029	-295900.0	-2646.0
ET63	-6711.0	620500.0	258.7	-41370.0	-0.00013	-100400.0	-912.0
ET64	-6809.0	433200.0	-209.4	44250.0	-0.00008	-92190.0	-720.2
ET73	NA	NA	-66.4	3338.0	-0.00010	66580.0	NA
ET108	NA	NA	-36.6	-9430.0	-0.00021	-658800.0	-1945.0
ET110	865.3	NA	-9377.0	1044000.0	-0.00038	-2149000.0	-3851.0

*Coefficients in RED indicate $p \le 0.05$

Pronghorn	**NDVI**	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
ET02	14.1	-1512.0	-0.19	0.0233	-0.119	0.575	NA
ET03	4.8	18.2	0.04	-0.0047	-0.106	-0.123	0.58
ET05	6.4	58.7	-0.04	-0.0142	0.468	-0.196	NA
ET07	1.8	-321.5	0.18	-0.0343	-0.237	0.528	-16.13
ET18	4.5	-675.2	0.22	-0.0150	0.126	-0.285	-18.67
ET21	19.4	-26490.0	0.43	0.1866	-0.026	0.754	1.02
ET24	-3.5	-1351.0	0.28	0.0151	-0.004	19.010	1.18
ET26	2.7	-661.5	0.01	0.0074	-0.074	-0.032	20.87
ET27	2.2	42.7	0.10	-0.0020	-0.287	-0.043	-14.86
ET29	2.7	-894.1	0.23	-0.0145	-0.119	-2.380	NA
ET30	-4.3	0.7	0.35	-0.0248	-0.063	17.300	NA
ET38	-8.2	-218.7	0.42	-0.0375	-0.199	-21.580	NA
ET41	3.4	-142.4	0.26	-0.0172	-0.302	0.103	0.87
ET46	8.1	555.1	0.04	-0.0857	-0.027	-0.557	NA
ET59	2.2	302.3	0.04	-0.0219	-0.135	0.609	-16.89
ET60	-48.4	514.1	2.84	-0.5007	-0.230	21.340	NA
ET62	1.4	-932.8	0.35	-0.0275	-0.039	1.006	-15.72
ET63	-6.8	-175.5	-0.01	-0.0027	0.051	0.654	NA
ET64	6.0	-2712.0	0.52	-0.0667	0.138	0.582	2.05
ET73	-0.5	94.3	-0.03	0.0039	0.014	17.720	NA
ET108	1.8	-76.1	-0.22	0.0196	0.047	-0.099	0.08
ET110	40.1	-1599.0	0.46	0.0098	0.313	-0.926	NA

*Coefficients in RED indicate $p \le 0.05$

Pronghorn	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
ET02	0.58	NA	NA	-17.23	1.5	NA	NA
ET03	0.21	-0.006	0.89	-16.05	-14.8	NA	-16.7
ET05	-0.08	NA	NA	NA	632.5	NA	NA
ET07	0.79	-16.500	-16.62	0.52	42.9	NA	NA
ET18	0.27	-18.610	NA	-17.84	-18.8	NA	NA
ET21	0.61	-17.250	NA	NA	2.4	NA	NA
ET24	NA	NA	0.73	0.14	NA	NA	NA
ET26	-0.04	0.328	-15.54	NA	NA	-14.7	-15.9
ET27	0.98	0.944	-15.30	NA	NA	NA	NA
ET29	-19.91	-20.110	NA	NA	NA	NA	NA
ET30	NA	NA	-0.61	2.60	NA	NA	NA
ET38	NA	-38.610	-38.07	NA	NA	NA	NA
ET41	-0.10	-0.417	0.37	-16.58	-17.1	-0.9	-17.5
ET46	-1.66	NA	NA	24.34	NA	NA	NA
ET59	0.68	-1.196	-16.79	NA	-15.8	1.5	0.3
ET60	NA	NA	NA	NA	NA	NA	NA
ET62	1.36	0.990	4.78	NA	NA	2.4	NA
ET63	0.09	2.831	-1.19	-16.10	-16.9	-17.0	-17.4
ET64	-0.81	-0.664	-0.02	-15.32	-13.1	NA	NA
ET73	0.59	0.521	NA	-0.23	NA	NA	NA
ET108	0.26	-17.530	-17.09	0.59	-16.8	NA	-17.4
ET110	0.25	-20.700	NA	NA	-23.5	NA	-22.6

*Coefficients in RED indicate $p \leq 0.05$

Pronghorn	**Paved Rd.**	**Paved Rd.^{2}**	**All Road**	**All Road^2**	**Near Well**	**Well Den.**	**Hydro. Den.**
ET118	NA	NA	843.4	-114800.0	-0.00002	-2450000.0	-1012.0
ET123	-2.3	27750.0	-211.4	19670.0	0.00015	-333900.0	-1588.0
ET125	NA	NA	-147.1	-4210.0	0.00009	1089000.0	-1971.0
ET126	1809.0	-367900.0	-124.3	10800.0	0.00012	-23810.0	-2391.0
ET128	-10330.0	1614000.0	10980.0	-1702000.0	-0.00046	1747000.0	-1048.0
ET130	NA	NA	-254.1	25550.0	-0.00002	-1082000.0	-666.0
ET135	-6498.0	1470000.0	-4507.0	NA	-0.00030	-510100.0	NA
ET137	-10330.0	NA	-123.3	13830.0	0.00013	960700.0	-473.0
ET138	-126300.0	22720000.0	-70.1	3463.0	0.00018	-51190.0	-382.4
ET139	NA	NA	-86.0	18560.0	0.00000	-438700.0	-498.3
ET140	-818.4	NA	50.8	-16830.0	0.00000	-2939000.0	-38740.0
ET141	629.7	-108200.0	34.8	-4209.0	0.00037	2687.0	-1447.0
ET142	NA	NA	379.9	-108200.0	-0.00002	-1551000.0	122.8
ET144	1059.0	-173900.0	-250.3	29620.0	0.00015	-54920000.0	-1277.0
ET145	NA	NA	-273.8	35950.0	0.00017	299200.0	-1421.0
ET148	NA	NA	-443.6	128200.0	0.00019	4147000.0	281.8
ET150	NA	NA	-2972.0	NA	0.00000	1035000.0	-39260.0
ET152	-10840.0	1301000.0	-797.8	74290.0	-0.00015	-1493000.0	NA
ET153	NA	NA	-711.6	108500.0	-0.00020	-1001000.0	74.3
ET154	-9815.0	500000.0	-178.6	29840.0	0.00017	-61160000.0	-973.6
ET156	-8115.0	945000.0	-29.4	-7195.0	-0.00009	1176.0	-1753.0
ET157	-762.1	148900.0	31.7	-15440.0	-0.00014	848200.0	148.5
ET158	NA	NA	2494.0	-422600.0	-0.00038	-1359000.0	-22080.0
ET159	-631.8	118100.0	154.0	-38210.0	0.00034	-51080000.0	-1500.0

*Coefficients in RED indicate $p \le 0.05$

Pronghorn	NDVI	VRM	SLOPE	SLOPE^2	ASPECT	GRASS	SHRUB
ET118	4.8	-76.0	-0.21	0.0175	-0.943	1.485	-16.46
ET123	5.1	-174.2	0.06	-0.0018	0.059	0.254	0.02
ET125	4.2	-99.9	-0.56	0.0413	0.566	-0.017	-16.49
ET126	2.9	-513.9	0.12	-0.0116	0.203	0.107	-17.18
ET128	1.5	-1261.0	0.15	-0.0423	-0.561	1.137	-17.92
ET130	2.7	-99.5	0.11	-0.0298	0.046	0.124	-17.01
ET135	-3.3	-99.5	-0.01	0.0109	-0.551	0.003	1.44
ET137	13.5	-171.1	-0.12	0.0045	-0.074	-0.009	-1.52
ET138	0.4	-36.1	0.01	0.0021	-0.047	1.271	-0.50
ET139	4.4	-304.1	0.14	-0.0089	0.048	-0.466	-0.32
ET140	6.9	-259.2	0.05	-0.0030	-0.192	-0.194	-1.52
ET141	2.8	-493.3	0.04	-0.0085	0.022	-0.096	-16.86
ET142	7.2	-152.3	-0.15	0.0098	0.217	-1.071	-1.31
ET144	1.3	-146.2	0.22	-0.0372	-0.290	0.914	0.86
ET145	1.8	-992.7	0.04	0.0013	0.405	0.494	0.86
ET148	13.8	-276.6	0.24	-0.0227	-0.291	0.439	0.43
ET150	-10.3	247.9	1.03	-0.1412	-0.036	19.960	0.32
ET152	-4.0	-660.0	0.05	-0.0075	0.235	0.519	0.51
ET153	4.7	-234.1	0.12	-0.0197	-0.059	0.504	0.43
ET154	3.2	-34.0	-0.22	0.0187	-0.002	-0.580	-1.29
ET156	6.4	-265.1	0.21	-0.0043	-0.295	0.495	-0.29
ET157	-4.8	-469.7	0.29	-0.0588	0.034	0.450	1.06
ET158	-5.5	13.2	0.03	-0.0166	-0.488	19.770	2.26
ET159	8.8	-85.3	-0.02	0.0055	-0.205	0.913	0.87

*Coefficients in RED indicate $p \leq 0.05$

Pronghorn	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
ET118	1.56	-15.480	NA	3.69	-17.5	NA	NA
ET123	-0.04	1.138	-0.32	-1.32	-13.9	NA	NA
ET125	0.27	-18.820	NA	NA	NA	NA	NA
ET126	-0.75	-17.110	-17.30	-1.03	-16.2	NA	NA
ET128	-25.39	-18.740	NA	NA	NA	NA	NA
ET130	-0.56	1.006	NA	NA	NA	NA	NA
ET135	NA	0.194	NA	NA	-0.7	NA	NA
ET137	-0.26	-17.780	NA	-16.69	-17.1	NA	-17.5
ET138	1.09	-18.250	-19.05	0.89	-128.8	NA	NA
ET139	0.49	-0.997	-16.11	-0.66	19.8	NA	-15.4
ET140	-17.81	-18.440	NA	0.21	3.1	NA	NA
ET141	-0.17	-17.170	-16.59	NA	1.2	NA	-15.0
ET142	-0.18	-1.749	NA	-16.40	2.7	NA	NA
ET144	1.32	NA	NA	0.83	-0.3	NA	-16.9
ET145	0.43	NA	NA	-15.39	NA	NA	NA
ET148	-16.43	NA	-16.80	-0.35	-18.8	NA	-16.9
ET150	NA	NA	NA	19.31	NA	NA	NA
ET152	-17.48	NA	NA	0.57	2.2	NA	NA
ET153	-0.50	NA	NA	0.54	-17.8	NA	NA
ET154	-1.41	NA	-19.70	-1.04	1.2	NA	NA
ET156	NA	-15.750	-16.35	0.35	0.7	NA	-0.5
ET157	0.26	NA	NA	0.24	1.2	NA	-15.4
ET158	2.54	NA	NA	19.56	NA	NA	0.2
ET159	1.18	NA	NA	0.47	-15.7	NA	NA

*Coefficients in RED indicate $p \leq 0.05$

Pronghorn	Paved Rd.	Paved Rd.^{2}	All Road	All Road^2	Near Well	Well Den.	Hydro. Den.
ET160	NA	NA	-810.6	130200.0	0.00016	-2355000.0	-459.2
ET161	-466.1	74380.0	699.4	-117000.0	-0.00017	-4730000.0	1092.0
ET163	-5744.0	493300.0	-209.8	23520.0	-0.00009	427900.0	-278.0
ET166	-5514.0	NA	249.8	-42520.0	0.00004	431100.0	-123.4
ET167	-256.3	-50280.0	43.8	-9053.0	-0.00029	-1255000.0	166.9
ET168	-27870.0	6019000.0	525.3	-133300.0	-0.00019	697300.0	NA
ET169	NA	NA	-2030.0	341600.0	0.00008	654900.0	551.2
ET171	-16740.0	2282000.0	-65.6	2165.0	0.00002	87730.0	-1315.0
ET174	NA	NA	-23770.0	1950000.0	0.00006	-2635000.0	-2165.0
ET182	NA	NA	-444.4	62370.0	-0.00048	-2076000.0	-40110.0
ET186	NA	NA	-5167.0	329500.0	0.00058	-300300.0	-3745.0
ET190	-3133.0	-4032000.0	371.1	-87760.0	-0.00077	-442400.0	2186.0
ET191	-3815.0	NA	180.2	-13110.0	-0.00029	-934300.0	323.5
ET193	-5714.0	407700.0	-1541.0	217400.0	-0.00057	1185000.0	-20.1
ET198	NA	NA	560.7	-131000.0	-0.00078	879000.0	2009.0
ET199	-2631.0	NA	-116.3	17420.0	-0.00027	-498300.0	-4149.0
ET1941	-4941.0	379000.0	-66.7	9831.0	-0.00001	39820.0	-1493.0
ET1943	NA	NA	1241.0	-219100.0	-0.00002	-63660.0	-361.0
ET1944	-2846.0	-52110.0	254.0	-59680.0	0.00001	-57220000.0	-1104.0
ET1945	NA	NA	-671.0	76340.0	0.00001	196500.0	-32910.0
ET1946	NA	NA	70750.0	-41010000.0	0.00011	119500.0	-115200.0

*Coefficients in RED indicate $p \leq 0.05$

Pronghorn	**NDVI**	**VRM**	**SLOPE**	**SLOPE^2**	**ASPECT**	**GRASS**	**SHRUB**
ET160	4.2	71.4	0.14	-0.0167	0.164	-0.912	-18.76
ET161	-7.7	-1219.0	0.03	0.0087	0.137	-0.245	0.53
ET163	2.7	-287.9	-0.08	0.0103	-0.048	0.051	-0.20
ET166	4.4	-83.2	-0.10	0.0003	-0.033	-0.352	-1.99
ET167	-4.1	-116.2	0.01	0.0026	-0.077	1.825	1.27
ET168	2.7	-57.2	-0.16	0.0107	-0.070	-0.166	-0.58
ET169	-1.3	122.8	-0.02	-0.0392	-0.095	0.493	-0.28
ET171	2.0	-696.6	0.04	-0.0018	0.017	-0.074	-0.63
ET174	-7.0	-747.8	0.23	-0.0435	-0.203	0.763	-0.59
ET182	17.8	-721.4	0.33	-0.0646	0.307	0.903	-17.64
ET186	4.8	0.5	-0.08	-0.0048	-0.908	17.940	20.44
ET190	-10.1	-95.0	-0.09	-0.0118	0.404	21.920	20.91
ET191	14.2	-1344.0	-0.07	-0.0188	-0.084	-0.092	-0.22
ET193	1.5	-604.4	0.07	-0.0541	0.076	-0.464	-0.39
ET198	2.2	-113.1	0.34	-0.0245	1.117	18.560	18.11
ET199	0.6	-207.8	0.08	-0.0110	-0.114	0.096	1.61
ET1941	5.0	-114.1	-0.14	0.0128	-0.051	-0.778	-16.16
ET1943	2.4	-65.6	-0.17	0.0027	0.411	1.543	1.21
ET1944	-9.1	13.7	0.24	-0.0252	-0.058	-0.311	-17.99
ET1945	-8.7	-1856.0	0.22	-0.0412	0.029	0.797	NA
ET1946	-10.5	-2555.0	0.02	0.0267	-0.312	1.372	NA

*Coefficients in RED indicate $p \leq 0.05$

Pronghorn	PPCROP	WETLAND	WATER	EXPOSED	DEVELOP	CONIF	DECID
ET160	0.33	-18.890	1.07	-0.41	-19.0	NA	-18.9
ET161	1.77	NA	NA	-14.03	1.3	NA	-0.4
ET163	-0.74	-0.446	-16.65	0.68	1.2	NA	-16.8
ET166	-0.34	-16.390	NA	-1.32	NA	NA	NA
ET167	2.36	-13.450	-13.64	1.87	2.6	NA	-13.6
ET168	-0.65	-16.030	NA	-0.99	-15.7	NA	-16.7
ET169	1.17	NA	NA	0.50	-14.4	NA	-16.1
ET171	-0.33	-16.480	-16.54	-0.24	0.4	NA	NA
ET174	NA	NA	NA	1.39	NA	NA	-17.2
ET182	-19.65	NA	NA	-18.57	NA	NA	NA
ET186	NA	NA	NA	1.54	NA	NA	NA
ET190	43.61	NA	NA	NA	180.9	NA	NA
ET191	0.80	0.282	NA	0.58	NA	NA	NA
ET193	0.65	-1.751	NA	NA	NA	NA	-15.1
ET198	NA	NA	NA	NA	NA	NA	NA
ET199	-0.25	-16.790	-16.85	NA	NA	NA	NA
ET1941	-0.95	NA	-15.80	NA	NA	NA	-16.3
ET1943	0.57	-14.900	-16.81	2.95	-16.7	NA	NA
ET1944	0.77	NA	NA	NA	NA	NA	NA
ET1945	0.83	NA	NA	NA	NA	NA	NA
ET1946	1.22	NA	-5.22	NA	NA	NA	NA

*Coefficients in RED indicate $p \leq 0.05$

Appendix 3.5: Pronghorn fall third-order scale migratory pathway selection comparing base (without road and well features included) and human (with road and well features included) models across the NSS from 2004-2010.

Pronghorn	Model1	AICc1	ΔAICc1	Model2	AICc2	ΔAICc2	w_{base}	w_{human}
ET03	Base	381.452	0	Human	396.191	14.739	0.999	0.001
ET26	Base	157.159	0	Human	172.942	15.783	1.000	0.000
ET27	Base	110.87	0	Human	159.798	48.928	1.000	0.000
ET28	Base	535.014	0	Human	538.195	3.181	0.831	0.169
ET30	Base	265.714	0	Human	268.351	2.637	0.789	0.211
ET31	Base	374.008	0	Human	389.093	15.086	0.999	0.001
ET39	Base	623.762	0	Human	626.198	2.436	0.772	0.228
ET41	Base	323.295	0	Human	336.855	13.559	0.999	0.001
ET51	Base	163.789	0	Human	179.638	15.849	1.000	0.000
ET62	Base	398.507	0	Human	410.264	11.757	0.997	0.003
ET63	Base	456.001	0	Human	460.322	4.321	0.897	0.103
ET73	Base	141.026	0	Human	153.382	12.356	0.998	0.002
ET113	Base	237.891	0	Human	246.703	8.812	0.988	0.012
ET123	Base	1221.7	0	Human	1224.66	2.961	0.815	0.185
ET125	Base	131.9	0	Human	149.664	17.764	1.000	0.000
ET130	Base	198.748	0	Human	220.141	21.393	1.000	0.000
ET131	Base	153.784	0	Human	188.54	34.755	1.000	0.000
ET138	Base	395.401	0	Human	402.526	7.125	0.972	0.028
ET140	Base	228.32	0	Human	231.791	3.471	0.850	0.150
ET141	Base	156.66	0	Human	175.365	18.705	1.000	0.000
ET142	Base	946.615	9.551	Human	937.064	0	0.008	0.992
ET145	Base	185.85	0	Human	193.843	7.993	0.982	0.018
ET148	Base	332.916	0	Human	335.481	2.565	0.783	0.217
ET150	Base	475.087	0	Human	481.353	6.266	0.958	0.042
ET154	Base	154.06	0	Human	170.175	16.115	1.000	0.000
ET159	Base	163.571	0	Human	181.96	18.389	1.000	0.000
ET163	Base	327.139	7.175	Human	319.965	0	0.027	0.973
ET165	Base	234.464	10.434	Human	224.03	0	0.005	0.995
ET166	Base	201.142	0	Human	209.9	8.759	0.988	0.012
ET167	Base	115.619	0	Human	135.808	20.190	1.000	0.000
ET168	Base	295.737	0.703	Human	295.034	0	0.413	0.587
ET169	Base	374.697	0	Human	377.819	3.123	0.827	0.173
ET171	Base	213.994	0	Human	221.678	7.684	0.979	0.021
ET174	Base	111.806	0	Human	137.166	25.360	1.000	0.000
ET179	Base	1605.65	0	Human	1606.16	0.504	0.563	0.437

Pronghorn	**Model1**	**AICc1**	**ΔAICc1**	**Model2**	**AICc2**	**ΔAICc2**	w_{base}	w_{human}
ET185	Base	383.854	0	Human	386.201	2.346	0.764	0.236
ET190	Base	176.647	0	Human	190.084	13.437	0.999	0.001
ET191	Base	244.111	0	Human	250.068	5.957	0.952	0.048
ET192	Base	257.088	0	Human	266.295	9.207	0.990	0.010
ET193	Base	1092.71	0	Human	1097.93	5.225	0.932	0.068
ET198	Base	113.84	0	Human	133.617	19.777	1.000	0.000
ET199	Base	317.783	0	Human	323.248	5.465	0.939	0.061
ET1944	Base	132.142	0	Human	160.943	28.801	1.000	0.000

Appendix 3.6: Pronghorn spring third-order scale migratory pathway selection comparing base (without road and well features included) and human (with road and well features included) models across the NSS from 2004-2010.

Pronghorn	Model1	AICc1	ΔAICc1	Model2	AICc2	ΔAICc2	w_{base}	w_{human}
ET02	Base	364.146	0	Human	372.627	8.480	0.986	0.014
ET03	Base	744.929	0	Human	750.112	5.182	0.930	0.070
ET05	Base	340.542	0	Human	351.116	10.573	0.995	0.005
ET07	Base	1030.47	9.084	Human	1021.39	0	0.011	0.989
ET18	Base	318.135	0	Human	328.14	10.005	0.993	0.007
ET21	Base	130.603	0	Human	166.598	35.996	1.000	0.000
ET24	Base	135.1	0	Human	150.917	15.817	1.000	0.000
ET26	Base	1041.88	0	Human	1045.91	4.034	0.883	0.117
ET27	Base	726.737	0	Human	728.098	1.362	0.664	0.336
ET29	Base	215.227	0	Human	220.771	5.544	0.941	0.059
ET30	Base	408.243	1.455	Human	406.788	0	0.326	0.674
ET38	Base	277.587	0	Human	286.065	8.478	0.986	0.014
ET41	Base	1234.09	0	Human	1234.32	0.227	0.528	0.472
ET46	Base	203.23	0	Human	214.53	11.300	0.996	0.004
ET59	Base	816.83	0	Human	824.967	8.137	0.983	0.017
ET60	Base	85.647	0	Human	97.3076	11.661	0.997	0.003
ET62	Base	395.375	16.307	Human	379.068	0	0.000	1.000
ET63	Base	482.826	1.863	Human	480.964	0	0.283	0.717
ET64	Base	457.012	0	Human	466.285	9.274	0.990	0.010
ET73	Base	607.926	0	Human	613.054	5.129	0.929	0.071
ET108	Base	898.332	3.591	Human	894.741	0	0.142	0.858
ET110	Base	112.29	0	Human	260.731	148.441	1.000	0.000
ET118	Base	181.393	0	Human	192.693	11.300	0.996	0.004
ET123	Base	1511.26	0	Human	1516	4.735	0.914	0.086
ET125	Base	176.792	0	Human	186.691	9.898	0.993	0.007
ET126	Base	667.989	0	Human	676.379	8.390	0.985	0.015
ET128	Base	182.718	0	Human	196.283	13.565	0.999	0.001
ET130	Base	372.104	0	Human	376.699	4.595	0.909	0.091
ET135	Base	284.134	0	Human	291.427	7.293	0.975	0.025
ET137	Base	590.703	0	Human	597.806	7.103	0.972	0.028
ET138	Base	1196.07	0	Human	1196.2	0.132	0.516	0.484
ET139	Base	1412.19	0	Human	1419.91	7.715	0.979	0.021
ET140	Base	357.056	0	Human	364.049	6.993	0.971	0.029
ET141	Base	839.636	10.256	Human	829.381	0	0.006	0.994
ET142	Base	221.534	0	Human	233.478	11.944	0.997	0.003

Pronghorn	**Model1**	**AICc1**	**ΔAICc1**	**Model2**	**AICc2**	**ΔAICc2**	w_{base}	w_{human}
ET144	Base	1194.17	0.066	Human	1194.1	0	0.492	0.508
ET145	Base	223.126	0	Human	232.542	9.417	0.991	0.009
ET148	Base	294.429	5.228	Human	289.201	0	0.068	0.932
ET150	Base	127.024	0	Human	139.804	12.780	0.998	0.002
ET152	Base	341.188	0	Human	343.935	2.748	0.798	0.202
ET153	Base	1075.93	0	Human	1077.1	1.168	0.642	0.358
ET154	Base	704.988	0.614	Human	704.375	0	0.424	0.576
ET156	Base	669.226	0	Human	677.433	8.207	0.984	0.016
ET157	Base	580.717	0	Human	587.98	7.264	0.974	0.026
ET158	Base	169.114	0	Human	174.598	5.483	0.939	0.061
ET159	Base	596.543	0	Human	597.004	0.461	0.557	0.443
ET160	Base	239.002	0	Human	244.165	5.163	0.930	0.070
ET161	Base	407.924	0	Human	417.217	9.293	0.990	0.010
ET163	Base	1932.73	0	Human	1938.27	5.541	0.941	0.059
ET166	Base	697.971	0	Human	707.646	9.675	0.992	0.008
ET167	Base	1774.62	12.546	Human	1762.07	0	0.002	0.998
ET168	Base	881.376	6.032	Human	875.343	0	0.047	0.953
ET169	Base	569.834	0	Human	570.764	0.929	0.614	0.386
ET171	Base	2256.79	0	Human	2265.32	8.521	0.986	0.014
ET174	Base	233.909	0	Human	242.468	8.559	0.986	0.014
ET182	Base	159.313	0	Human	166.956	7.643	0.979	0.021
ET186	Base	142.576	0	Human	154.933	12.357	0.998	0.002
ET190	Base	180.391	4.731	Human	175.66	0	0.086	0.914
ET191	Base	199.298	0	Human	206.71	7.412	0.976	0.024
ET193	Base	443.954	18.261	Human	425.693	0	0.000	1.000
ET198	Base	98.2575	0	Human	121.352	23.094	1.000	0.000
ET199	Base	1003.73	4.743	Human	998.99	0	0.085	0.915
ET1941	Base	906.655	0	Human	917.133	10.478	0.995	0.005
ET1943	Base	283.039	0	Human	292.465	9.426	0.991	0.009
ET1944	Base	360.605	0	Human	368.316	7.711	0.979	0.021
ET1945	Base	156.444	0	Human	166.046	9.602	0.992	0.008
ET1946	Base	96.0477	0	Human	129.265	33.218	1.000	0.000

Appendix 3.7: Pronghorn seasonal second-order scale migratory pathway selection comparing base (without road and well features included) and human (with road and well features included) models across the NSS from 2004-2010.

Season	Model1	AICc1	ΔAICc1	Model2	AICc2	ΔAICc2	w_{base}	w_{human}
Fall	Base	10476	126	Human	10350	0	0	1
Spring	Base	26115	690	Human	25425	0	0	1

Appendix 3.8: Seasonal migratory pathway models for pronghorn across the NSS, using data from 2004-2010.

Fall Migratory Pathway

Third-order [S3-FM]:

Exp ((0.103494* "Water") +(0.148301* "Exposed") + (0.472095* "Development") + (0.180811* "Shrubland") + (0.184663* "Wetland") + (-0.03519* "Grassland") + (0.106225* "Pasture and Perennial Crop") +(-17.7893* "Conifer Forest") + (0.873643* "Deciduous Forest") + Con ("VRM (Vector Ruggedness Measure)" > 0.036048, -112.459 * 0.036048, -112.459*"VRM (Vector Ruggedness Measure)") + Con ("Slope"> 23.1682, 0.084232* 23.1682, 0.084232 *"Slope ") + Con ("Slope^2" > 536.7655, -0.00496 * 536.7655, -0.00496*"Slope^2 ") + (-0.19316* "Aspect") + Con ("Hydrology 1:1000000 – 750m Density"> 0.00192799, 1.4080409* 0.00192799, 1.4080409*"Hydrology 1:1000000 – 750m Density") + Con ("NDVI for 16 day period at mean fall migration for population "> 0.7954, -0.17663* 0.7954, -0.17663 *"NDVI for 16 day period at mean fall migration for population") + Con ("All Roads^2 – 100m Density"> 0.000203, 10020.612* 0.000203, 10020.612*"All Roads^2 – 100m Density ") + Con ("All Wells – 1000m Density"> 3.63E-05, -43866.1* 3.63E-05, -43866.1*"All Wells – 1000m Density ") + Con ("All Roads – 100m Density" > 0.014238, -62.25068595* 0.014238, -62.25068595* "All Roads – 100m Density") + Con ("Paved Roads – 100m Density"> 0.0133921, -1059.1* 0.0133921, -1059.1* "Paved Roads – 100m Density") + Con ("Paved Roads^2 – 100m Density"> 0.000179347, 103299.45* 0.000179347, 103299.45*"Paved Roads^2 – 100m Density") +(2.37e-05 * "Drilled Well))

Note: Conditional statements (i.e. "Con") were added to cap the maximum value for each continuous parameter so that results could be expanded and displayed across the entire Northern Sagebrush Steppe.

Second-order [S2-FM]:

Exp((-1.496e+00 * "Water") + (7.015e-01 * "Exposed") + (5.278e-01 * "Development") + (1.089e-01 * "Shrubland") + (-1.287e-01 * "Wetland") + (1.046e+00 * "Grassland") + (1.569e-01 * "Pasture and Perennial Crop") + (-2.633e+00 * "Conifer Forest") +(-5.794e-01 *"Deciduous Forest") + (-4.109e+01 * "VRM (Vector Ruggedness Measure)") + (1.999e-01 * "Slope") + (-1.625e-02 * "Slope^2") + (-2.739e-01 * "Aspect") + (4.249e+02 * "Hydrology 1:1000000 – 1000m Density") + (-3.627e+02 * "All Roads – 1000m Density") + (-3.668e+04 * "All Wells – 1000m Density") + (-6.245e+02 * "Paved Roads – 1000m Density"))

Integrated Map [SI-FM]:

[SI-FM] = [S3-FM]*[S2-FM]

Note: The "Drilled Well" coefficients were not mapped in any of the three maps due to temporal nature of the parameter. The parameter measured for each use/available point, the distance to nearest drilled well during a 16-day period centered on the day each well was drilled.

Spring Migratory Pathway

Third-order [S3-SM]:

Exp ((0.417234 * "Water") +(0.239087 * "Exposed") + (0.950094 * "Development") + (0.146144 * "Shrubland") + (-0.05446 * "Wetland") + (0.126842 * "Grassland") + (0.150884 * "Pasture and Perennial Crop") +(1.821801 * "Conifer Forest") + (-0.20747 * "Deciduous Forest") + Con ("VRM (Vector Ruggedness Measure)" > 0.065912, -83.3975* 0.065912, -83.3975 *"VRM (Vector Ruggedness Measure)") + Con ("Slope"> 29.5743, 0.038436* 29.5743, 0.038436 *"Slope") + Con ("Slope^2" > 874.6392, -0.00103 * 874.6392, -0.00103*"Slope^2") + (-0.05288* "Aspect") + Con ("Hydrology 1:1000000 – 750m Density"> 0.00152903, -1011.985* 0.00152903, -1011.985 *"Hydrology 1:1000000 – 750m Density") + Con ("NDVI for 16 day period at mean spring migration for population "> 0.7951, 2.641317 * 0.7951, 2.641317*"NDVI for 16 day period at mean spring migration for population") + Con ("All Roads^2 – 100m Density"> 0.000524, 7649.3941* 0.000524, 7649.3941*"All Roads^2 – 100m Density") + Con ("All Wells – 1000m Density"> 3.18E-05, -25059.4 * 3.18E-05, -25059.4*"All Wells – 1000m Density") + Con ("All Roads – 100m Density" > 0.0228988, -55.88419019* 0.0228988, -55.88419019* "All Roads – 100m Density") + Con ("Paved Roads – 100m Density"> 0.0171048, 536.4258* 0.0171048, 536.4258 * "Paved Roads – 100m Density") + Con ("Paved Roads^2 – 100m Density"> 0.000292576, -66718.5 * 0.000292576, -66718.5*"Paved Roads^2 – 100m Density") + (-1.5e-05 * "Drilled Well"))

Note: Conditional statements (i.e. "Con") were added to cap the maximum value for each continuous parameter so that results could be expanded and displayed across the entire Northern Sagebrush Steppe.

Second-order [S2-SM]:

Exp ((-9.48e-01*"Water") + (1.066 * "Exposed") + (4.227e-01 * "Development") + (1.746e-01 * "Shrubland") + (-6.524e-02 * "Wetland") + (1.074 * "Grassland") + (-3.104e-01 * "Pasture and Perennial Crop") +(-2.566 *"Conifer Forest") + (-1.028 *"Deciduous Forest") + (-5.360e+01 *"VRM (Vector Ruggedness Measure)") + (1.417e-01 * "Slope") + (-1.358e-02 * "Slope^2") + (-1.241e-01 * "Aspect") +(-8.878e+02 * "Hydrology 1:1000000 – 1000m Density") + (-6.431e+02 * "All Roads – 1000m Density") + (-7.805e+04 * "All Wells – 1000m Density") + (3.728 * "NDVI for 16 day period at mean spring migration for population") + (1.42e-06 * "Drilled Well"))

Integrated Map [SI-SM]:

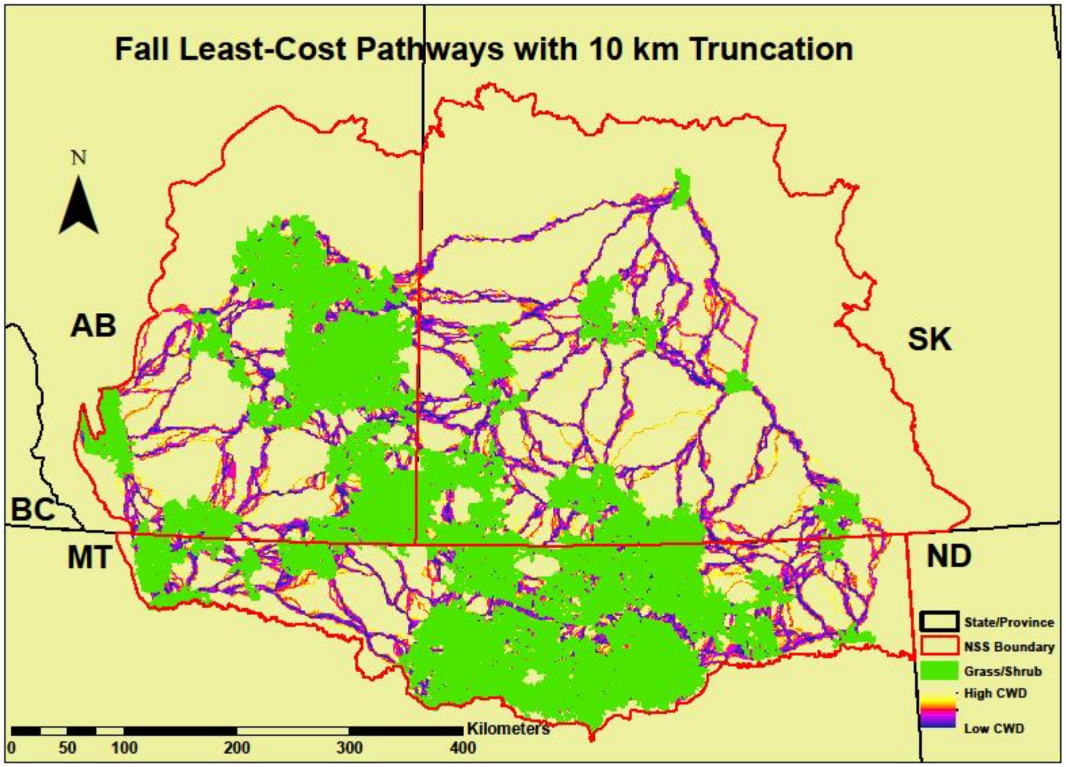
[SI-SM] = [S3-SM]*[S2-SM]

Note: The "Drilled Well" coefficients were not mapped in any of the three maps due to temporal nature of the parameter. The parameter measured for each use/available point, the distance to nearest drilled well during a 16-day period centered on the day each well was drilled.

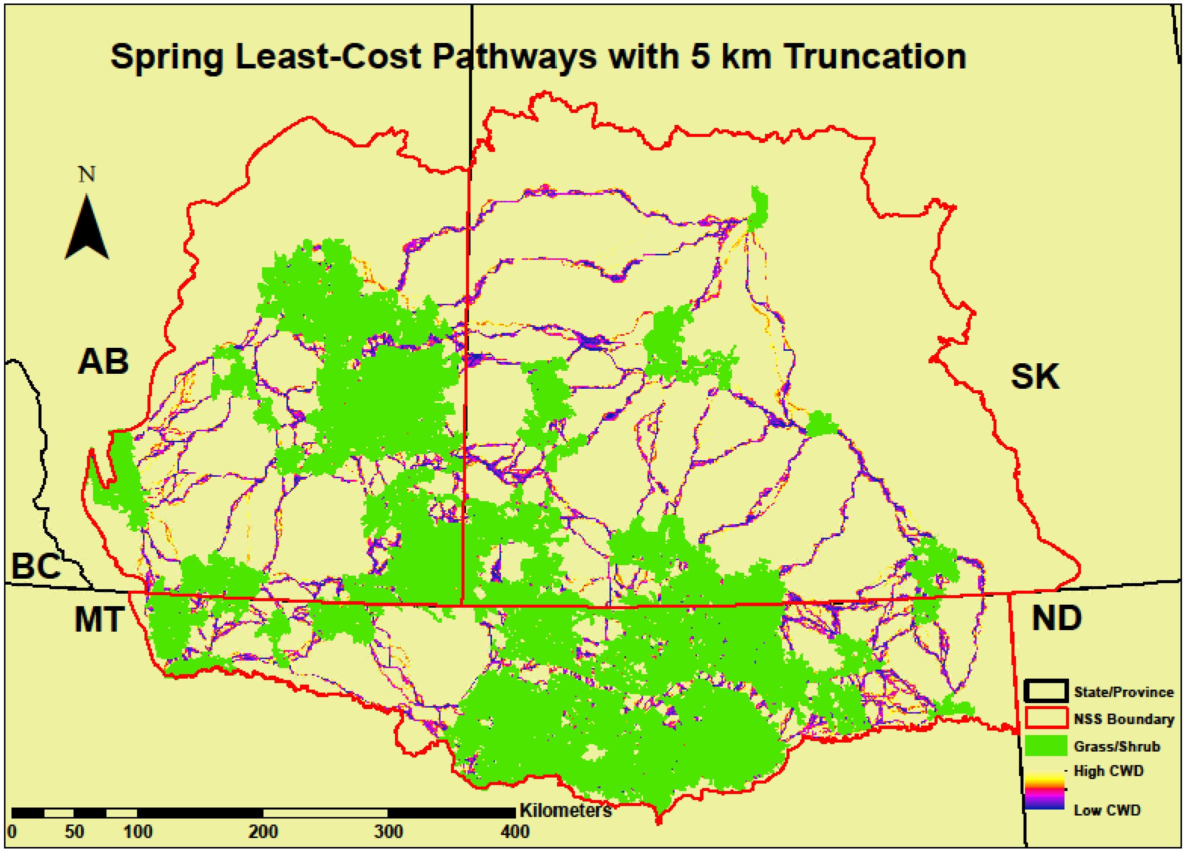
CHAPTER 4 APPENDICIES

Appendix 4.1 (a-b): 10 km-wide fall (a) and 5 km-wide spring (b) least-cost pathways results. Pathways were truncated to identify seasonal migratory corridors based on optimal corridor widths for pronghorn across the NSS, using data from 2004-2010.

(a)



(b)


Spring Least-Cost Pathways with 5 km Truncation
N
AB
SK
BC
MT
ND
State/Province
NSS Boundary
Grass/Shrub
High CWD
Low CWD
Kilometers
0
50
100
200
300
400