SOCIO-ECOLOGICAL DRIVERS OF RESOURCE SELECTION AND HABITAT USE BY MOOSE IN INTERIOR ALASKA

By

Casey L. Brown

RECOMMENDED:

Dr. Roger Ruess
Advisory Committee Member

Dr. Todd Brinkman
Advisory Committee Member

Dr. Scott Brainerd
Advisory Committee Member

Eugenie Euskirchen
Dr. Eugenie Euskirchen
Co-Advisory Committee Chair

Dr. Knut Kielland
Advisory Committee Chair

Dr. Diane Wagner
Chair, Department of Biology and Wildlife

APPROVED:

Paul W Layer
Dr. Paul Layer
Dean, Natural Science and Mathematics

John C Eichelberger
Dr. John Eichelberger
Dean of the Graduate School

27 July 2016
Date

SOCIO-ECOLOGICAL DRIVERS OF RESOURCE SELECTION AND HABITAT USE BY MOOSE IN INTERIOR ALASKA

A

DISSERTATION

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By

Casey L. Brown, M.S.

Fairbanks, Alaska

August 2016

ABSTRACT

Sustainably managing wildlife with diverse utilization values is one of the greatest challenges facing contemporary wildlife management. These challenges can be amplified under changing environmental and socio-economic conditions. In Alaska, boreal forest systems are experiencing rapid change as a result of climate warming. Alaska's boreal region has warmed twice as rapidly as the global average, affecting a host of processes including an increase in wildfire frequency, extent, and severity. Wildfire is the most common ecological disturbance in the Alaskan boreal forest and an important driver of landscape heterogeneity, burning on average 1 to 2 million acres per year. Fire severity is a particularly important factor dictating the regeneration of deciduous species, and one that can influence the overall quality of habitat for herbivores, such as moose (*Alces alces)*. However, the relationships between the availability and duration of biomass production and moose habitat selection are largely unknown. Additionally, the effects of fire on wildlife resources in Alaska can have important consequences for boreal social-ecological systems as well. Fire-related changes to the community composition of forest stands would likely affect the densities of species that human communities rely on for hunting and trapping. In Interior Alaska, where natural wildfire is the primary means of increased browse production for moose, managers may want to consider incorporating burns into management plans while paying particular attention to hunter accessibility. However, an increase in hunter activity into moose habitat could result in changes to moose distribution and activity patterns near trails and roads. To examine these questions I utilized telemetry data from 26 moose along with methods in spatial ecology, plant-animal interactions, resource selection and human dimensions of wildlife research to predict the influence of an ecological disturbance (fire) and an anthropogenic disturbance (hunter activity) on moose habitat use. I used dynamic Brownian bridge movement models (dBBMM) in conjunction with browse assessment surveys to examine how fire severity, via its control over vegetation composition, forage production and nutritional quality, affect habitat use patterns of moose across their seasonal home ranges and core use areas. To assess the effects of hunter activity on moose habitat use, I created fine-scale step-selection models to test whether habitat selection and movement patterns were affected by spatio-temporal variation in risk from hunting activity. Additionally, from August-October, I used a camera trap array to collect field data on human activity (off-road vehicles, automobiles, 4x4 trucks, dirt bikes, and hunters afoot) together with the RandomForests algorithm to create high-resolution hunter distribution models. Finally, to integrate my research within a social-ecological framework, I examined the interactions between wildfire, forage production and hunter access on management scenarios overtime. In winter, moose preferred low-severity sites more than high and moderate-severity sites, but in summer, moose selected for high-severity sites. Forage biomass production ranged from 62 to 243 kg/ha/yr across all sites during winter within the Hajdukovich Creek Burn, but production and availability varied depending on fire severity and browse species. These results indicate that differing distributions of wildfire severity across a landscape can create a dynamic, mosaic of habitat patches that may optimize and extend the value of burns over time for moose. I found that while moose selected habitat closer to trails and roads, they also avoided areas with more hunting activity. Finally, my management scenarios provide a framework for managers to adapt goals and actions to changing conditions that can affect moose-hunter systems. I recommend that wildlife conservation and management decisions consider these methods as we seek to sustainably manage wildlife for future generations during a time of rapid socio-ecological change in Alaska.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

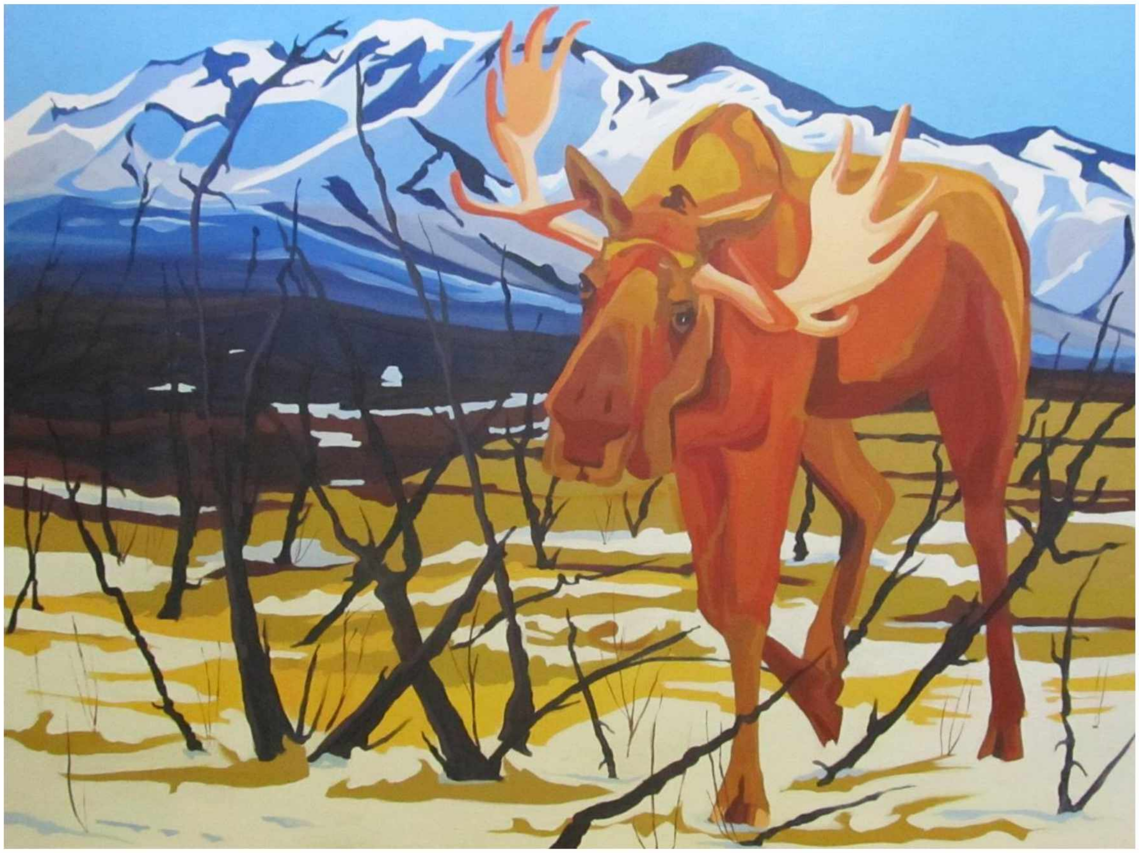
LIST OF EQUATIONS

PREFACE

I owe a great deal of thanks and gratitude to my major advisors Knut Kielland and Eugenie Euskirchen for their helpful guidance, good humor, and constant encouragement throughout my doctoral education. I am also deeply grateful to all of the members of my graduate committee, Todd Brinkman, Scott Brainerd, and Roger Ruess for their invaluable advice, suggestions, and support. I am thankful to my collaborator and co-author, Kalin Season, for her help preparing manuscripts, research advice, and productive discussions. Thank you so much to everyone who helped collect and process data in the field, especially Darren Bruning Ellie Mason, Bob Schmidt, Kimberley Maher, Dash Feierabend, Molly Tedesche, Todd Brinkman and Jack Staker. I am also grateful to the Washington State University Wildlife Habitat/Nutrition Lab for processing and analyzing our forage samples. Thank you to Tom Paragi and Tom Seaton for sharing their knowledge on plant-based sampling of forage species. Thank you also to Sophie Gilbert, Brendan Oates, Jana Canary, and Ron Barry for contributing valuable advice regarding statistical and habitat selection modeling approaches. Logistical support, field gear, and transportation were also generously provided by Todd Brinkman, Darren Bruning Laura Prugh, and Bob Schmidt. This research would not have been possible without the undying support from my friends and family, especially my fiancé, Andy Baltensperger, who has provided me with endless love, companionship, encouragement and guidance over the past five years. Funding for this research was provided by an National Science Foundation grant "Integrative Graduate Education and Research Traineeship: Global-Local Interactions: Resilience and Adaption of Social-Ecological Systems in a Rapidly Changing North" (#0654441), a Joint Fire Science Program Graduate Innovation Award, an American Association of University Women Dissertation Fellowship, a University of Alaska Fairbanks Graduate

School Dissertation Completion Fellowship, an Arctic Institute of North America Grant-In-Aid, a John F. Marooney Memorial Scholarship, a David Burnett Dunn Memorial Scholarship, a Kathryn and John Doyle Scholarship, and the Alaska Department of Fish and Game Wildlife Diversity Program. Permission to camera trap and to handle and collar moose was obtained from the Institutional Review Board (#620457-1), the International Animal Care and Use Committee (#617031-2) and from the Alaska Department of Fish and Game (ADF&G; #2012-033)

Finally, I am incredibly appreciative for the opportunity to study and explore Alaska's boreal forests, it's agent of change (wildfire), and the moose that call this extraordinary place home. I am deeply grateful for the opportunity to develop my own sense of place in this remarkable landscape. This experience has been a transformative experience both personally and professionally, and it's meaning for me can be best conveyed by the following piece of art by Iris Sutton titled, *His Grandfathers Fire.*



His Grandfathers Fire by Iris Sutton 2016.

CHAPTER 1. INTRODUCTION

1.1. GENERAL INTRODUCTION

Sustainably managing wildlife with diverse values is a challenge for natural resource managers across Alaska. These challenges can be amplified under changing environmental and socio-economic conditions. Due to the complex nature of these relationships, interdisciplinary methods are often necessary to understand the broad spectrum of effects associated with natural and anthropogenic disturbances on wildlife populations. My dissertation applied a research design that incorporated methods in spatial ecology, plant-animal interactions, resource selection and human dimensions of wildlife research to predict the influence of an ecological disturbance (fire) and an anthropogenic disturbance (hunter activity) on moose (*Alces alces*) habitat use. Additionally, I examined how socio-ecological variables can be monitored, and incorporated, into interior Alaska moose management plans.

1.2. CHAPTER 2 BACKGROUND

The effects of fire on wildlife resources in Alaska can have important consequences for boreal social-ecological systems (Chapin et al. 2008). Fire-related changes to the community composition of forest stands can affect the densities of species that human communities rely on for hunting and trapping (Nelson et al. 2008). Wildfire characteristics, such as fire severity, are important drivers of post-fire succession in boreal forests. Fire severity can alter the spatial heterogeneity of habitat for wildlife by influencing the composition, age structure, and regeneration patterns of forest patches (Johnstone and Kasischke 2005, Duffy et al. 2007, Shenoy et al. 2011). The regeneration of early successional habitats following fire is especially important for herbivores such as moose. Moose constitute the largest terrestrial subsistence resource in interior Alaska (Nelson et al. 2008) making fire-related habitat shifts especially important given that stable populations are an important ecosystem service.

Although it is generally accepted that burns can sustain or increase moose populations via forage regeneration, this may not result in increased hunter success. For example, environmental conditions, such as the rate of deciduous biomass production, can change over time and affect habitat use by moose. Additionally, landscape variables (e.g., trail condition) or economic variables (e.g., price of gas) can influence whether hunters are able to access burned areas to hunt. Thus, a combination of dynamic socio-ecological variables can have management implications on the effectiveness of burns in providing ecosystem services.

Most current wildlife management issues require a broad, interdisciplinary framework that draws on the concepts of both natural and social sciences. There is a growing consensus that most resource management issues are best understood within a social-ecological framework (Chapin et al. 2009). As recognition of the importance of social-ecological science in natural resource management increases, new interdisciplinary linkages are required (Collins et al. 2010). When studying the response of social-ecological systems to changing conditions, it is important to pay particular attention to the processes that link ecological and social components (Figure 1.1).

One method of monitoring the effects of changing environmental conditions on wildlife is to examine key drivers that can affect wildlife resources following perturbations. Although the overall functioning of wildlife-hunter systems typically involves more than one variable, their trajectories are usually influenced by a handful of controlling or “slow” variables (Figure 1.1; Walker and Salt 2006). Slow variables are those that can strongly influence social-ecological systems, but remain fairly stable because they are buffered by feedbacks which prevent rapid change (Carpenter and Turner 2000). In contrast, "fast" variables (e.g., annual forage offtake) are typically more sensitive to daily, seasonal, or inter-annual variations (Chapin et al. 2009). Fast variables are usually of foremost interest to ecosystem users because they are often considered ecosystem goods and services over the short term. The objectives of this chapter were: 1) to quantify key slow and fast variables in a moose-hunter system in Alaska following a wildfire event, and 2) to integrate these findings into management scenarios.

1.3. CHAPTER 2 RESEARCH QUESTIONS

In Chapter 2, *Applications of resilience theory in a moose-hunter system in Alaska,* I addressed the following research questions:

Question 1: What are the slow and fast social-ecological variables in our system? How do these variables change over time?

Question 2: What management actions can be linked to the long-term monitoring of social-ecological variables in our system?

1.4. CHAPTER 3 BACKGROUND

Wildfire is the most ubiquitous ecological disturbance in the boreal forest and recent studies predict an increase in frequency, extent, and severity of fire in interior Alaska under a changing climate regime (Duffy et al. 2007). High-severity fires (i.e., those that burn through the organic soil layer exposing the mineral soil) are favorable for seedling establishment of deciduous shrubs and trees (Johnstone and Kasischke 2005). Additionally, the recruitment and establishment of deciduous species in high-severity patches continues for several decades post-fire shifting the composition from black spruce to deciduous-dominated forests (Shenoy et al. 2011).

Such a shift could influence a broad suite of ecosystem processes, including the production of early successional forage patches dispersed within areas of continuous cover (McCarthy 2001). The effect of fire severity on spatial heterogeneity exhibited in the distribution of deciduous forage and cover species may be a key variable influencing habitat use by boreal herbivores such as moose (Lord and Kielland 2015). The effects of fire severity on woody browse production are especially important during winter when moose must maintain a neutral to negative energy balance.

However, it is unknown whether moose preferentially select for high severity habitat patches in relation to low/medium severity patches or other landscape features (e.g., riparian habitat) that may occur across their home range. Second, if severity is an important variable influencing moose habitat selection, more information is needed on the effects of fire severity on habitat characteristics (i.e., duration of production, % cover, and quality of browse species) that may affect moose nutrition. The objective of this research is to evaluate the influence of a regenerating burn, paying particular attention to fire severity, on seasonal (winter and summer) moose habitat use.

1.5. CHAPTER 3 RESEARCH QUESTIONS

In Chapter 3, *Fire-mediated patterns of habitat use by moose in boreal Alaska,* I addressed the following research questions:

Question 1: At the home range scale, how does a regenerating burn influence habitat selection of moose compared to other landscape features?

Question 2: Within a regenerating burn, does the fire severity of habitat patches affect moose habitat selection?

Question 3: How does fire severity affect the overall duration of browse production in a regenerating burn?

Question 4: How does fire severity affect the nutritional quality of browse species in a regenerating burn?

1.6. CHAPTER 4 BACKGROUND

Just as Alaska's boreal forest are undergoing transition under a changing climate regime, Alaska residents are experiencing dramatic socio-economic and cultural transitions. For example, rural residents in the state are increasingly moving to urban areas (Martin et al. 2008). As a result of burgeoning urban populations, areas accessible along the road system have become increasingly important to hunters throughout the state. An increase in human disturbance along road and trails can induce behavioral responses in ungulates like heightened levels of vigilance and increased flight distance (Stankowich 2008). Moose can be particularly sensitive to anthropogenic disturbance including human activities associated with hunting and transportation (Shanley and Pyare 2011). In addition, hunting has been shown to affect ungulate populations directly via mortality, and indirectly by eliciting risk-avoidance behavior (Bender et al. 1999, Conner et al. 2001). Moose may respond to hunting pressure by selecting spatial refugia (i.e., vegetative cover) or by shifting diurnal movement patterns (Ericsson and Wallin 1996). Therefore, the possibility of human-related mortality during hunting season can cause animals to adjust resource selection strategies to avoid risk.

Understanding the effects of hunting on ungulate habitat use is critical for effective wildlife management. For example, if hunter and wildlife distributions do not overlap the link between wildlife abundance and hunting opportunities may weaken, resulting in hunter dissatisfaction (Heberlein 2002). Hunter dissatisfaction might become further exacerbated if wildlife avoid or select habitat away from accessible travel corridors. In rural communities, the ability to access wildlife populations can be a critical driver of hunting opportunities (Berman and Kofinas 2004, Kofinas et al. 2010, Brinkman et al. 2014). To account for this, researchers have proposed an availability framework that not only considers the abundance of the game species in question, but also incorporates indices of seasonal distribution and hunter access (Brinkman et al. 2013). Based on this, it is important to consider that if hunters focus their effort on habitats that provide the best access (i.e., close to roads or areas with high visibility), they may not overlap with the species they are hunting.

The objectives for this chapter were to explore how variations in human activity during hunting season affect moose habitat selection and activity patterns. Specifically, I 1) examined temporal variation in habitat selection patterns (before and during hunting season) for two groups of moose, 2) quantified the effects of hunter risk across the landscape on moose habitat selection, and 3) analyzed differences in moose activity before and during hunting seasons.

1.7. CHAPTER 4 RESEARCH QUESTIONS

In Chapter 4, *Connecting moose movement and habitat selection to spatio-temporal variation in risk during hunting season,* I addressed the following research questions:

Question 1: How do moose habitat selection patterns vary before and during moose hunting season?

Question 2: How does spatial variation in hunter activity affect fine-scale moose habitat selection patterns?

Question 3: How does the hunting season affect moose movement patterns?

1.8. FIGURE

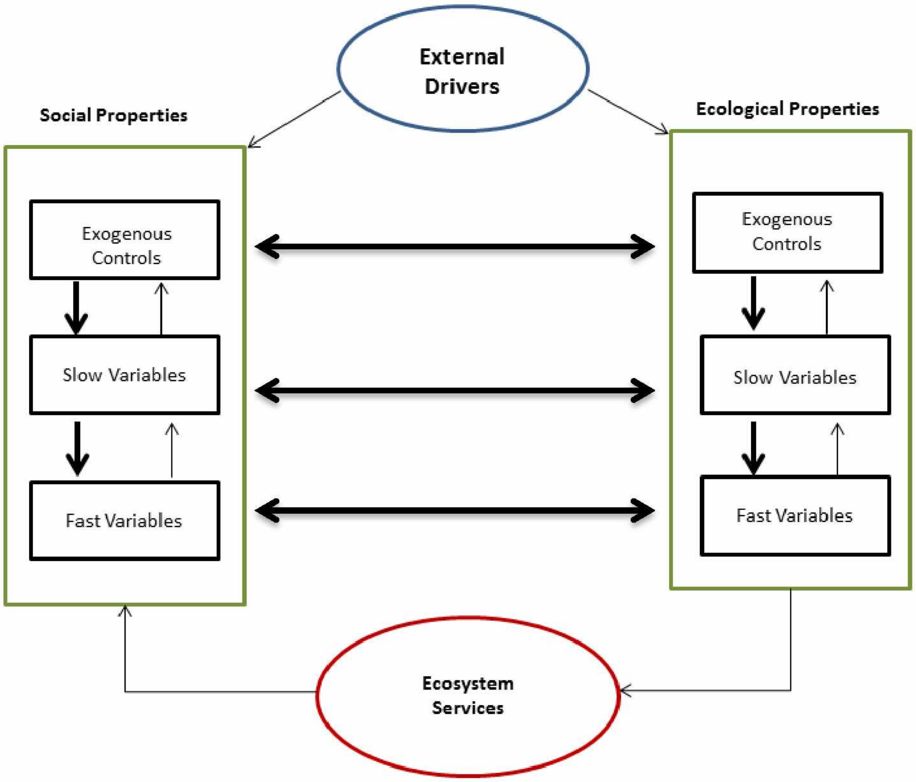


Figure 1.1. Integrated Social-Ecological System Framework

Exogenous controls affect slow variables, which, in turn can impact fast variables that change quickly. If transitions to fast variables persist over time, these effects can propagate upward to impact slow variables. Changes to both slow and fast social-ecological variables can impact ecosystem services. Adapted from Chapin et al. (2009) and Collins et al. (2010).

1.9. REFERENCES

Bender, L. C., D. E. Beyer Jr., and J. B. Haufler. 1999. Effects of short-duration, high-intensity hunting on elk wariness in Michigan. Wildlife Society Bulletin **27**:441-445.

Berman, M. and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. Ecological Economics **49**:31-46.

Brinkman, T., G. Kofinas, W. Hansen, F. S. Chapin III, and S. Rupp. 2013. A New Framework to Manage Hunting. The Wildlife Professional **7**:38-43.

Brinkman, T., K. T. B. Maracle, J. Kelly, M. Vandyke, A. Firmin, and A. Springsteen. 2014. Impact of fuel costs on high-latitude subsistence activities. Ecology and Society **19**:18. http://dx.doi.org/10.5751/ES-06861-190418

Carpenter, S. R. and M. G. Turner. 2000. Hares and tortoises: interactions of fast and slow variables in ecosystems. Ecosystems **3**:495-497.

Chapin III, F. S., S. F. Trainor, O. Huntington, A. L. Lovecraft, E. Zavaleta, D. C. Natcher, A. D. McGuire, J. L. Nelson, L. Ray, and M. Calef. 2008. Increasing wildfire in Alaska's boreal forest: pathways to potential solutions of a wicked problem. BioScience **58**:531-54

Chapin III, F. S., G. P. Kofinas, C. Folke, S. R. Carpenter, P. Olsson, N. Abel, R. Biggs, R. L. Naylor, E. Pinkerton, and D. M. S. Smith. 2009. Resilience-based stewardship: strategies for navigating sustainable pathways in a changing world. Pages 319-337 Principles of ecosystem stewardship. Springer.

Collins, S. L., S. R. Carpenter, S. M. Swinton, D. E. Orenstein, D. L. Childers, T. L. Gragson, N. B. Grimm, J. M. Grove, S. L. Harlan, and J. P. Kaye. 2010. An integrated conceptual framework for long-term social-ecological research. Frontiers in Ecology and the Environment **9**:351-357.

Conner, M. M., G. C. White, and D. J. Freddy. 2001. Elk movement in response to early-season hunting in northwest Colorado. The Journal of Wildlife Management **65**:926-940.

Duffy, P. A., J. Epting, J. M. Graham, T. S. Rupp, and A. D. McGuire. 2007. Analysis of Alaskan burn severity patterns using remotely sensed data. International Journal of Wildland Fire **16**:277-284.

Ericsson, G. and K. Wallin. 1996. The impact of hunting on moose movement. Alces **32**:31-40.

Heberlein, T. A. 2002. Peer-Reviewed Articles Too Many Hunters or Not Enough Deer? Human and Biological Determinants of Hunter Satisfaction and Quality. Human Dimensions of Wildlife **7**:229-250.

Johnstone, J. F. and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post fire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research **35**:2151-2163.

Kofinas, G. P., F. S. Chapin, S. Burnsilver, J. I. Schmidt, N. L. Fresco, K. Kielland, S. Martin, A. Springsteen, and T. S. Rupp. 2010. Resilience of Athabascan subsistence systems to interior Alaska's changing climate. Canadian Journal of Forest Research **40**:1347-1359.

Lord, R. and K. Kielland. 2015. Effects of variable fire severity on forage production and foraging behavior of moose in winter. Alces **51**:23-34.

Martin, S., M. Killorin, and S. Colt. 2008. Fuel costs, migration, and community viability. Prepared for the Denali Commission. Institute of Social and Economic Research, Anchorage, Alaska, USA.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environmental Reviews **9**:1-59.

Nelson, J. L., E. S. Zavaleta, and F. S. Chapin III. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems **11:**156-171.

Shanley, C. S. and S. Pyare. 2011. Evaluating the road-effect zone on wildlife distribution in a rural landscape. Ecosphere **2**:1-16.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management **261**:381-390.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation **141**:2159-2173.

Walker, B. and D. Salt. 2006. Resilience thinking: sustaining ecosystems and people in a changing world. Island Press.

CHAPTER 2. APPLICATIONS OF RESILIENCE THEORY IN MANAGEMENT OF A MOOSE HUNTER SYSTEM IN ALASKA[1]

2.1. ABSTRACT

We investigated wildfire-related effects on a slow ecological variable, i.e., forage production, and fast social-ecological variables, i.e., seasonal harvest rates, hunter access, and forage offtake, in a moose–hunter system in interior Alaska. In a 1994 burn, average forage production increased slightly (5%) between 2007 and 2013; however, the proportional removal across all sites declined significantly (10%). This suggests that moose are not utilizing the burn as much as they have in the past and that, as the burn has aged, the apparent habitat quality has declined. Areas with a greater proportion of accessible burned area supported both high numbers of hunters and harvested moose. Our results suggest that evaluating ecological variables in conjunction with social variables can provide managers with information to forecast management scenarios. We recommend that wildlife managers monitor fast variables frequently, e.g., annually, to adapt and keep their management responsive as resources fluctuate; whereas slower variables, which require less frequent monitoring, should be actively incorporated into long-term management strategies. Climate-driven increases in wildfire extent and severity and economically driven demographic changes are likely to increase both moose density and hunting pressure. However, the future resilience of this moose–hunter system will depend on integrated management of wildfire, hunter access, and harvest opportunities.

---

[1] Brown, C. L., K. A. Kellie, T. J. Brinkman, E. S. Euskirchen, and K. Kielland. 2015. Applications of resilience theory in management of a moose-hunter system in Alaska. Ecology and Society **20**: 16. http://dx.doi.org/10.5751/ES-07202-200116

2.2. INTRODUCTION

Sustainably managing wildlife species with diverse utilization values is one of the greatest challenges for contemporary wildlife management agencies. Management decisions can become especially difficult near communities that rely on available wildlife populations for ecosystem services such as hunting. In North America, managers will often focus on one variable (e.g., abundance) to address decisions related to harvest. In doing so, other variables (e.g., seasonal wildlife distribution, fluctuating habitat conditions, and hunter participation) are typically ignored, despite their obvious relevance to sustainable management.

In Alaska, hunting remains an integral practice to state wildlife management. Alaska is unique compared to the contiguous United States in that many rural residents rely on the seasonal harvest of wild game to maintain food security (Loring and Gerlach 2009). Even in urban centers like Anchorage, many families consume wild-caught fish and game, even if they did not harvest these resources themselves (Titus et al. 2007). Alaska has not experienced the sharp declines in hunter activity compared to the contiguous U.S. (Leonard 2007, Schuett et al. 2009). However, Alaska is undergoing dramatic socio-economic and cultural transitions. For example, rural residents of the state are increasingly moving to urban areas (Martin et al. 2008) and due to this burgeoning urban population, areas that are accessible along the road system have become increasingly important to hunters throughout the state.

Just as human communities are undergoing transition, Alaska's boreal forests are experiencing rapid change as a result of climate warming. This warming has triggered Alaska's boreal region to warm twice as rapidly as the global average (Markon et al. 2012), affecting a host of processes including an increase in plant disease and insect outbreaks (Berg et al. 2006), thawing of permafrost (Jorgenson et al. 2010), earlier snowmelt and later freeze-up (Euskirchen et al. 2010), and increased wildfire frequency (Kasischke et al. 2010). Wildfire, in particular, is the most common ecological disturbance in the boreal forest (Viereck 1973, Kasischke et al. 2002), and recent studies predict an increase in frequency, extent, and severity of fire in Interior Alaska under a changing climate regime (Duffy et al. 2005). Wildfire affects habitat quality and subsequent utilization patterns of several boreal wildlife species (Nelson et al. 2008, Kofinas et al. 2010). The immediate impact following a fire is typically a reduction in wildlife numbers; however, as vegetation begins to regenerate, populations of some species can rebound and even increase (Nelson et al. 2008).

Moose (*Alces alces*) can benefit nutritionally from post-fire regeneration of deciduous browse (Schwartz and Franzman 1989). Fires create and maintain spatially heterogeneous moose habitat. In Interior Alaska, moose are the primary terrestrial, subsistence resource (Scott et al. 2001, Nelson et al. 2008) and moose hunting has been identified as an important cultural and recreational activity to hunters throughout the state (Brinkman et al. 2013). Prescribed burns have been identified as a management option in Interior Alaska, but the lack of resources during fire prescription and limited public support has restricted the application of this habitat improvement effort (Boertje et al. 2009). Thus, natural post-fire habitat characteristics can have important consequences for the social-ecological interactions among hunters, moose, and the environment (moose-hunter system).

Like many highly valued consumptive resources, moose are challenging to manage due to lack of timely information regarding population parameters and competing interests from a variety of user groups. Changing conditions associated across multiple temporal and spatial scales can also create unexpected management scenarios. As a result, wildlife managers will have to adapt decisions to account for this variability. One approach to assessing the effects of changing environmental conditions on wildlife is to incorporate aspects of resilience theory (i.e., crossing thresholds) into management decisions. In particular, monitoring the effects of key variables (drivers) following perturbations can allow managers to forecast changes to wildlife populations. The ability of managers to target and monitor key variables and their interactions will also provide important information on ecosystem function over time. The objectives of this paper are to: 1) investigate the effects of a wildfire event on ecological and social variables in a moose-hunter system (forage production, browse offtake, hunter access, and harvest success) and; 2) highlight strategies that incorporate these variables into Alaskan moose management.

2.3. MATERIALS AND METHODS

2.3.1. Methodological Framework

The moose-hunter system consists of a set of social and ecological components that are affected by a disturbance (wildfire) (Figure 2.1). Social components in this system include: 1) proximity of wildfire to human infrastructure; 2) hunter access via motorized vehicle and; 3) hunter opportunities. The proximity of wildfire to travel corridors (i.e., roads, off-road vehicle trails) could better facilitate access, or the ability of hunters to travel through burned areas. Alaskan hunters will often utilize motorized vehicles (e.g., ATV's and snow machines) to travel more efficiently though remote or rugged terrain (Shanley et al. 2013). Access into regenerating moose habitat through travel corridors will strongly influence hunter opportunities (Berman and Kofinas 2004) and may affect the overall harvest rate of entire units (Schmidt et al. 2005). Alternatively, proximity of wildfire to human infrastructure may also interact with regional and local fire management regarding wildfire suppression efforts. Thus, regional/local fire management can also impact the relative magnitude of these interactions.

The ecological components in this system include: 1) fire severity effects on soil properties; 2) deciduous forage production and; 3) removal of deciduous forage production by moose. Wildfire characteristics, such as severity, interact strongly with ecological components of the system (Figure 2.1). Fire severity is linked to deciduous forage production due to the negative relationship between depth of the residual soil mat and recruitment of deciduous seedlings (Johnstone and Kasischke 2005, Johnstone and Chapin 2006). More recent findings suggest that the effects of the depth of burning in the organic soil layer on forest recovery can persist over several decades converting stands from black spruce to aspen (Shenoy et al. 2011). Moose selectively feed on deciduous plant species (e.g., willow and aspen) that are more likely to establish in high severity sites (Lord 2008). It is also important to note that other variables in this system that can affect moose habitat use, such as predation. Predators play a significant role in moose systems, in regions with low-density moose populations (Gasaway et al. 1992), and their presence should also be considered when investigating the influence of fire on moose densities.

2.3.2. Study Area

Our research took place in Game Management Unit (GMU) 20, located in Interior, Alaska. GMU 20 is divided into 6 subunits (A, B, C, D, E, F) comprising ~130,000 km^2. Our study was focused in GMU 20D located in the southeastern portion of GMU 20 (Figure 2.2). We chose this area because GMU 20D supports some of the highest moose densities in the state, with corresponding high levels of harvest, and has a history of large wildfires (Dubois 2010). Unit 20D has been subdivided into 4 areas for moose management purposes, and our research was located within two of these subunits: southwestern GMU 20D (SW20D), the area south of the Tanana River from the Johnson River to the Delta River and northeastern GMU 20D

(NE20D), the area north of the Tanana River and east of the Volkmar River. Land in GMU 20D varies from canopy forest and agricultural fields to subalpine terrain. Both subunits have experienced wildfire over the past twenty years and aerial surveys estimated that moose populations increased steadily until recently (Dubois 2010). However, access into these regions is very different for local hunters. SW20D has an extensive trail network that can be easily accessed via all-terrain vehicles and 4x4 trucks, whereas NE20D is difficult to access except for areas along the Tanana River and a few landing strips.

Data collection for moose forage production and removal took place within SW20D in the 19-year old Hajdukovich Creek Burn located 25 miles east of Delta Junction. In 1994, the fire burned approximately 8,900 ha of a forest dominated by black spruce stands and a few mixed stands of aspen and spruce (Johnstone and Kasischke 2005). Fire severity classes were determined by Michalek et al. (2000) and ground-truthed by Shenoy et al. (2011) (Figure 2.3). Post-fire satellite imagery and field-based comparisons of the degree of soil organic matter consumed (SOM) classified 61% of the burn as low-severity, 6% as medium severity, and 33% as high-severity.

2.3.3. Ecological Components

Browse surveys are one approach that evaluates forage conditions and the nutritional status of moose population (Seaton 2002, Boertje et al. 2007, and Paragi et al. 2008). To measure forage production and removal, we used 20 pre-established sites (Johnstone and Kasischke 2005, Lord 2008, Shenoy et al. 2011) stratified by fire severity (Figure 2.3). We sampled vegetation during the spring of 2013 before leaf emergence (March 25-April 10th) within 30 m-diameter circular plots. We randomly located three plants from each forage species (*Salix scouleriana*, *S. bebbiana*, *S. glauca*, and *S. arbusculoides*, *Populus tremuloides*, and *Betula neoalaskana*) that were of foraging height for moose (0.5m-3.0m). For each plant, we recorded species, height, dead material (%) by volume, and estimated the number of current annual growth twigs (CAG). Calipers were used to record the diameter of base of CAG for 10 twigs per plant as well as the diameter at the point of browsing (DPB) if twigs were browsed. When necessary, more than three plants were sampled until 30 twigs or all of the twigs available in the plot were measured. Total plant densities/plot were then estimated for each forage species.

We used regression coefficients established by Paragi et al. (2008) that relate diameter and dry mass of forage species and the number of twigs per plant to estimate production and removal (Telfer 1969). We used diameter of CAG to predict production and diameter of DPB to predict removal. Proportional offtake of forage biomass was estimated by the following equation:

$$\hat{B}_k = \Sigma \frac{M_{jk}}{m_{jk}} \Sigma \frac{N_{ijk}}{n_{ijk}} \Sigma \hat{z}_{hijk} \qquad \text{[Eq. 2.1]}$$

$\hat{B}_k$ is the site estimate of production or forage offtake (g/ha). Twigs are represented by *h,* plants are represented by *i,* species by *j,* and the sites by *k*. *M* and *m* are the total and sampled plants in each plot, while *N* and *n* are the total and sampled twigs. Individual twig biomass is represented by $\hat{z}$.

$$Forage\ offtake = \left(\frac{\sum biomass\ removal\ from\ all\ plants\ sampled}{\sum CAG\ biomass\ produced\ from\ all\ plants\ sampled}\right) \qquad \text{[Eq. 2.2]}$$

We used a program developed in R software, version 2.14.1, by the Alaska Department of Fish and Game (ADF&G) to read plot counts, twig diameters, diameter-biomass pairs, and dry-weight conversions and then estimate the diameter-biomass relationships and production and removal (kg/ha) on the basis of plant, species, plot and study area (Paragi et al. 2008). Tukey's adjustments for pairwise comparisons were used to test for differences among severity classes. Finally, we compared our results to a previous study (Lord 2008) that utilized the same sites and surveying technique.

2.3.4. Social Components

We used a set of spatial layers to develop an index of hunter accessibility into burns. We used statewide fire maps from the Alaska Interagency Coordination Center (AICC 2013) for fires that burned between 1994-2009, corresponding to the same years in our hunter-harvest database. We also used a statewide infrastructure layer that includes all major highways, roads, trails and other linear features (e.g., power lines, pipelines, seismic lines, etc.) (Figure 2.4). In ArcGIS 10.1 (ESRI, Redlands, CA) we used a 2 km buffer to define the areas accessible to hunters via linear features. We chose this buffer distance based on the assumption that hunters would travel within this distance from travel corridors to hunt moose. We intersected this buffered area with fires within GMU 20 to produce a map of burned areas accessible to hunters. We then calculated the accessible area burned for SW20D, NE20D, and the Hajdukovich Creek burn.

After a moose is harvested, licensed hunters in Alaska must return their harvest tag to ADF&G. Annual harvest rates (based on returned harvest tags) provide wildlife managers with information on the relative "success" of hunters within a given area. These tickets include information on the location of hunts, # of permits issued, # of hunters, and percent success. We compared local harvest statistics from SW20D and NE20D from 1994-2009 (Dubois 2010). We chose this timeframe because both subunits experienced wildfires during those decades and moose forage production is typically abundant 10-20 years post-burn (Gasaway et al. 1989, Loranger et al. 1991). However, hunter access in the two subunits is very different.

2.3.5. Management Scenarios

To integrate the interactions between the social-ecological components of our system, we devised four management scenarios that could be implemented following a wildfire disturbance in Interior Alaska. We chose the same social-ecological variables to monitor in each scenario (forage production, offtake, hunter access, and harvest success). However, each scenario represents different magnitudes for each variable (e.g., low production rate, low offtake rate, low harvest rate). Each scenario also included a set of management actions at two different timescales (1-10 and 10-20 years post-burn) to account for temporal variation.

2.4. RESULTS

2.4.1. Ecological Components

Nearly 200 kg/ha of forage biomass was produced across all sites within the Hajdukovich Creek Burn. However, production estimates were highly variable depending on the fire severity at each site. High-severity sites produced a mean of 267 (SE=26) kg/ha, medium severity sites produced 61 (SE=5) kg/ha, and low severity sites produced a mean of 172 (SE=16) kg/ha.

The proportion of annual browse production which was consumed by moose (offtake) averaged 23%, but offtake varied among fire severities. Offtake was highest in medium severity sites at 33% (SE=7%), whereas high severity sites had a proportional removal of 27% (SE=6%), with 11% (SE=4%) in low severity sties. There was no significant difference between high and medium severity sites ($t=-0.5, p=0.6$) or between medium and low severity sites ($t=2.4, p=0.09$). However, There was a significant difference in forage offtake between high severity and low severity sites ($t=2.2, p=0.05$).

Whereas the average forage production has increased slightly (5%) since 2007 (Lord 2008), the proportional removal across all sites has declined significantly from 33% in 2007 (Lord 2008) to 23% in 2013. This decline is especially apparent in high severity sites where proportional removal has declined by half between 2007 and 2013 (Lord 2008). These results suggest that moose are not utilizing the burn as much as they have in the past, and that as the burn has aged the apparent habitat quality has declined.

2.4.2. Social Components

GMU 20 contains 12,110 km of infrastructure available for hunter access (Figure 2.4). SW20D encompasses 770 km of infrastructure whereas NE20D has 480 km of infrastructure. Between 1994-2007, approximately 3 million ha burned within GMU 20. Of this area, 371,931 ha of burned land are available to hunters via travel corridors. In SW20D, 48,141 ha burned leaving 11,675 ha accessible to hunters. The total land burned in NE20D (93,885 ha) was approximately twice the size of burned land in SW20D. However, less than100 ha of that land is accessible to hunters in NE20D. By contrast, in the Hajdukovich Creek Burn (8,900 ha) 64% (~5,700 ha) is accessible to hunters.

During 1994-2009, 1577 moose were harvested during the Resident General Season Hunt in SW20D (Appendix 2.1). This resulted in 55% of the Unit 20D harvest. The average success rate of SW GMU20D was 28% (SE=1%). During that same period, hunters in NE20D harvested moose resulting in 6% of the total harvest in GMU 20D. However, average success rates in NE20D were 36% (SE=3%) and significantly higher ($t=-2.7$, $p=0.01$) than those from SW20D. Just as SW20D supported over half of the total moose harvested in the Unit, the area also supported 52% of the total number of reported hunters in GMU 20D (Appendix 2.1). By contrast, NE20D represented only 5% of the total number of hunters in the unit (Appendix 2.1).

In our study region, SW20D encompassed a greater portion of accessible burned area, supporting both high numbers of hunters and harvested moose.

2.4.3. Management Scenarios

Managers in Alaska can link the monitoring of both social and ecological variables to create management strategies for moose harvest following a wildfire (Table 2.2). For example, if managers find increasing levels of offtake accompanied by signs of habitat degradation due to high densities of moose, managers may want to increase levels of harvest by actively providing access into a burn such as maintaining ATV trails and developing access points (Scenario 3, Table 2.2). Or, if monitoring indicates high rates of browse production but low levels of offtake in a regenerating burn, managers may need to incorporate additional management strategies such as aerial surveys to monitor predator and moose habitat use (Scenario 2, Table 2.2). Alternatively, if managers observe low rates of production as well as offtake over time, they may want to discontinue monitoring the area and re-focus management efforts elsewhere (Scenario 1, Table 2.2). Finally, if managers find areas with no access but high harvest rates, this would suggest that hunters are using alternative forms of transportation like aircraft or boat (Scenario 4, Table 2.2). It is important for managers to understand that other variables in this system can affect moose densities and subsequent harvest rates. For example, in our study area the role of predation is likely less important in SW20D compared to NE20D and other more remote areas of Alaska (Boertje et al. 2009). Hunter access is not only increasing moose harvest, but also harvest of predators via trapping and hunting. The consequences of hunting and trapping predators can result in higher moose densities available for hunters. Management scenarios focusing on key drivers in the systems may help elucidate when additional management actions are needed.

Management scenarios can also be used to forecast changing habitat conditions of wildlife for the human communities that rely on them for ecosystem services. Our results suggest that proportional forage offtake has declined considerably over the past 7 years as the burn in 20DSW has aged. Local managers can use these results to forecast changing conditions for both moose and hunters in the region. Management actions will likely vary depending on the time scale of the disturbance (Table 2.2). It will be important for managers to consider the temporal scale of social-ecological variables on the system when making management decisions.

2.5. DISCUSSION

The overall functioning of social-ecological systems is usually influenced most strongly by a handful of controlling or "slow" variables. Slow variables can strongly influence these systems but remain fairly stable because they are buffered by feedbacks that prevent rapid change (Carpenter and Turner 2000). For example, slow variables might include the presence of functional types of plants/animals, disturbance regimes (e.g., fire or grazing), and the capacity of soils to supply vital nutrients (Walker and Salt 2006). Fast variables are those with substantial intra-annual variation and are more sensitive to daily, monthly, or seasonal changes (Chapin et al. 2009). Resource management decisions often focus on fast variables because they are considered ecosystem goods and services, such as annual crop production or abundance of a favored game species (Walker et al. 2012), despite the influence of slow variables on system functioning. When incorporating slow and fast variables into contemporary management, it is crucial to understand how these variables might enhance or weaken aspects of the system (Walker and Salt 2006). By identifying and monitoring key slow and fast variables, managers can better predict and adjust management goals and actions to changing dynamics that might affect wildlife-hunter systems.

The effects of fire severity can have important consequences for slow and fast social-ecological variables. For example, post-fire conditions promote deciduous forage production (slow variable) translating into more food for moose. As moose move into burns, the rate of forage removal also increases (fast variable). It will be important for wildlife managers to assess severity after a fire event. Monitoring one of the slow ecological variables in our system every few years (forage production) can provide managers with information regarding the overall habitat potential for moose, whereas monitoring the fast ecological variable every year (forage offtake) can provide managers with valuable insight into moose habitat use patterns. In areas that have been influenced by wildfire, hunter access to roads and trails (slow variables) can strongly influence seasonal harvest (fast variable).

In Alaska, wildlife researchers have proposed an availability framework that not only considers the abundance of the game species in question, but also incorporates indices of seasonal wildlife distribution and hunter access when setting management objectives (e.g., Brinkman et al. 2013). If managers want to incorporate natural wildfires into management plans, we also propose using a hunter accessibility metric that accounts for the proximity of regenerating burns to human communities and the availability of travel infrastructure within the area. In addition, monitoring the quality and quantity of roads in popular hunting areas may also be needed when assessing access. Our results suggest that evaluating local harvest tickets in conjunction with access is especially important when accounting for relative success rates. In our study area, the overall harvest success rate was lower in an area with good access (SW20D). The ease of access in this area could actually be affecting the harvest success rates due to competition between hunters. However, how “success” rate is calculated (proportion of successful harvest tickets returned) may not fully represent hunting opportunities in an area. For example, where there are few hunters, success rates are almost always higher, but the number of moose that a given area is producing for harvest is low. Thus, wildlife managers may need to develop metrics that incorporate hunter success from the landscape perspective (e.g., # moose harvested/km^2). More research will also be needed on the effects of access on the quality of the hunt (e.g., experience) and effects on wildlife (e.g., shifting distribution due to anthropogenic disturbance).

Managers will need to have a strong understanding of the system components when choosing which variables to monitor. Ultimately, managers in most situations will have to choose which variables to monitor to constrain logistical and financial costs. We recommend that wildlife managers monitor fast variables on a frequent basis (e.g., annually) in order to adapt and keep their management responsive as resources fluctuate. On the other hand, slower variables may require less monitoring unless the manager is actively attempting to change them through their management strategy. Within this general framework, wildlife managers can use several outlets to respond to a fluctuating moose population following a disturbance including: (1) collaboration with fire managers to assess severity in areas where moose may increase (e.g., in high severity burns); (2) monitor both moose forage offtake and local harvest rates to track annual use patterns; (3) adapt seasons and bag limits for increasing densities of moose; (4) actively monitor predator densities and trapping records; (5) provide on-going education regarding the relationships between access, moose numbers and predators so that community members can adapt to these new opportunities and limitations.

As wildfire characteristics, such as severity, continue to change under a warming climate, managers can expect new and often challenging management scenarios will follow. Here we offer a framework that includes monitoring slow and fast social-ecological variables overtime to forecast changes to wildlife resources following a disturbance. Wildlife management must be adaptive by nature because managers have to continually assess fluctuating wildlife populations and adjust harvest actions accordingly. This approach is novel because it allows managers to use social and ecological metrics as well as their interactions overtime to help steer management decisions. Understanding the slow habitat variables that are driving wildlife population dynamics will become especially important when setting long-term management goals. Yet, mangers must also account for fast social-ecological variables to adapt short-term management strategies. In a time of rapid change across northern ecosystems, resilience-based wildlife management may offer an opportunity to better predict how wildlife-hunter systems will be affected by changing resource conditions.

2.6. ACKNOWLEDGEMENTS

The research for this paper was supported by National Science Foundation grant “Integrative Graduate Education and Research Traineeship: Global-Local Interactions: Resilience and Adaption of Social-Ecological Systems in a Rapidly Changing North” (Grant # 0654441). The views expressed in the paper are those of the author(s) and do not represent the National Science Foundation. We gratefully acknowledge the Alaska Department of Fish and Game, specifically the Delta Junction Area Office, for providing valuable assistance in the field with data collection. We thank S. Dubois, D. Haggstrom, T. Paragi, T. Seaton for consultation and advice on the project. We thank A. Baltensperger for field assistance and help with analysis of spatial data. Funding to support this research was provided by grants from the University of Alaska Fairbanks Resilience and Adaptation Program.

2.7. FIGURES

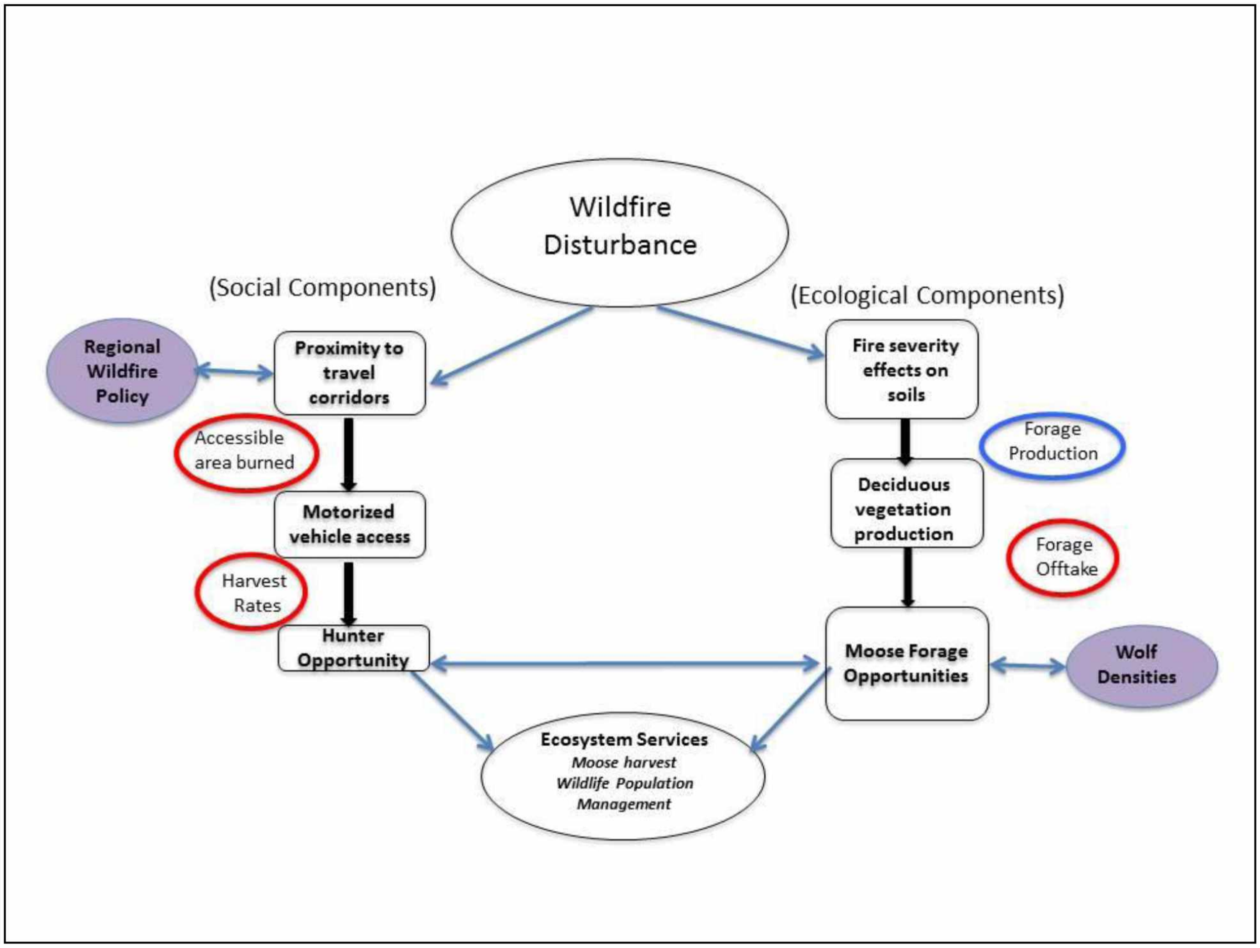


Figure 2.1. Diagram of the Social and Ecological Components

The social and ecological components in a moose-hunter system following a wildfire disturbance in interior Alaska. Arrows represent the interactions between components. Research in our system focused on a slow variable (oval with blue outline) and fast variables (ovals with red outline). Purple ovals represent exogenous variables that can also affect system components.

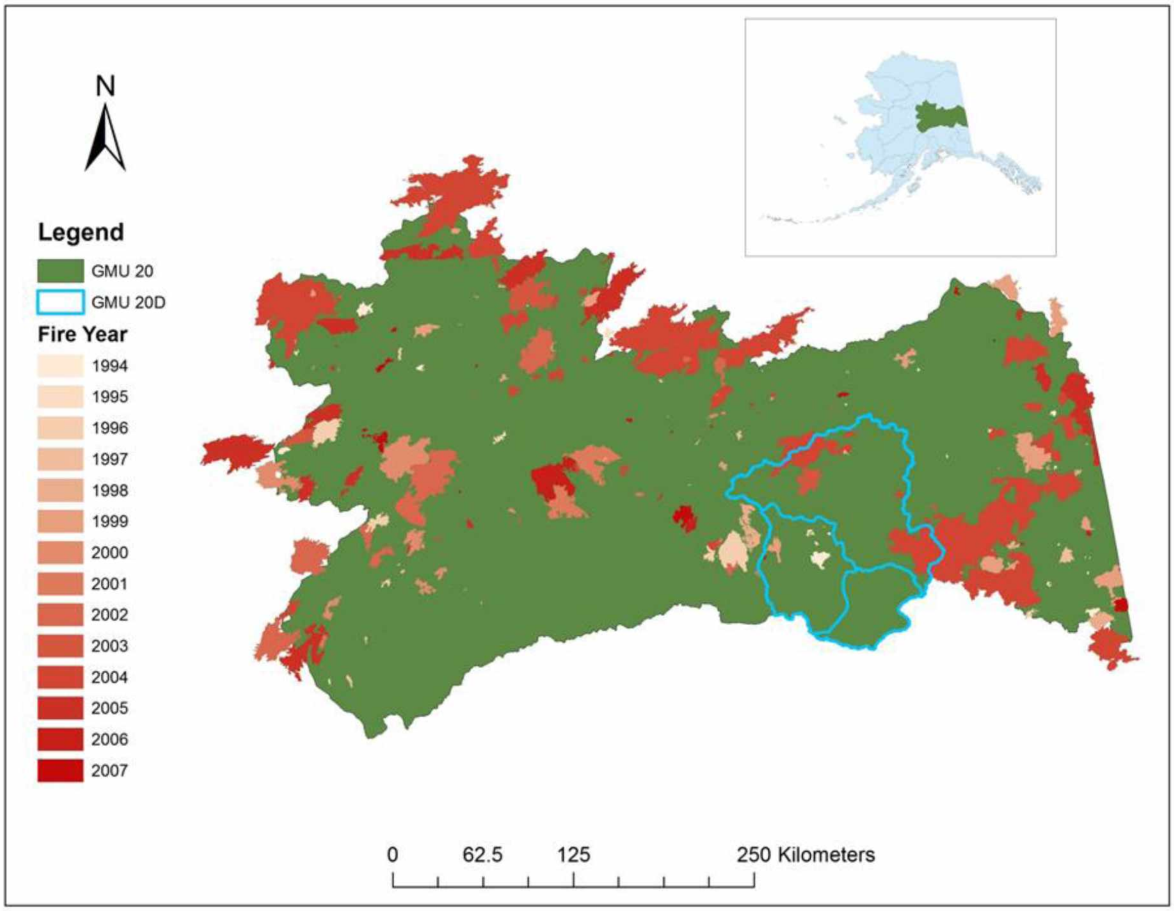


Figure 2.2. Map of Game Management Unit 20 Burned Areas.

The region highlighted with blue represents the location of our case study in game management unit 20D.

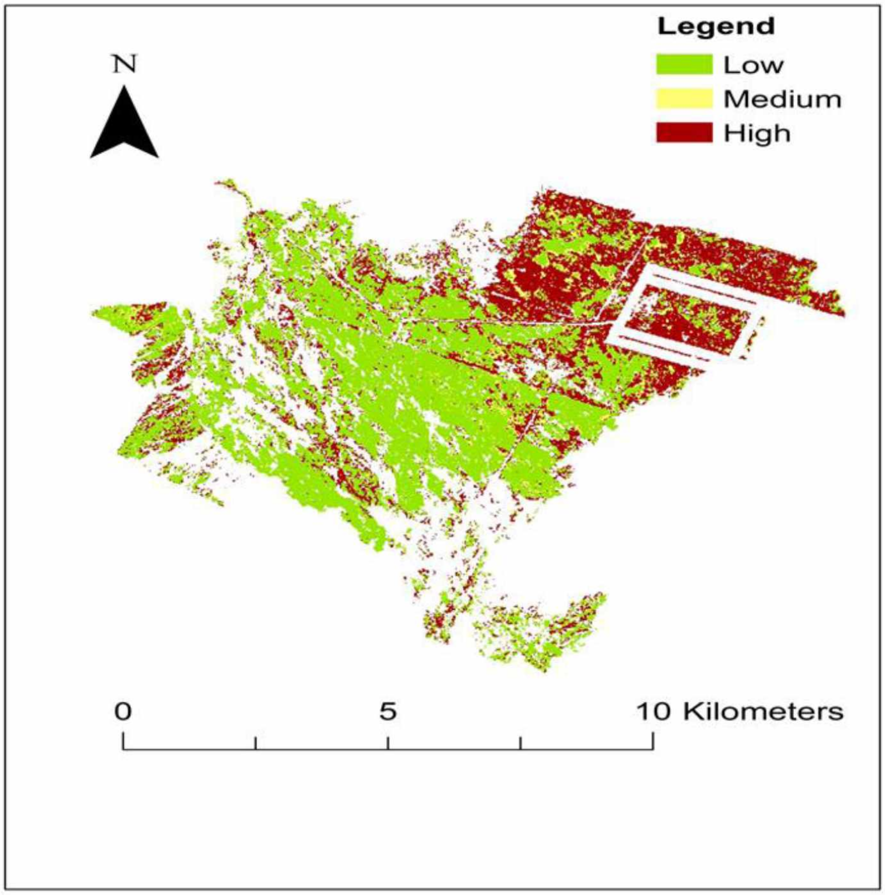


Figure 2.3. Fire-severity Map of Hajdukovich Creek Burn.

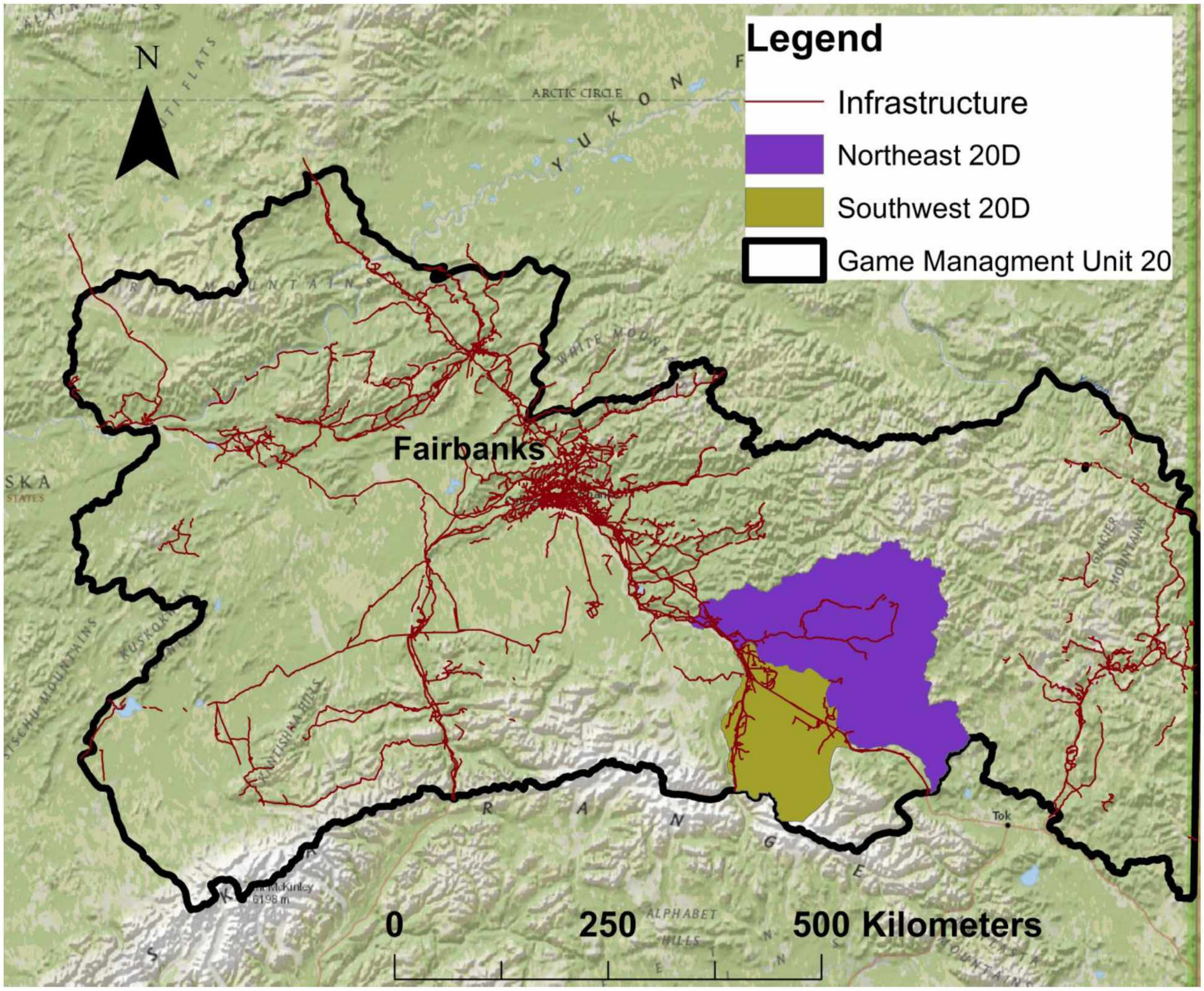


Figure 2.4. Map of Transportation Infrastructure

Infrastructure line on map encompasses all major highways, roads, trails, and other linear features, e.g., powerlines, pipelines, seismic lines, and major rivers, across Game Management Unit 20.

2.8. TABLES

Table 2.1. Management Scenarios: Initial Prioritization

Initial prioritization (1-2 years) allows managers to rank burns that have habitat potential for moose (*Alces alces)* and evaluate whether hunters will be able to utilize these areas in the future. Together these metrics allow managers to priortize areas as high, moderate, and low for continued management.

	Fire Severity	**Hunter Access**	**Forage Production**	**Forage Offtake**	**Harvest Rate**	**Management Action**
Scenario 1	Low	No	Low production rate	Low offtake rate	Low	***Initial Prioritization: LOW*** If the fire is categorized as a low severity burn, it can be expected that coniferous tree species could dominate the forest stands. An area with no access suggests hunters will need to find alternative transportation methods (e.g., aircraft) when accessing the area. ***Continued Monitoring:*** Low production and offtake rates indicate that vegetation is slow to recover and moose are not utilizing the area. If monitoring efforts indicate little to no hunter activity as well as low harvest rates, hunters are not using burn. *Management Action:* Reduce monitoring efforts as this area will likely not become suitable for moose harvest and focus management efforts elsewhere.

Table 2.1. cont.

Scenario 2	High	Yes	High Production rate	Low offtake rate	Low	***Initial Prioritization: MODERATE*** High severity fires with high-levels of forage production would indicate that moose habitat potential exists for this area. Thus, managers will want to investigate whether the area support hunter access. ***Continued Monitoring:*** Annual browse surveys to monitor habitat potential overtime can provide managers with benchmarks regarding habitat potential in a high severity burn. However, an area with quality moose habitat but low offtake rates suggests that moose have not dispersed into the burn due to already low populations (potentially limited by predation or philopatric migration behavior). The lack of available moose populations would translate over to low harvest rates. *Management Action*: Aerial surveys should be utilized to measure moose and predator densities. If surveys indicate adequate moose densities in surrounding forest patches, managers may need to initially restrict hunting to allow moose populations to disperse into the burn. Active communication with hunters regarding alternative areas to hunt will also be important to mitigate hunter disapproval. If surveys indicate low moose populations, but high predator densities, managers may want to shift management efforts to alternative burn sites.
Scenario 3	Moderate-High	Moderate	High production rate	High offtake rate	Low	***Initial Prioritization: HIGH*** An area that has some access or has the potential for future access suggests hunters will have to find alternative transportation or managers will have to create access. *Management Action:* Develop a hunter accessibility metric (e.g., area accessible to hunters) to strategize where access may already exist and communicate this information to the public. If access does not exist, wildlife managers will need to collaborate with resource managers regarding the sustainability of trail clearing, building, etc. ***Continued Monitoring:*** If forage production is high accompanied with high offtake rates, moose are utilizing the burn. If proportional offtake is high, accompanied by signs of plant mortality and low twinning rates, moose may be nutritionally stressed and management actions should be considered.

Table 2.1 cont.

Scenario 4	High	No	High production rate	High offtake rate

High	***Initial Prioritization: HIGH*** An area with no access but high harvest rates suggests that hunters that do enter these areas are utilizing aircraft or boats. Hunters that are able to gain access have less competition from other hunters and will likely have good hunting opportunities. *Management Action:* Continue to monitor browse production annually as the burned area continues to regenerate. ***Continued Monitoring:*** If production is still high accompanied with signs of use, there is still habitat potential for moose. Managers should monitor both growth and the potential for overbrowsing. *Management Action:* Same as 1-10 years post burn.

Table 2.2. Management Scenarios: Long-term Monitoring (3-15 years).

	Forage Production	**Forage Offtake**	**Hunter Access**	**Harvest Rate**	**Management Action**
Scenario 1	Low production rate	Low offtake rate	No	High	***1-10 years post-burn:*** An area with little access and high harvest rates suggest hunters Low production and offtake rates indicate that vegetation is slow to recover and moose are not utilizing the area. Management Action: Continue to conduct browse surveys and monitor access every 2 years as fire regenerates. Communicate with fire managers to determine the severity of the burn. ***11-20 years post-burn*:** If monitoring efforts still indicate little to no hunter activity along road corridors as well as low harvest rates, hunters are still not using burn. Management Action: Reduce monitoring efforts as this area will likely not become suitable for moose harvest.
Scenario 2	High Production rate	Low offtake rate	Yes	Low	***1-10 years post-burn:*** An area with good access and high harvest rates indicate that hunters have the ability to access the area. However, low harvest rates indicate little hunter success. High severity fires could indicate increased production rates of deciduous species overtime suggesting quality moose habitat exists, but, moose are not using the burn. Management Action: Continue to conduct annual browse surveys to monitor habitat potential. Conduct aerial surveys to assess moose and predator distribution across a larger area (moose may not have dispersed into the burn or moose densities may be limited by predation). Communicate with hunters regarding alternative areas to hunt. **11-20 years post-burn:** An area with historically high production rates and low offtake rates suggests that moose have not dispersed into the burn due to already low populations (potentially limited by predation or philopatric migration behavior). Low harvest rates are likely due to lack of available moose populations to hunt. Management Action: Assess whether the burn still has habitat potential (i.e., has forage grown out of moose browsing height). If forage is on average > 3m, abandon monitoring efforts.

Table 2.2. cont.

Scenario 3	High production rate	High offtake rate	No	Low	***1-10 years post-burn:*** An area with no access and low harvest rates suggests that hunters are not utilizing the area. However, high production rates and proportionally high offtake rates suggest that moose are using the area. *Management Action:* Continue to monitor browse production annually as the burned area continues to regenerate. Develop a hunter accessibility metric (e.g., area accessible to hunters) to strategize where access may already exist and communicate this information to the public. If access does not exist, wildlife managers will need to collaborate with resource managers regarding the sustainability of trail clearing, building, etc. Monitor the nutritional condition of moose in the area. If proportional offtake is high, accompanied by signs of plant mortality and low twinning rates, moose may be nutritionally stressed and management actions (i.e., liberalized hunts) should be considered to decrease the population once access is established. **11-20 years post-burn:** If production is still high accompanied with signs of use, there is still habitat potential for moose. Managers should monitor both growth and the potential for overbrowsing. *Management Action:* Same as 1-10 years post burn, but active and decisive management will be needed
Scenario 4	High production rate	High offtake rate	No	High	***1-10 years post-burn:*** An area with no access but high harvest rates suggests that hunters that do enter these areas are utilizing aircraft or boats. Hunters that are able to gain access have less competition from other hunters and will likely have good hunting opportunities. *Management Action:* Continue to monitor browse production annually as the burned area continues to regenerate. ***11-20 years post burn:*** If production is still high accompanied with signs of use, there is still habitat potential for moose. Managers should monitor both growth and the potential for overbrowsing. *Management Action:* Same as 1-10 years post burn.

2.9. REFERENCES

(AICC) Alaska Interagency Coordination Center. 2013. Alaska Fire Center. Fort Wainwright, AK, USA. [online] URL: http://fire.ak.blm.gov/predsvcs/maps.php.

Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. Forest Ecology and Management **227**:219-232.

Berman, M. and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches for analyzing climate effects of subsistence hunting in an Arctic community. Ecological Economics **49**:31-46.

Boertje, R. D., K. A. Kellie, C. T. Seaton, M. A. Keech, D. D. Young, B. W. Dale, L. G. Adams, and A. R. Aderman. 2007. Ranking Alaska moose nutrition: Signals to begin liberal antlerless harvests. Journal of Wildlife Management **71**:1494-1506.

Boertje, R. D., M. A. Keech, D. D. Young, K. A. Kellie, and C. Seaton. 2009. Managing for elevated yield of moose in Interior Alaska. The Journal of Wildlife Management **73**:314-327.

Brinkman, T. J., G. Kofinas, W. D. Hansen, F. S. Chapin III, T.S. Rupp. 2013. A new framework to manage hunting: why we should shift focus from abundance to availability. The Wildlife Professional **7**:38-43.

Carpenter, S. R. and M. G. Turner. 2000. Hares and Tortoises: Interactions of Fast and Slow Variables in Ecosystems. Ecosystems **3**:495-497.

Chapin III, F. S., G. P. Kofinas, C. Folke, and M. C. Chapin. 2009. Principles of ecosystem stewardship: resilience-based natural resource management in a changing world. Cambridge University Press, Cambridge, UK.

DuBois, S. D. 2010. Unit 20D moose. Pages 380–409 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2007–30 June 2009. Alaska Department of Fish and Game. Juneau, AK, USA.

Duffy, P. A., J. E. Walsh, J. M. Graham, D. H. Mann, and T. S. Rupp. 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. Ecological Applications **15**:1317-1330.

Euskirchen, E., A. McGuire, F. S. Chapin III, and T. Rupp. 2010. The changing effects of Alaska's boreal forests on the climate system. Canadian Journal of Forest Research **40**:1336-1346.

Gasaway, W. C., S. D. Dubois, R. D. Boertje, D. J. Reed, and D. T. Simpson. 1989. Response of radio-collared moose to a large burn in central Alaska. Canadian Journal of Zoology **67**:325–329.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs **120**:1-59.

Johnstone, J. F. and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post fire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research **35**:2151-2163.

Johnstone, J. F. and F. S. Chapin III. 2006. Effects of burn severity on patterns of post-fire tree recruitment in boreal forests. Ecosystems **9**:14–31.

Jorgenson, M. T., V. Romanovsky, J. Harden, Y. Shur, J. O'Donnell, E. A. Schuur, M. Kanevskiy, and S. Marchenko. 2010. Resilience and vulnerability of permafrost to climate change. Canadian Journal of Forest Research **40**:1219-1236.

Kasischke, E. S., D. Williams, and D. Barry. 2002. Analysis of the patterns of large fires in the boreal forest region of Alaska. International Journal of Wildland Fire **11**:131-144.

Kasischke, E. S., D. L. Verbyla, T. S. Rupp, A. D. McGuire, K. A. Murphy, R. Jandt, J. L. Barnes, E. E. Hoy, P. A. Duffy, and M. Calef. 2010. Alaska's changing fire regime-implications for the vulnerability of its boreal forests. Canadian Journal of Forest Research **40**:1313-1324.

Kofinas, G. P., F. S. Chapin, S. Burnsilver, J. I. Schmidt, N. L. Fresco, K. Kielland, T. S. Rupp. 2010. Resilience of Athabascan subsistence systems to Interior Alaska's changing climate. Canadian Journal of Forest Research **40**:1347-1359.

Leonard, J. 2007. Fishing and hunting recruitment and retention in the U.S. from 1990-2005. Addendum to the 2001 National Survey of Fishing, Hunting, and Wildlife Associated Recreation. Arlington, VA: U.S. Fish and Wildlife Service.

Loranger, A. J., T. O. Osbornet, T. F. Paragi, J. L. Bodkin, and N. Johnson. 1991. Extent, cause, and timing of moose calf mortality in western Interior Alaska. Alces **27**:24-30.

Lord, R. E. 2008. Variable fire severity in Alaska's boreal forest: implications for forage production and moose utilization patterns. M.S. Thesis. University of Alaska Fairbanks, Fairbanks, AK.

Loring, P. A. and S. C. Gerlach. 2009. Food, culture, and human health in Alaska: an integrative health approach to food security. Environmental Science & Policy **12**:466-478.

Markon, C. J., S. F. Trainor, and F. S. Chapin III, eds., 2012. The United States National Climate Assessment Alaska Technical Regional Report: U.S. Geological Survey Circular 1379, 148p.

Martin, S., M. Killorin, and S. Colt. 2008. Fuel Costs, Migration, and Community Viability. Prepared for The Denali Commission. Anchorage: Institute of Social and Economic Research, 22p.

Michalek, J., N. French, E. Kasischke, R. Johnson, and J. Colwell. 2000. Using Landsat TM data to estimate carbon release from burned biomass in an Alaskan spruce forest complex. International Journal of Remote Sensing **21**:323-338.

Nelson, J. L., E. S. Zavaleta, and F. S. Chapin III. 2008. Boreal fire effects on subsistence resources in Alaska and adjacent Canada. Ecosystems **11**:156-171.

Paragi, T. F., C. T. Seaton, and K. A. Kellie. 2008. *Identifying and evaluating techniques for wildlife habitat management in Interior Alaska: moose range assessment*. Project 5.10, Alaska Department of Fish and Game, Juneau, Alaska.

Schmidt, J. I., J. M. Ver Hoef, J. A. Maier, and R. T. Bowyer. 2005. Catch per unit effort for moose: a new approach using Weibull regression. Journal of Wildlife Management **69**:1112-1124.

Schuett, M. A., D. Scott, and J. O'Leary. 2009. Social and Demographic Trends Affecting Fish and Wildlife Management. In *Wildlife and Society*, eds. M. Manfredo, J. J. Vaske, P. J. Brown, D. J. Decker, and E. A. Duke. Island Press, Washington, D.C., USA.

Schwartz, C. C. and A. W. Franzman. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces **25**:1-10.

Scott, C., L. A. Brown, G. B. Jennings, and C. J. Utermohle. 2001. Community Profile Database for Access 2000 (version 3.12). Alaska Department of Fish and Game, Division of Subsistence, Juneau, AK, USA.

Seaton, C. T. 2002. *Winter foraging ecology of moose in the Tanana Flats and Alaska Range Foothills*. M.S. Thesis. University of Alaska Fairbanks, Fairbanks, AK.

Shanley, C. S., G. P. Kofinas, and S. Pyare. 2013. Balancing the conservation of wildlife habitat with subsistence hunting access: A geospatial-scenario planning framework. Landscape and Urban Planning **115**:10-17.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in Interior Alaska. Forest Ecology and Management **261**:381-390.

Telfer, E. 1969. Weight-diameter relationships for 22 woody plant species. Canadian Journal of Botany **47**:1851-1855.

Titus, K., T. L. Haynes, and T. R. Paragi. 2007. The importance of moose, caribou, deer and small game in the diets of Alaskans. Alaska Department of Fish and Game Report, Anchorage, AK, USA.

Viereck, L. A. 1973. Wildfire in the taiga of Alaska. Quaternary Research **3**:465-495.

Walker, B. and D. Salt. 2006. *Resilience thinking: sustaining ecosystems and people in a changing world*. Island Press, Washington, D.C., USA.

Walker, B. H., S. R. Carpenter, J. Rockstrom, A. S. Crepin, and G. D. Peterson. 2012. Drivers," slow" variables," fast" variables, shocks, and resilience. Ecology and Society **17**:30.

2.10. APPENDIX

Appendix 2.1 Moose harvest statistics

Southwest (SW) and northeast (NE) GMU 20D reported the number of moose harvested, the number of hunters, and success Adapted from Dubois (2010).

Regulatory Year	SW Moose Harvested	NE Moose Harvested	Total Moose Harvested 20D	SW Hunters	NE Hunters	Total Hunters 20D	SW Success Rate	NE Success Rate
1994-1995	61	9	128	339	33	709	18%	27%
1995-1996	60	12	138	301	42	645	20%	29%
1996-1997	103	16	211	320	35	693	32%	46%
1997-1998	88	19	202	325	46	683	27%	41%
1998-1999	122	16	227	431	43	795	28%	37%
1999-2000	107	12	177	358	29	644	30%	41%
2000-2001	140	18	240	355	35	657	35%	51%
2001-2002	101	14	178	425	41	744	24%	34%
2002-2003	119	5	204	426	39	836	28%	13%
2003-2004	124	13	212	447	41	794	28%	32%
2004-2005	107	14	197	415	42	772	26%	33%
2005-2006	126	13	219	407	30	721	31%	43%
2006-2007	155	19	286	517	44	915	30%	43%
2007-2008	164	12	273	535	39	995	31%	31%

CHAPTER 3. FIRE-MEDIATED PATTERNS OF HABITAT USE BY MALE MOOSE IN BOREAL ALASKA[1]

3.1. ABSTRACT

Wildfire is the most ubiquitous ecological disturbance in Alaska's boreal forests. It is the primary driver of secondary succession in these forests and directly influences available habitat for many Alaskan wildlife species. Fire severity is an important control over regeneration of deciduous species and can influence the overall quality of habitat for herbivores, such as moose (*Alces alces)*, but the relationships between the availability and duration of biomass production and moose habitat use are largely unknown. The purpose of this research was to evaluate the relative influence of a regenerating burn on seasonal moose habitat use. Additionally, we examine the effects of stand regeneration on utilization patterns in relation to fire severity. To examine these relationships, we used data from 15 GPS collared moose in the 20-year-old regenerating Hajdukovich Creek Burn (HCB) in Interior Alaska. We conducted winter browse surveys to measure forage production, forage offtake, nutritional quality and other habitat characteristics (i.e., plant mortality and architecture class), that were stratified across fire severities. We used dynamic Brownian bridge movement models (dBBMM) to examine how fire severity, via its control over vegetation composition and forage production, affects habitat use patterns of moose across their seasonal home ranges and core use areas. Within HCB, moose selected for low-severity sites more than high and moderate-severity sites during the winter. In summer, however, moose selected for high-severity sites. Forage biomass production ranged

---

[1] Submitted to Journal of Wildlife Management as Brown, C. L., K. Kielland, E. S. Euskirchen, R. W. Ruess, K. A. Kellie, and T. J. Brinkman. Fire-mediated patterns of habitat use by male moose in boreal Alaska (2016).

from 62 to 243 kg/ha/yr across all sites during winter within the HCB, but production and availability varied depending on fire severity and browse species. These results indicate that differing distributions of wildfire severity across a landscape can create a dynamic mosaic of habitat patches that may optimize and extend the value of burns over time for moose.

3.2. INTRODUCTION

Spatial heterogeneity of landscapes can have important effects on wildlife by influencing patch size and shape, as well as the composition and distribution of habitat types across landscapes (Turner 1989, Li and Reynolds 1994). These changing habitat characteristics can influence predator-prey interactions (Pierce et al. 2000, Kauffman et al. 2007), population dynamics (Dempster and Pollard 1986), community structure (Pacala and Roughgarden 1982), and animal movement and distribution (Kie et al. 2002, Boyce et al. 2003). Both natural (e.g., wind, drought and fire) and anthropogenic disturbances (e.g., agriculture and logging) can be considered sources of large-scale spatial heterogeneity. In forest-dominated landscapes, disturbances, such as fire, produce spatial heterogeneity by creating new patches of early successional habitat within the forest matrix (McCarthy 2001).

Wildfire is the most common ecological disturbance in the Alaskan boreal forest, burning on average 1 to 2 million acres per year (Chapin et al. 2008). Black spruce (*Picea mariana*) forests are the most common forest type in Interior Alaska. These forests typically follow a post-fire successional trajectory of self-replacement where the dominant pre-fire stand replaces itself shortly after low-severity fires (Van Cleve and Viereck 1981). However, recent studies in Interior Alaska and Canada have shown fire severity, in particular, is an important driver for post-fire succession in boreal forests (Johnstone et al. 2010). High-severity fires (i.e., those that burn through the organic soil layer exposing the mineral soil) have been shown to be favorable for seeding deciduous shrubs and trees (Johnstone and Kasischke 2005). It has also been shown that the recruitment and establishment of deciduous species in high-severity patches persists for several decades post-fire shifting the composition from black spruce to hardwood-dominated forests (Shenoy et al. 2011). Fire severity is also linked to an increase in fire extent across Alaska (Duffy et al. 2007). Thus, fire severity can alter the spatial heterogeneity within boreal forests by influencing the composition, age structure, and size of habitat patches.

A fire-mediated shift to a deciduous-dominated forest could affect a broad suite of ecosystem processes, including the production and duration of important forage and cover species for boreal herbivores such as moose (*Alces alces*). The effects of fire severity on spatial heterogeneity manifested in the distribution of forest cover and vegetation in early successional patches may be a key variable influencing habitat use by moose (Lord and Kielland 2015). Throughout the year, moose must balance the costs and benefits associated with accessing forage and finding cover against predation and weather conditions (Hansson 1994). The effects of fire severity on woody browse production are especially important during winter when moose maintain a neutral to negative energy balance. An increase in winter forage production in high-severity sites may be accompanied with greatly increased forage offtake (Lord and Kielland 2015). Therefore burned areas could represent habitat mosaics of productive forage patches dispersed within areas of continuous cover. It remains unknown, however, whether moose select for high-severity habitat patches in relation to low/moderate-severity patches or other unburned features (e.g., riparian habitat) that may occur within their home range.

Despite recent research on the effects of fire severity on forest recruitment (Johnstone and Kasischke 2005, Shenoy et al. 2011), the duration of post-fire browse availability for moose is less understood. Numerous studies have found that moose populations respond strongly to the increased production of shrub habitat post-fire (Lutz 1960, Spencer and Hakala 1964, DuBois 2008). Schwartz and Franzmann (1989) found that moose populations increased 15 years after a burn on the Kenai Peninsula in Alaska, and most research suggests that favorable moose habitat conditions peak between 11 and 30 years following wildfire (MacCracken and Viereck 1990, Maier et al. 2005).

Browse quality of selected diets by ungulates may also differ between habitats that are burned and unburned (Blair 1997, Van de Vijver et al. 1999). For example, Hobbs and Spowart (1984) found that bighorn sheep (*Ovis canadensis*) and mule deer (*Odocoileus hemionus*) diets had higher crude protein and digestibility in burned habitat compared to non-burned habitat during the winter season. However, the effects of fire severity on nutritional quality are unknown. Low-severity sites are typically characterized by cool, moist soils that are generally less-productive; whereas high-severity sites have warmer, dry soils that are more productive soils (Johnstone et al. 2010, Shenoy et al. 2013). Nitrogen, in particular, is a limiting nutrient to plant growth in boreal regions (Bryant et al. 1983) and dietary nitrogen can act as a nutritional constraint for moose in these environments (McArt et al. 2009). If wildfire does have significant impacts on forage quality, these differences will be important during the winter when forage quality is at its nadir and moose are typically in a negative energy /protein balance (Oldemeyer et al. 1977, Van Soest et al. 1991).

The objective of this research was to evaluate the influence of a regenerating burn on seasonal (winter and summer) moose habitat use. We used GPS telemetry data from 15 moose to examine how the regenerating burn affected habitat-use patterns. We also examined if fire severity influenced the use of habitat patches within individual winter core use areas (i.e., 40% use area), and performed winter browse assessment surveys to assess forage production, offtake and nutritional quality across high and low severity sites within a regenerating burn. We hypothesized that moose are still utilizing habitat with a regenerating burn 20 years post-fire. Additionally, we hypothesized that moose prefer habitat within the burn compared to unburned areas during both winter and summer. Within the burn, we expected individual moose to exhibit greater preference for high-severity sites versus low-severity sites during both winter and summer due to the greater abundance and quality of woody browse in the high-severity sites.

3.3. METHODS

3.3.1. Study Area

Research was conducted in the vicinity of the 20-year old Hajdukovich Creek Burn (HCB) 40 km east of Delta Junction, Alaska (Figure 3.1), located on the northern side of the Alaska Range. The terrain within the HCB consists of a relatively flat glacial outwash plain lying between the Alaska Range to the south, and the Tanana River to the north. Agriculture fields border the northern edges of the burn and high-elevation hills run along the southern perimeter. Riparian corridors including the Gerstle River and Sawmill Creek border the eastern and western edges, respectively. Soils in the HCB consist predominantly of silt loam overlying sand and gravel deposits, with some areas having a layer of stream-deposited cobble on top of the silt (Johnstone and Kasischke 2005). The climate is continental and mean annual precipitation is approximately 28.6 cm, most of which is received as rain during May to September. Winter temperatures during our study ranged from - 10°C to - 42°C, whereas summer temperatures ranged between 0°C to 30°C (Brown unpublished data, 2014). Mean snow depth during winter months is 0.43 m ±0.01 and does not differ significantly between fire severities (p=0.97, Brown unpublished data). Predators in the study area include wolves (*Canis lupus*), brown bears (*Ursus arctos*), and black bears (*U. americanus*). Good road and trail access for trapping and hunting in the region is likely limiting local predator densities and the role of predation may be less important compared to other areas in the state.

3.3.2. Fire Severity Classification

In June-September 1994, the fire burned approximately 8,900 hectares of predominantly mature black spruce (*Picea mariana)* stands with few mixed stands of aspen and spruce (Johnstone and Kasischke 2005, Michalek et al. 2000). Vegetation composition in high-severity patches is dominated by deciduous trees and shrubs, such as willow (*Salix scouleriana, Salix bebbiana, Salix glauca),* aspen *(Populus tremuloides)* or Alaska birch (*Betula neoalaskana*), whereas low-severity patches are primarily composed of black spruce, willow (*Salix* spp.) and few aspen and birch (Shenoy et al. 2011). In 1996, fire severity classes were determined using post-fire satellite imagery and later ground-truthed with field measurements of soil organic matter (SOM) combustion (Michalek et al. 2000). In total, 43% of the HCB burn scar perimeter was classified as low-severity, 4% as moderate-severity, and 23% as high-severity, and 29% as unburned (Figure 3.1).

3.3.3. Habitat Classification

We merged 2001 National Land Cover Data (NLCD) with the HCB perimeter (Michalek et al. 2000) to produce a map of relevant habitat types for the study area. We condensed habitat types into 7 habitat classes: *evergreen forest, deciduous forest, shrubs, mixed forest, open water, agriculture*, and *burn*. We are aware that a diversity of habitats may exist within burns; however, our first step was to compare habitat use in burned versus unburned areas. The *burn* class represented areas within the HCB perimeter. The *evergreen forest, deciduous forest, shrubs, mixed forest, open water,* and *agriculture* were all unburned habitat types outside of the HCB. We validated our reclassified NLCD layer with 243 point locations that were ground-truthed within the study area. We found that 88% of the ground-truthed locations outside the HCB were classified accurately by our NLCD habitat layer.

In addition, we utilized a recent habitat layer to examine the dominant forest types found within the entire HCB. This layer was ground-truthed in 2013 using 88 point locations. We reclassified vegetation types to consist of *Agriculture, Black spruce/Willow (Picea mariana, Salix sp.)*, *Coniferous (Picea mariana and Picea glauca), Deciduous* (*Populus tremuloides, Betula neoalaskana*, *Salix sp.*), *Mixed (coniferous sp. and deciduous sp.), Open water, Shrub* (*low-lying Salix sp.* and *Betula nana), and Tundra* (Figure 3.2). We intersected these layers in Geospatial Modeling Environment 0.7. 2.0 (Beyer 2012) to calculate the proportion of vegetation types within each fire severity class.

3.3.4. Browse Production and Quality

To estimate forage composition within fire severity classes, we used 16 pre-established sites (Johnstone and Kasischke 2005, Lord 2008, Shenoy et al. 2011) (low, n=6; high, n=10) for browse assessment surveys. The sites were distributed along the trail system within the burn scar and accessed via snow machine in March 2013. We did not include data from moderate-severity sites due to low sample size (n=3) and the fact that a small percentage of the burn was classified as moderate severity (6% moderate severity versus 61% for low severity and 33% for high severity, as described above). At each site, we established one 30-m diameter circular plot and randomly selected three plants of each forage species within each plot. We defined forage species as willow (*Salix scouleriana, S. bebbiana, S. glauca),* aspen *(Populus tremuloides)* or Alaska birch (*Betula neoalaskana*) that were of foraging height for moose (0.5–3 m; Peek et al. 1976, Risenhoover 1989). Whereas willows were identified to species in the field, they were grouped into *Salix* spp. for final analysis. For each plant, we recorded species, height, percent dead material by volume, and architecture class. Plant architecture classes were categorized as the percentage of the current growth by volume of the plant arising from lateral branching that was due to moose herbivory, defined as: unbrowsed (< 5%), browsed (5 - 50%), and broomed (> 50%) (Seaton et al. 2011). Stem densities can be used to estimate the abundance of forage species and to estimate cover for moose (i.e., depending on age class and degree of browsing, high numbers of stems/m^2 is equivalent to thicker cover, Dussault et al. 2005). To estimate stem densities (m^2), we divided 30-m diameter plots into quadrants, counted the number of stems of all forage species and non-forage species above 0.5 in each quadrant, summed the total number of forage and non-forage species per plot, and divided this sum by the area of the plot.

We estimated biomass production and browse offtake at each site following techniques from Seaton et al. (2011). We randomly located 3 plants of each forage species that were within foraging height for moose (0.5 m to 3.0 m): willow (i.e., *Salix scouleriana*, *S. bebbiana*, *S. glauca*, *S. arbusculoides*), aspen, and Alaska birch. For each plant, we recorded the diameter of the base of current annual growth (CAG) for 10 twigs per plant as well as the diameter at the point of browsing (DPB) if twigs were browsed. When necessary, more than 3 plants were sampled until 30 twigs per species or all of the twigs available in the plot were measured. Total twig densities were then estimated for each plant sampled.

Biomass was calculated using the estimated dry weights from mass-diameter regression equations. The formula used for estimating biomass production and offtake was:

$$\hat{B}_k = \Sigma \frac{M_{jk}}{m_{jk}} \Sigma \frac{N_{ijk}}{n_{ijk}} \Sigma Z_{hijk} \qquad \text{[Eq. 3.1]}$$

Where, B is the site estimate of offtake or production biomass in grams. Twigs are denoted by h, plants by i, species by j, and the sites by k. M and m are the total and sampled plants in each plot, respectively, while N and n are the total and sampled twigs, respectively. Individual twig biomass is represented by z (Seaton et al. 2011). We used a program developed in R 2.14.1 (R Development Core Team 2011) by the Alaska Department of Fish and Game using plot counts, twig diameters, diameter-biomass pairs and dry weight conversions to estimate and production and removal (kg/ha/yr; Paragi et al. 2008). All models were checked to ensure that they met basic assumptions of normality and homogeneity of variance. To test differences between stem densities, biomass and offtake estimates, we used Tukey's adjustment for pairwise comparisons. To examine the duration of browse production in the burn, we compared our results to a previous study that used the same browse survey methods (Lord 2008) and utilized the same sites to estimate biomass production and removal. To test for differences between years, we used Wilcoxon signed rank tests. Values reported are means with standard error in parentheses.

Additionally, at 4 sites we randomly sampled twigs from 4-5 individual plants of the following species: willow (*Salix bebbiana*), aspen, and Alaska birch. All twig samples were within the defined foraging height for moose. Samples were kept frozen until they were freeze-dried in the lab. Freeze-dried twig samples were ground in a Wiley mill over a 20-mesh (1mm) screen and stored in airtight containers prior to chemical analysis. Nitrogen concentrations (N) were analyzed on a Truspec C-N Analyzer. Tannin-protein precipitation capacity (PPC) was determined with bovine serum albumin (BSA) using the method of Martin and Martin (1983). Sequential fiber analysis was conducted on all forages according to the methods of Van Soest et al. (1991) yielding neutral detergent fiber (NDF). All samples are reported on a dry matter basis.

Finally, digestible protein concentration was calculated using the equation of Robbins et al. (1987):

$$DP = -3.97 + (0.9283CP) - (11.82 \times PPC) \qquad \text{[Eq. 3.2]}$$

where DP is digestible protein as a percentage of dry matter, CP is crude protein as a percentage of dry matter (6.25 X N concentration), and PPC is protein precipitation capacity (µg/ µg). We analyzed our entire dataset with a mixed-model ANOVA (R Version 3.2) with species and fire severity category (high vs. low) as explanatory variables. We added Site ID as a random factor to account for within-site dependency among the observations. The dependent variables were nitrogen concentration (N), protein precipitation capacity (PPC), and digestible protein (DP).

3.3.5. Estimating Home Range and Core Areas

In October 2012, 15 adult male moose were captured in the HCB by darting from helicopter. We fitted the captured moose with GPS radio collars (TDW-4780, Telonics, Mesa, Arizona) equipped with ARGOS connectivity. Collars were programmed to collect one location every hour from August 16th to October 15th, and once every 2 hours for the rest of the year. The increase rate of GPS fixes during late-summer was for an additional research question not addressed here. Location data (n=220,000) were downloaded weekly between October 2012 and November 2014. One animal died in December 2012 and was excluded from all analyses. Two additional mortalities occurred in spring 2013 and these two moose were only included in the winter 2012 analysis.

We used dynamic Brownian bridge movement models (dBBMM; Kranstauber et al. 2012) to estimate the utilization distribution (UD) for each individual moose based on movement data collected from the GPS collars (Figure 3.3). The UD is a probability density function that quantifies an individual's relative use of space (Kernohan et al. 2001). The UDs were calculated for the winter (November 1–April 1) and summer (May 1–September 1) seasons. Traditional Brownian bridge movement models (BBMM) are continuous-time stochastic movement models that predict the probability of occurrence by incorporating the distance and elapsed time between consecutive locations, the location error, and an estimate of the animal's mobility, referred to as the Brownian motion variance (σ^2_m; Horne et al. 2007). The BBMM assumes a constant σ^2_m along the entire movement path. However, animal movement is often composed of a series of behaviorally unique movements that change over time (e.g., diurnal versus nocturnal movement patterns). Moose movement, in particular, can change daily between foraging, bedded, or traveling behaviors (Moen et al. 1996) and seasonally during rut (Miquelle 1990). Therefore, we used the dBBMM, which allows the σ^2_m to vary along a path corresponding to changes in the animal's behavior over time (Kranstauber et al. 2012). The σ^2_m is essentially an average of multiple σ^2_m for each time step executed via a sliding window. Thus, the dBBMM allows for a more precise estimate of the UD by introducing changing behavioral states into the estimate of the σ^2_m.

We calculated UDs using the Brownian.bridge.dyn function (move package) in R. Moose home range boundaries were defined by 95% isopleth values. Core use areas were defined by isopleths that divided intensively used areas from peripheral home range areas (Vander Wal and Rodgers 2012). To calculate core use areas we fit an exponential regression to a plot of UD area against UD volume (i.e., isopleth value) and determined the point at which the slope of the line fitted was equal to 1 (Vander Wal and Rodgers 2012, Feierabend and Kielland 2014). This point represents a limit where the home range area begins to increase at a greater rate than the probability of use and the corresponding UD volume defines the boundary of the core area. Core use isopleths ranged between the winter 31%–47% (X=40%, SD=4%) and summer season 61%–67% (X=64%, SD=2%).

3.3.6. Habitat Use

Each pixel within the home range and core use areas was assigned a UD value denoting the probability that the individual was located within that pixel during a given period relative to all other pixels within the home range or core use area. The sum of these probabilities associated with occurrence in one of the seven types of habitat classified, as described above was equal to the total probability of occurrence within that habitat type (Marzluff et al. 2004). Habitat consisted of unburned types (*evergreen forest, deciduous forest, shrubs, mixed forest, open water, agriculture*) and *burn* habitat. We define availability as the proportion of habitat types within moose home ranges or core use areas. To estimate selection for a particular habitat type, we divided the total probability of occurrence by its availability for each individual, referred to as 'concentration of use' (Neatherlin and Marzluff 2004, Bjørneraas et al. 2012). Concentration of use is an index measuring habitat use relative to its availability. This index is similar to other use/availability selection coefficients (e.g., Manly et al. 2002). However, this approach incorporates variation of use within habitat types instead of assigning space "used" versus "unused" (Neatherlin and Marzluff 2004). We then divided the sum of all UD values associated with a particular habitat by the availability. We scaled the concentration of use index to a value between 0 and 1 within each individual home range and core area (Bjørneraas et al. 2012). We compared use of the HCB relative to other habitat types (see below) across individual seasonal home ranges by defining availability as the proportion of habitat types inside the 95% isopleth boundary. To test whether moose preferred certain habitats, we compared the concentration of use across all habitat types among individual home ranges.

To examine use of fire severity patches within the burn, we defined availability as the proportion of habitat types inside the 40% (winter) and 64% (summer) core use areas. We compared the concentration of use of burn habitat across all fire severity types among individual core use areas. Fire severity types consisted of *high*, *moderate*, and *low*-severities, as well as *unburned* patches. The unburned class was composed of pixels that were within the HCB boundary but were not consumed by fire. We utilized Michalek et al.'s (2000) fire severity classifications for this analysis. In this case, availability was the proportion of fire severity classes within individual core use areas.

We used linear mixed effects models using the lme4 package in R to examine whether moose preferred some habitat types or fire severity classes to others by comparing mean concentration of use of different habitat types and fire severity classes between home range and core use areas. We added individual moose as a random factor to account for within-individual dependency among the observations. To examine habitat preference we compared mean concentration of use estimates to the mean probability of occurrence expected for random use of habitat types within home ranges and core use. For example, if there were 5 habitat categories of equal area within an individual's home range, the mean probability of occurrence for random use of each habitat type would be 20%. We defined "preference" as a mean (+/- 95% CI) greater than the mean probability of occurrence for random use. We defined "avoidance" as a mean (+/- 95% CI) less than the mean probability of occurrence. To compare concentration of use among all habitat types within moose home ranges, we used a mixed model one-way analysis of variance (ANOVA).

3.4. RESULTS

Spatial reclassification of dominant vegetation types indicates that low-severity sites were predominately composed of *Black spruce/Willow* (40%) and *Shrub* (29%) classes (Figure 3.2). High-severity sites were heavily dominated by the *Deciduous* (71%) class. Moderate-severity sites were also composed of the *Deciduous* class (75%); however, these sites had a moderate *Coniferous* (15%) component as well. Lastly, unburned areas were composed of a mixture of *Shrub* classes (46%), *Black spruce/Willow* (26%), *Deciduous* (38%).

Stem density of deciduous browse within the HCB varied significantly across fire severity classes ($F_{1,15}$=6.0, p=0.03), averaging willow, aspen and birch within high and low-severity sites. The mean stem density of all deciduous species in high-severity sites was more than twice that of low-severity sites (1.2 ± 0.18 stems/m^2 vs. 0.40 ± 0.09 stems/m^2, respectively). Willow spp. were the most abundant forage species across all sites; spruce was the most abundant overall tree species in low-severity sites. Although high-severity sites had the highest stem densities, they also had higher percentage of brooming (54% ± 4%) compared to low-severity sites (38% ±7%). Additionally, high-severity sites had much higher proportion of dead stems by volume compared to low-severity sites at (38% and 3%, respectively). High-severity sites also had more mature trees (i.e., > 3 m) that had escaped moose browsing height (0.28 ± 0.04 trees/m^2) relative to low-severity sites (0.06 ± 0.04 trees/m^2).

An average of 186 ± 5.7 kg/ha/yr of browse biomass was produced across all sites within the burn. High-severity sites produced an average of 252 ± 51 kg/ha/yr while low-severity sites produced 141 ± 33 kg/ha/yr, but this difference were not statistically significant ($F_{1,15}$= 3.2, p = 0.07). Proportional offtake was higher in high-severity sites 27% ±6% than in low-severity sites 17% ± 4%, but this difference was not statistically significant ($F_{1,15}$= 2.4, p = 0.20). When examining biomass production by species, we found that high-severity sites produced more aspen (132 ± 38 kg/ha/yr) than low-severity sites (29 ± 15 kg/ha/yr). However, low- severity sites produced more Salix biomass (109 ± 31 kg/ha/yr) than high-severity sites (95± 25 kg/ha/yr), but the site differences between aspen ($F_{1,15}$=2.9, p=0.08) and Salix production ($F_{1,15}$=0.15, p=0.70) was not significant

Between 2007 and 2013, the total forage production across all sites has remained essentially the same. However, in low-severity sites, browse production of *Salix* spp. increased more than 2-fold (p = 0.05, Table 3.1). We also found a significant increase in *Alaska birch* in high severity sites (p=0.01, Table 3.1). The average proportional removal across all sites declined from 41% in 2007 to 24% in 2013. This decline is especially apparent in high-severity sites where proportional removal has declined ~50% between 2007 and 2013.

We analyzed indices of plant nutritional quality (PPC, CP and DP and NDF), and although there were several differences among species we found no chemical effects of fire severity. The greatest differences we found were for digestible protein in aspen relative to other browse species due to their very low protein precipitation capacity (Table 3.2).

We estimated 50 UDs across 2 years (26 winter, 24 summer) from radio-collared moose throughout our study. During the winter season, home range size was (20.5 ± 2.3 km^2) and core area size was (1.2 ± 0.10 km^2). In the summer months, home range size was (32.3 ± 1.9 km^2) and core area size was (6.3 km^2 ± 0.40 km^2). We found no significant difference in core area size among years (2012–2014), so data were pooled across years to analyze seasonal habitat use. *Burn* habitat was most abundant during both winter (34% ± 6%) and summer (42% ±7%) seasons across individual home ranges followed by the unburned evergreen and deciduous forest types (Figure 3.4a).

During the winter, moose selected for shrub habitat within home ranges most (Figure 3.5a). Concentration of use values for shrub habitat were also significantly greater than those within the burn ($F_{1,25}$=9.6, p=0.003). During summer, moose tended to select for shrub habitats and sites within the burn perimeter, while avoiding agricultural habitats and open water (e.g., lakes, Figure 3.5c). However, the only significant difference when comparing concentration of use values for the burn and other habitat types was for open water ($F_{1,23}$=3.6, p 0.05). Within winter core areas, moose strongly selected for shrub habitats and sites within the burn scar while strongly avoiding open water, agricultural fields and mixed habitat types. However, selection for burn and deciduous ($F_{1,25}$=0.05, p=0.81), evergreen ($F_{1,25}$=0.04, p=0.83), and shrub ($F_{1,25}$=0.02, p=0.87) habitats did not vary statistically (Figure 3.5b). During summer, moose showed a slight preference for shrub and deciduous habitat within core areas (Figure 3.5d).

Moose showed strong selection for low-severity or otherwise unburned patches during the winter season (Figure 3.6). Concentration of use values were significantly greater for low-severity sites than moderate ($F_{1,25}$=32, p= 0.0008) and high-severity patches ($F_{1,25}$=3.9, p= 0.05). Concentration of use did not differ between low-severity and unburned patches ($F_{1,25}$=0.02, p = 0.90) or high-severity and unburned patches ($F_{1,25}$=2.5, p=0.12). However, during summer, moose selected high-severity patches significantly more than low-severity patches ($F_{1,23}$=4.4, p = 0.04) and moderate-severity patches ($F_{1,23}$=5.3, p = 0.02). Just as in winter, the concentration of use did not significantly differ between high-severity patches and unburned patches ($F_{1,23}$=0.02, p = 0.88), which also tended to be preferred relative to availability.

3.5. DISCUSSION

Our results indicate that moose made extensive use of post-fire habitats in this 24-year old burn. Moreover, moose responded to changes in vegetation composition related to differences in burn severity. We found that the HCB was the most abundant habitat class across individual moose home range and core use areas. Moose selected core use areas that had high availability of willow biomass (i.e., low-severity sites) more than areas that had the most total available woody browse biomass (i.e., high-severity sites) during the winter season. By contrast, in summer, moose selected for high-severity sites more than low-severity sites. The increase in selection for high-severity sites in summer may be due to cover provided by deciduous tree and shrub species (as discussed below) as well as availability of forage in the form of leaves. However, at the home range scale, it appears that selectivity for burns decreases during winter relative to summer.

Despite an abundance of burned habitats in seasonal home ranges, concentrations of use values for the burn were not significantly greater than shrub, deciduous, evergreen, and mixed forest classes outside the burn perimeter, suggesting that moose need resources from a variety of different habitat categories. Telfer (1984) categorized the full range of moose habitats as consisting of boreal forest, mixed forest, large delta floodplains, tundra, subalpine shrubs, and stream communities. The importance of each habitat type may also vary throughout the season. For example, at the beginning of winter, moose often select open areas dominated by woody shrubs and then use closed canopy types during late-winter when high quality forage has been depleted (Peek et al. 1976, Crête and Jordan 1982). We found that moose preferred shrub habitats over other vegetation types during winter. Shrub habitats in our study area were predominately located at higher elevations and consisted of low-willows. Moose also selected for coniferous and deciduous habitats during both winter and summer. Mature coniferous trees can provide thermal cover, whereas in summer deciduous forests offer more diverse understory layers that can provide abundant forage as well as shade (Dussault et al. 2005).

We found that moose core use areas overlapped with the burn more in the winter than in summer months. This is likely due to the availability of woody browse species found across a successional gradient during the winter within the burn. Although we did not detect significant differences in biomass production estimates, recent trends suggest that low-severity sites, in particular, have been slower to regenerate since time of fire (Shenoy et al. 2013). However, we found that willow biomass production has more than doubled in low-severity burns, now surpassing willow browse production in high-severity patches. Additionally, when classifying vegetation with the HCB, we found that low-severity sites were predominately composed of low-lying willow and black spruce and moose seem to be responding to changing successional conditions by increased use of these low-severity sites during the winter. High-severity sites have experienced a slight increase in biomass production. However, these sites also have high levels of plant mortality, increased rates of brooming, and greater prevalence of mature trees, which likely results in the reduction of proportional removal. Despite greater numbers of stem densities and offtake rates in high-severity sites, we speculate that forage availability has started to decline, while production of high-quality browse is still increasing in low-severity sites as indicated by the large increases in willow production.

By comparing biomass production estimates over time, we gained considerable insight into the longevity of habitat availability that is likely an important driver of moose habitat use. Moreover, changing biomass estimates across our low-severity sites demonstrate how repeated measures of the same ecological parameters over time can reveal the temporal patterns of shifting controls over vegetation dynamics pertinent to moose populations. However, low statistical power from small sample sizes makes our conclusions conservative. Therefore, in the future, we recommend using a large number of plots to reduce variance and increase precision of biomass and offtake estimates (Seaton et al. 2011).

Although we had expected to see higher concentrations of DP and CP in browse species in high-severity sites, we did not find significant differences between severity classes. The lack of significance could be due to several factors including the age of the HCB, past browsing history, and plant physiological mechanisms. For example, the increased growth of the deciduous forest canopy in high-severity sites is likely affecting the amount of light reaching the forest floor influencing photosynthesis and decomposition rates. Additionally, the effects of past herbivory on plant chemical responses, especially in high-severity sites, could explain higher protein precipitating capacity of tannins. Lastly, there could be seasonal differences in plant nutritional quality across high- and low-severity sites. Vartanian (2011) found that wildfires created heterogeneity in forage and diet quality, but only during the summer months. We did find significant differences in the nutritional quality between species. Digestible protein and crude protein concentrations were consistently higher in aspen than Alaska birch and willow. Oldemeyer et al. (1977) also found aspen winter twig samples to be more digestible than willow and paper birch. Although high-severity sites produced more aspen, moose were still selecting low-severity sites characterized by willow, which had the lowest digestible protein. However, aspen can also have high concentration of phenolic glycosides (Donaldson and Lindroth 2007), which we did not measure in this study, and could affect selective pressure from moose (Bryant and Kuropat 1980).

The seasonal shift of habitat use patterns within the burn also suggests that patches of different fire severity can offer different resources depending on the time of year. During summer, moose select for high-severity sites over low-severity sites. Despite the high rates of brooming and plant mortality, these sites exhibit a more abundant understory layer (e.g., stem densities) providing both summer forage as well as shade. During summer months, ambient air temperatures above 14° C can be stressful for moose and as a result, moose may seek out vegetative cover during hot days (Dussault et al. 2004). Moose also seek vegetative cover to minimize risk of predation, by wolves and bears which is a strong limiting factor to moose recruitment in most parts of Interior Alaska (Gasaway et al. 1992).

Other factors could also influence the utilization of burned areas by moose in Alaska. For instance, fires can leave behind large amounts of downed wood (i.e., slash) creating difficult travel conditions. It is possible that the distribution of slash volume modified movement corridors within burned areas and may affect moose movement (MacCracken and Viereck 1990). This could explain preference for non-burned habitat patches by moose within the HCB during both the winter and summer seasons. Pre-fire population densities may also impact dispersal rates into burned areas, since moose appear to only use burns that overlap with their pre-fire home ranges (Gasaway and Dubois 1985). We speculate that relatively high-density moose populations are likely to colonize recent burns more rapidly than a low-density population. A density-driven mismatch in timing of colonization could allow woody shrubs to grow out of browsing height and reduce the duration of forage availability. However, this relationship should be investigated further with future research. Lastly, females relative to males may exhibit different habitat use patterns within burned area. For example, females with calves will often avoid habitat in open areas to minimize predation risk (Dussault et al. 2005, Bjørneraas et al. 2011). Thus, females may avoid low-severity patches and select edge habitat that offers more cover.

Combining habitat assessment surveys with dBBMM's has allowed us to effectively monitor habitat conditions and subsequent habitat use by moose in a post-disturbance landscape. Walter et al. (2015) found that home range estimators that incorporate a temporal component (e.g., BBMM and dBBMM) into model estimation typically perform better than traditional first- and second-generation estimators (e.g., fixed kernel home range and local convex hull). Movement-based estimators are further refined by including behaviorally distinct movement patterns as well as a dynamic variance estimates (Kranstauber et al. 2012). Moreover, by incorporating a 'concentration of use' metric that relates habitat use relative to its availability, we can assess preferential habitat utilization patterns associated with post-fire browse availability.

As Alaska's boreal forest continues to change as a result of rapid warming, it can be expected that fires will increase in both frequency and severity (Calef et al. 2015), with concomitant changes to forest canopy dominance from coniferous to deciduous species (Johnstone et al. 2010, Shenoy et al. 2011). Thus, fire severity will likely be an important habitat modifier for moose in other boreal regions. Additionally, the effects of fire severity on forest recovery can persist for several decades following a fire (Shenoy et al. 2011). If the relationship between fire-severity, forage production, and habitat heterogeneity persists across northern latitudes, moose populations in the short term (i.e., 20 years post-fire) should benefit from changing habitat conditions that follow forest disturbance.

3.6. ACKNOWLEDGEMENTS

All moose captures were carried out with approval from the Alaska Department of Fish and Game Institutional Animal Care Use and Committee (#2012-033). Our research was supported by National Science Foundation grant "Integrative Graduate Education and Research Traineeship: Global-Local Interactions: Resilience and Adaption of Social-Ecological Systems in a Rapidly Changing North" (grant #0654441). The views expressed are those of the author(s) and do not represent the National Science Foundation. Funding to support this research was provided by grants from the Joint Fire Science Program Graduate Research Innovation Award and the American Association of University Women "American Fellowship". We gratefully acknowledge the Alaska Department of Fish and Game, specifically the Delta Junction Area Office, for providing valuable assistance in the field with data collection.

3.7. FIGURES

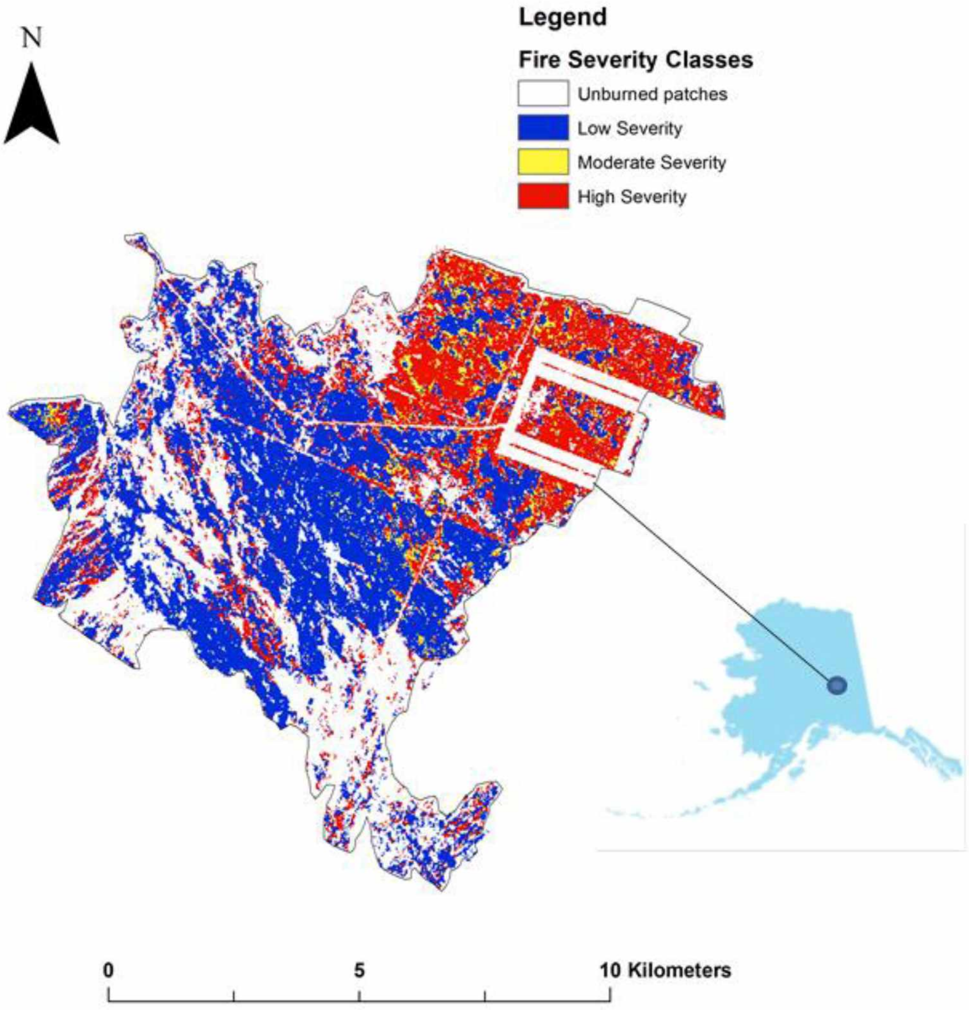


Figure 3.1. Fire-severity Map of Hajdukovich Creek Burn

The HCB is located 40 km southeast of Delta Junction, Alaska (Michalek et al. 2000). Red pixels denote high-severity, yellow pixels are moderate-severity, and blue pixels denote low severity. There were some areas within the fire perimeter that did not burn and are in white.

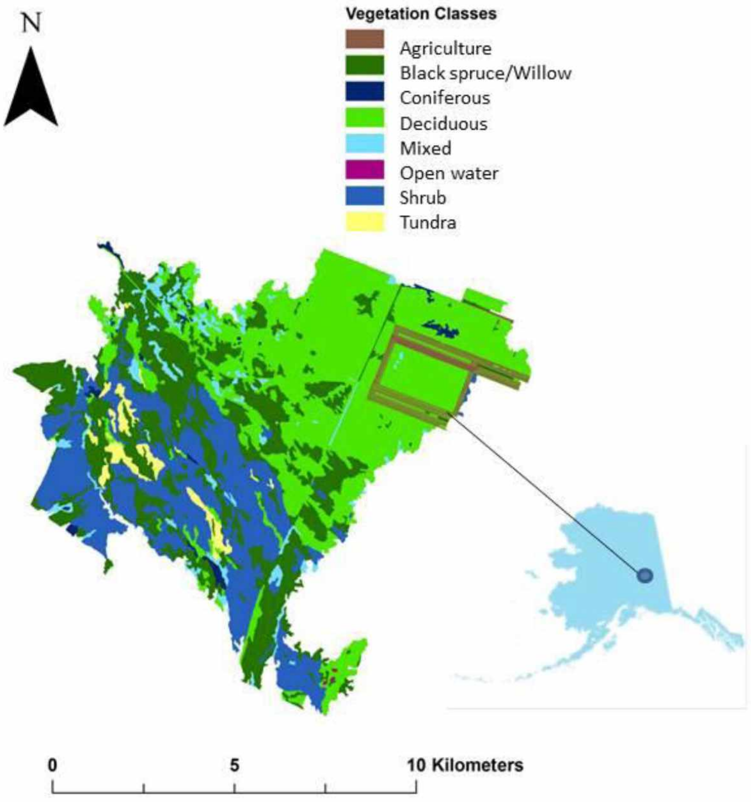


Figure 3.2. Map of Habitat Types Across Hajdukovich Creek Burn

Habitat types consisted of *Agriculture, Black spruce/Willow (Picea mariana, Salix sp.), Coniferous (Picea mariana and Picea glauca), Deciduous* (*Populus tremuloides, Betula neoalaskana, Salix sp.*), *Mixed (coniferous sp. and deciduous sp.), Open water, Shrub* (*low-lying Salix sp.* and *Betula nana), and Tundra.*

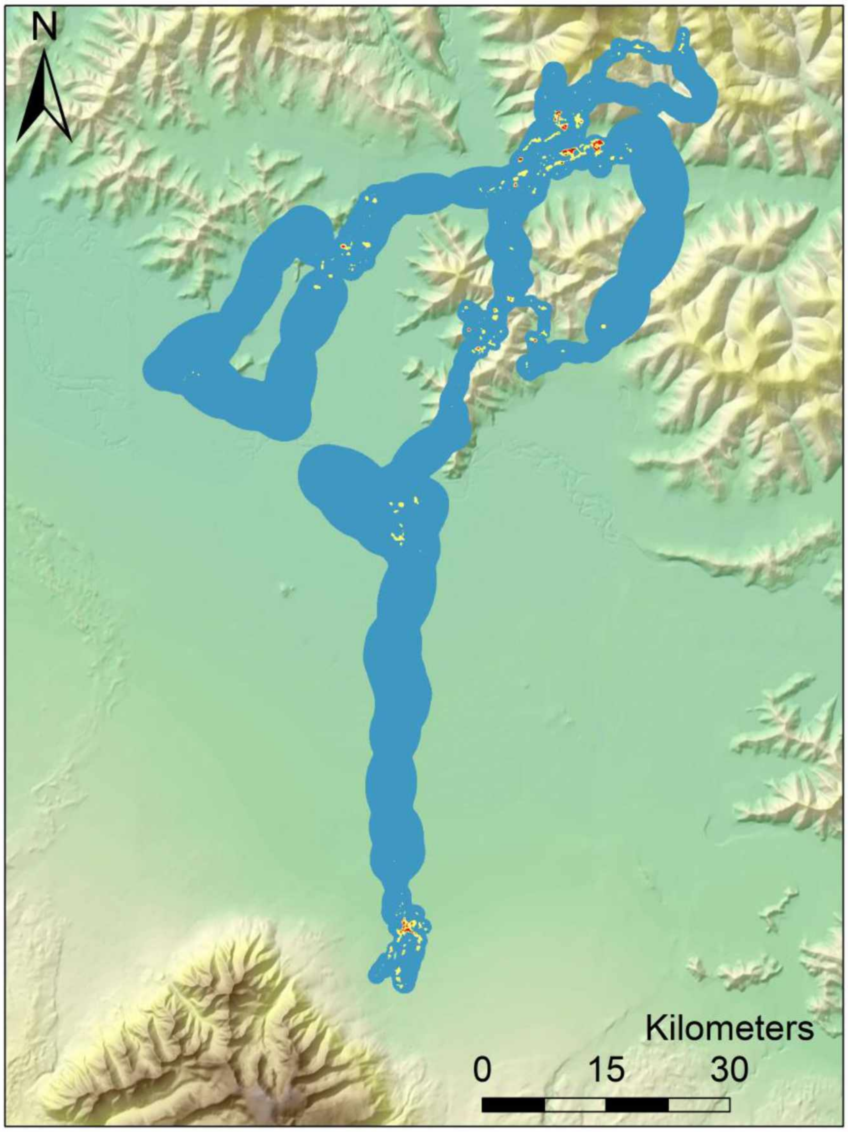


Figure 3.3. Home Range Map

An example of a utilization distribution (95% isopleth boundary) for one moose generated from the dynamic Brownian Bridge movement model. The warm colors represent areas that have a higher probability of use.

a)

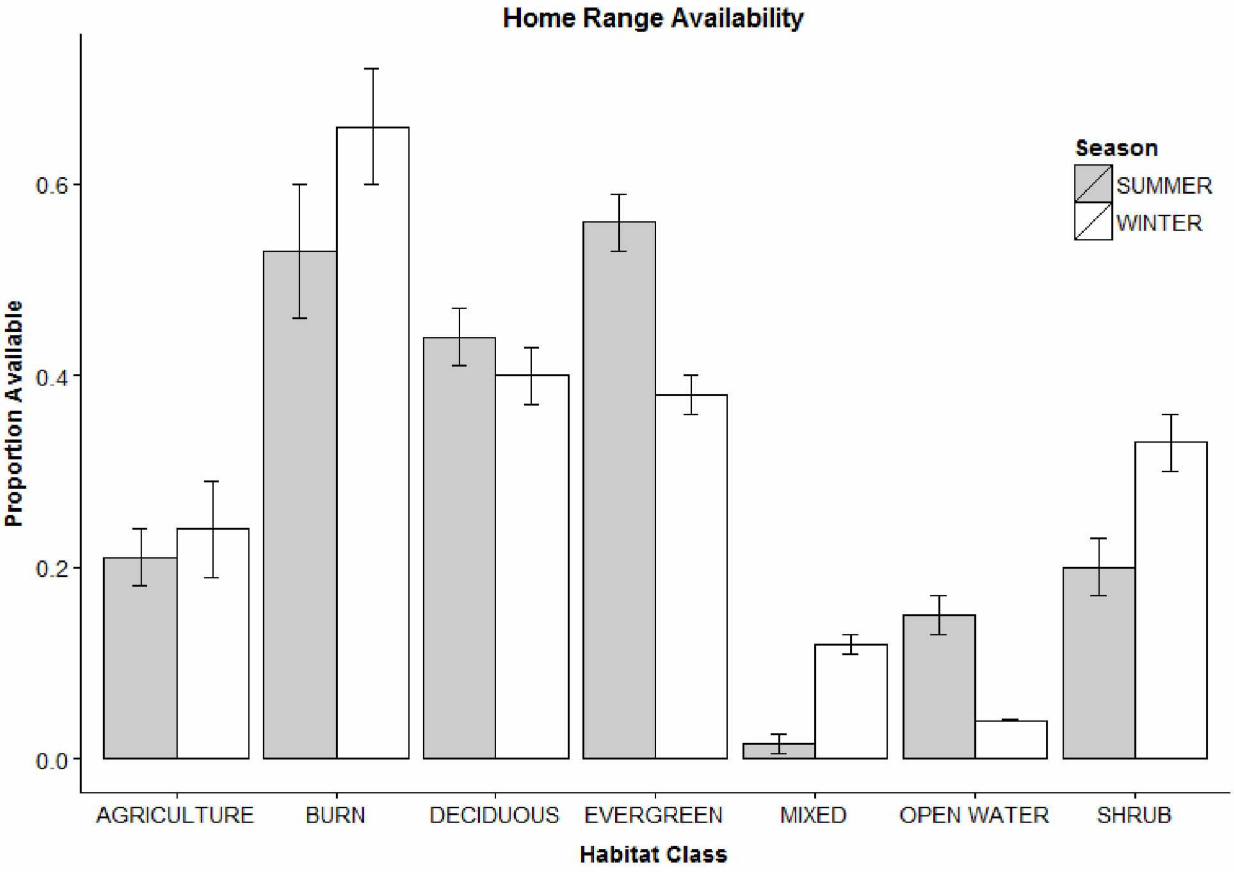
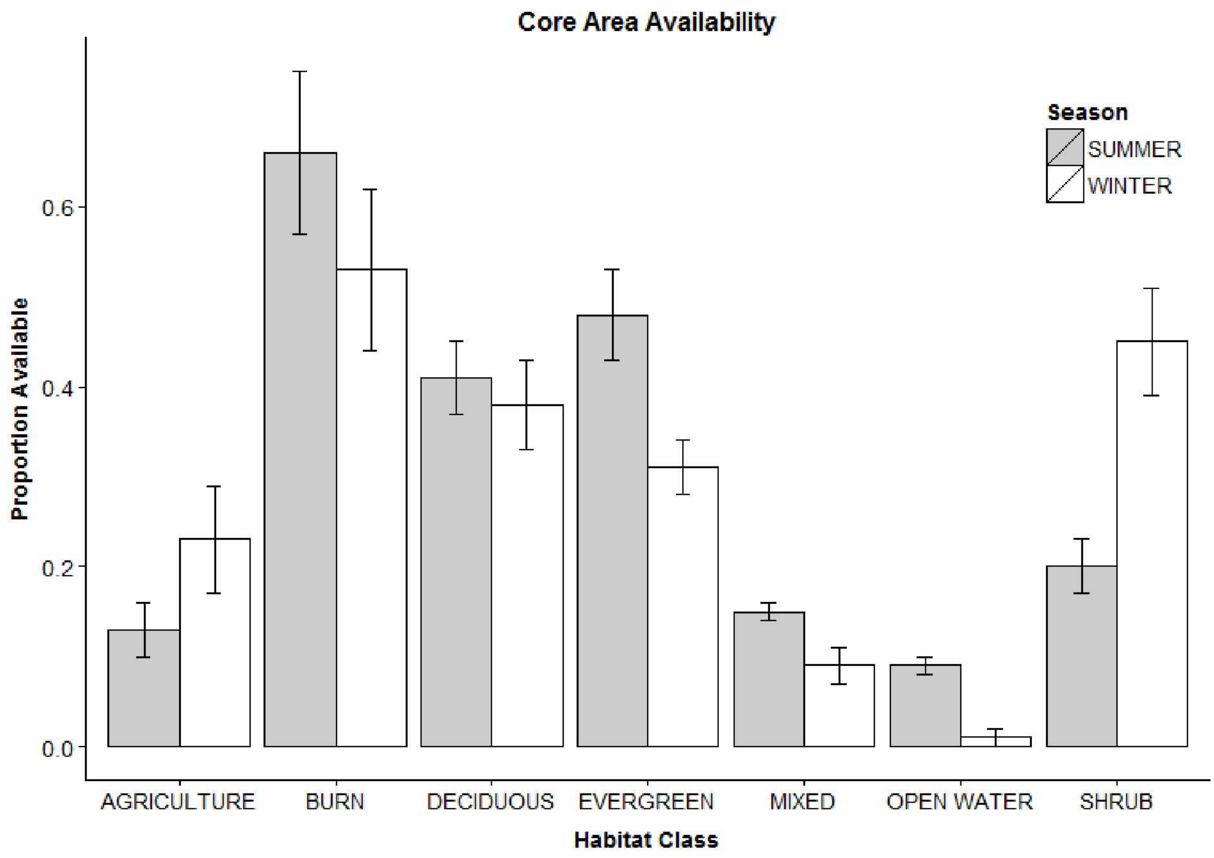


Figure 3.4. Home Range and Core Area Habitat Availability

a) Proportion of habitat types within 95% UD estimated by dBBMM for moose during winter and summer seasons (2012-2014). Parameter variables are from linear mixed effects models. The *BURN* class represents area within the boundary of the 1994 Hajdukovich Creek Burn. b) Proportion of habitat types within 40% and 64% UD estimated by dBBMM for moose during winter and summer seasons (2012-2014). The *BURN* class denotes area within the boundary of the 1994 Hajdukovich Creek Burn. Bars represent Mean ± 95% CI (n=26 winter, 24 summer).

b)


Core Area Availability
Season
SUMMER
WINTER
Proportion Available
0.0
0.2
0.4
0.6
AGRICULTURE
BURN
DECIDUOUS
EVERGREEN
MIXED
OPEN WATER
SHRUB
Habitat Class

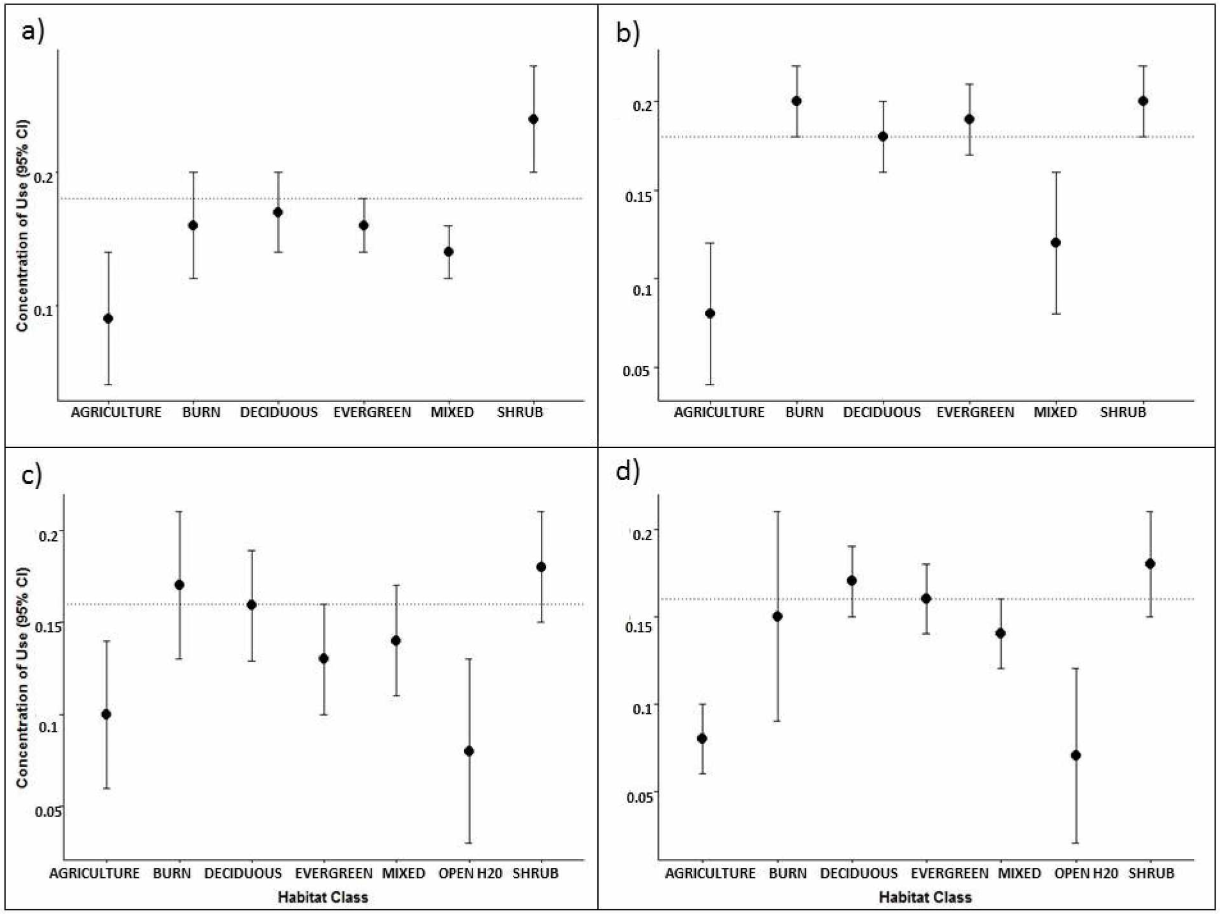


Figure 3.5. Concentration of Use Values for Habitat Types

Concentration of use values for: a) Winter home ranges; b) Winter core areas; c) Summer home ranges; d) Summer cores areas. Here, we show mean concentration of use (95% CI) for each habitat type within moose home ranges and core use areas. The dashed line indicates mean probability of occurrence expected for random use of habitat types within home ranges given that all habitat types are included in each home range and core use area CI > mean probability of occurrence indicate the habitat type is selected. CI< mean probability of occurrence indicate the focal habitat type is avoided. Mean ± 95% CI (n=26 winter, 24 summer).

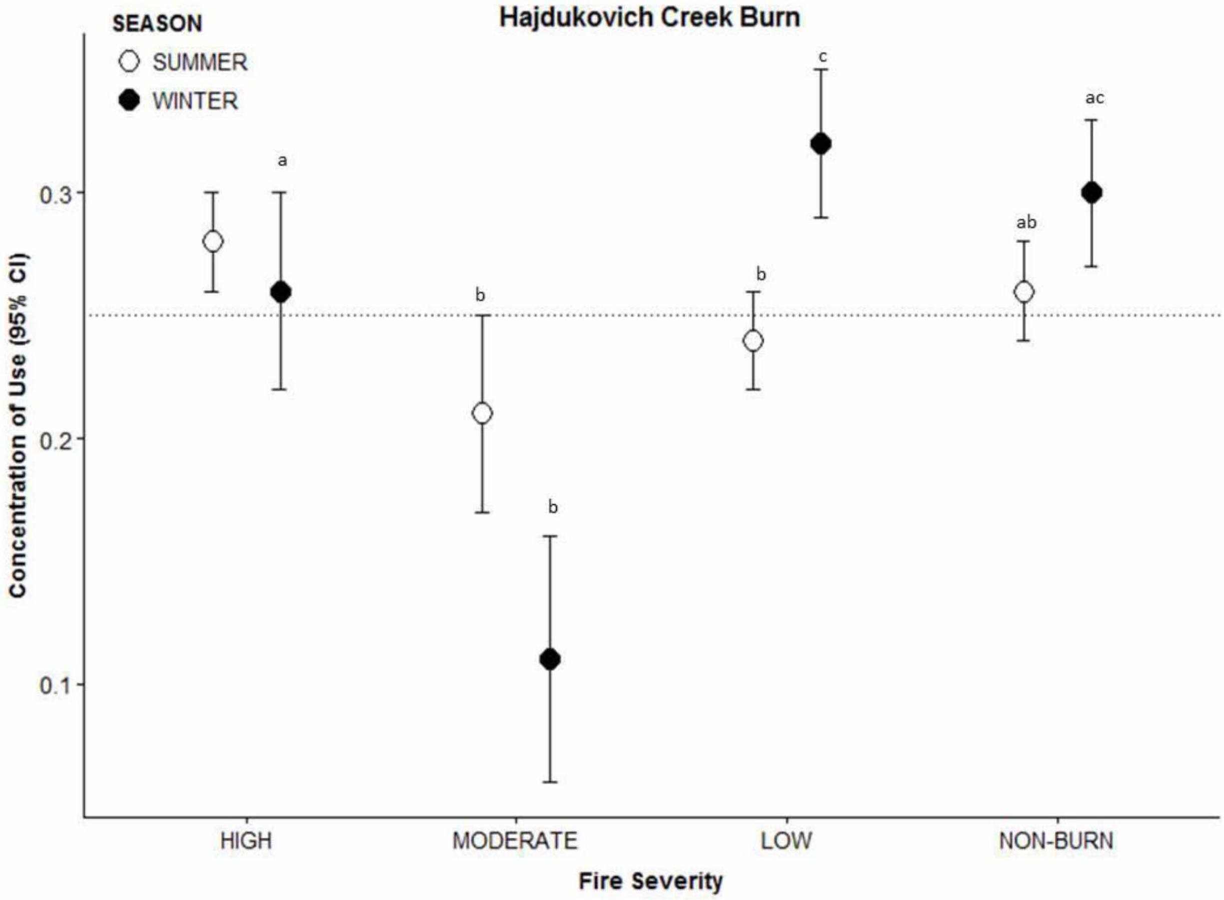


Figure 3.6. Concentration of Use Values for Fire-severity

Fire severity classes were first determined by post-fire satellite imagery and ground-truthed with field based comparisons of the degree of SOM (Michalek et al. 2000). The *NON-BURN* variable refers to areas within the burn perimeter that were not consumed by fire. The sum of all core UD values associated with a fire severity class is the total probability of occurrence. The dashed line indicates mean probability of occurrence expected for random use of habitat types within home ranges given that all habitat types are included in each home range and core use area. We defined "preference" as a mean (+/- 95% CI) greater than the mean probability of occurrence for random use. We defined "avoidance" as a mean (+/- 95% CI) less than the mean probability of occurrence. Mean ± 95% CI (n=23 winter, n = 18 summer). Letters a, b and c represent statistically significant differences between fire severities for the winter and summer seasons.

3.8. TABLES

Table 3.1. Browse Assessment Results (2007, 2013)

Results from 2007 HCB browse assessment surveys (Lord 2008) and 2013 HCB browse assessment surveys. BENA represents *Betula neoalaskana*, POTR represents *Populus tremuloides,* and SASP represents all willow species *(e.g., Salix scouleriana, Salix bebbiana, Salix glauca, Salix arbusculoides*). Values are reported as means and standard errors. Significance of Wilcoxon signed rank test is indicated by asterisks ** $p < 0.10$; **** $p < 0.05$.

Species	**Biomass Production 2007**	**Biomass Production 2013**
High Severity		
BENA	4 ± 3	11 ± 6****
POTR	77 ± 12	132 ± 38
SASP	157 ±21	126 ± 25
TOTAL	*238 kg/ha/yr*	*269 kg/ha/yr*
Low Severity		
BENA	1 ± 0.1	5 ±3 **
POTR	41 ± 25	20 ± 15
SASP	55 ± 13	138 ±65 ****
TOTAL	*97 kg/ha/yr*	*163 kg/ha/yr*
	Biomass Offtake 2007	**Biomass Offtake 2013**
High Severity		
BENA	1 ± 0.3	4 ± 2 **
POTR	45 ± 7	26 ± 9
SASP	76 ± 10	52 ± 13 **
TOTAL	*122 kg/ha/yr*	*82 kg/ha/yr*
Low Severity		
BENA	0.08 ± 0.02	2 ± 1
POTR	6 ± 1	7 ± 4
SASP	10 ± 2	15 ± 5
TOTAL	*17 kg/ha/yr*	*24 kg/ha/yr*

Table 3.2. Nutrition Results

Comparison of digestible protein concentrations, crude protein concentrations, and protein precipitating capacity of tannins of winter woody browse species in the HCB. Within a group of factors, rows with different lowercase letters are significantly different from each other (Tukey's hsd, $p<0.05$). Values are reported as LS means and standard errors.

	Digestible Protein (% DM)	Crude Protein (%DM)	Neutral Detergent Fiber (%DM)	Protein Precipitating Capacity (g/g)
Fire Severity				
High	2.0^{a} (0.30)	6.9^{a} (0.31)	49^{a} (0.96)	0.038^{a} (0.006)
Low	1.8^{a} (0.32)	6.4^{a} (0.32)	47^{a} (1.1)	0.030^{a} (0.007)
Species				
Salix bebbiana	0.71^{a} (0.23)	5.8^{a} (0.25)	53^{a} (1.04)	0.10^{a} (0.003)
Populus tremuloides	3.1^{b} (0.22)	7.5^{b}(0.24)	45^{b}(0.93)	0.00^{b} (0.000)
Betula neoalaskana	1.4^{c} (0.29)	6.2^{a} (0.30)	47^{a} (1.3)	0.051^{c} (0.004)

3.9. REFERENCES

Bjørneraas, K., I. Herfindal, E. J. Solberg, B.-E. Sæther, B. van Moorter, and C. M. Rolandsen. 2012. Habitat quality influences population distribution, individual space use and functional responses in habitat selection by a large herbivore. Oecologia **168**:231-243.

Bjørneraas, K., E. J. Solberg, I. Herfindal, B. V. Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology **17**:44-54.

Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology **78**:2359-2368.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience **10**:421-431.

Bryant, J. P., F. S. Chapin III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40**:357-368.

Bryant, J. P. and P. J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. Annual Review of Ecology, Evolution and Systems **11**:261-285.

Calef, M. P., A. Varvak, A. D. McGuire, F. S. Chapin III, and K. B. Reinhold. 2015. Recent changes in annual area burned in Interior Alaska: the impact of fire management. Earth Interactions **19:**1-17.

Chapin III, F. S., S. F. Trainor, O. Huntington, A. L. Lovecraft, E. Zavaleta, D. C. Natcher, A. D. McGuire, J. L. Nelson, L. Ray, and M. Calef. 2008. Increasing wildfire in Alaska's boreal forest: pathways to potential solutions of a wicked problem. BioScience **58**:531-540.

Crête, M. and P. Jordan. 1982. Population consequences of winter forage resources for moose, *Alces alces*, in southwestern Quebec. Canadian Field-Naturalist **96**: 467-475.

Dempster, J. and E. Pollard. 1986. Spatial heterogeneity, stochasticity and the detection of density dependence in animal populations. Oikos **50**:413-416.

Donaldson, J. R. and R. L. Lindroth. 2007. Genetics, environment, and their interaction determine efficacy of chemical defense in trembling aspen. Ecology **88**:729-739.

DuBois, S. D. 2008. Unit 20D moose. Pages 386–423 in P. Harper, editor. Moose management report of survey and inventory activities 1 July 2005 through 30 June 2007. Alaska Department of Fish and Game, Project 1.0, Juneau, USA.

Duffy, P. A., J. Epting, J. M. Graham, T. S. Rupp, and A. D. McGuire. 2007. Analysis of Alaskan burn severity patterns using remotely sensed data. International Journal of Wildland Fire **16**:277-284.

Dussault, C., J. -P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience **11**:321-328.

Dussault, C., J. -P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography **28**:619-628.

Feierabend, D. and K. Kielland. 2014. Movements, activity patterns, and habitat use of snowshoe hares (Lepus americanus) in interior Alaska. Journal of Mammalogy **95**:525-533.

Gasaway, W. C. and S. D. DuBois. 1985. Initial response of moose, *Alces alces*, to a wildfire in interior Alaska. Canadian Field-Naturalist **99**:135-140.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs **120**:3-59.

Hansson, L. 1994. Vertebrate distributions relative to clear-cut edges in a boreal forest. Landscape Ecology **9**:105-115.

Hobbs, N. T. and R. A. Spowart. 1984. Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. The Journal of Wildlife Management **48**:551-560.

Horne, J. S., E. O. Garton, S. M. Krone, and J. S. Lewis. 2007. Analyzing animal movements using Brownian bridges. Ecology **88**:2354-2363.

Johnstone, J. F. and E. S. Kasischke. 2005. Stand-level effects of soil burn severity on post fire regeneration in a recently burned black spruce forest. Canadian Journal of Forest Research **35**:2151-2163.

Johnstone, J. F., T. N. Hollingsworth, F. S. Chapin III, and M. C. Mack. 2010. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Global Change Biology **16**:1281-1295.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecology Letters **10**:690-700.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Radio tracking and animal populations. Academic Press, San Diego, California, USA, 125-166.

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

Kranstauber, B., R. Kays, S. D. LaPoint, M. Wikelski, and K. Safi. 2012. A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. Journal of Animal Ecology **81**:738-746.

Li, H. and J. F. Reynolds. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology **75**:2446-2455.

Lord, R. E. 2008. Variable fire severity in Alaska's boreal forest: implications for forage production and moose utilization patterns. M.Sc. thesis. University of Alaska. Fairbanks, USA.

Lord, R. E. and K. Kielland. 2015. Effects of variable fire severity on forage production and foraging behavior of moose in winter. Alces **51**:23-34.

Lutz, H. J. 1960. History of the early occurrence of moose on the Kenai Peninsula and other sections of Alaska. Annual Publication: Alaska Forest Research Center 1.

Maier, J. A., J. M. Ver Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research **35**:2233-2243.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L McDonald, and W. P. Erickson. 2002. Resource selection by animals. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Marzluff, J. M., J. J. Millspaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's jays. Ecology **85**:1411-1427.

Martin, J. S. and M. M. Martin. 1983. Tannin assays in ecological studies Precipitation of ribulose-1, 5-bisphosphate carboxylase/oxygenase by tannic acid, quebracho, and oak foliage extracts. Journal of Chemical Ecology **9**:285-294.

MacCracken, J. G. and L. A. Viereck. 1990. Browse regrowth and use by moose after fire in interior Alaska. Northwest Science **64**:11-18.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology **90**:1400-1411.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environmental Reviews **9**:1-59.

Michalek, J., N. French, E. Kasischke, R. Johnson, and J. Colwell. 2000. Using Landsat TM data to estimate carbon release from burned biomass in an Alaskan spruce forest complex. International Journal of Remote Sensing **21**:323-338.

Miquelle, D. G. 1990. Why don't bull moose eat during the rut? Behavioral Ecology and Sociobiology **27**:145-151.

Moen, R., J. Pastor, Y. Cohen, and C. C. Schwartz. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management **60**:659-668.

Neatherlin, E. A. and J. M. Marzluff. 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. Journal of Wildlife Management **68**:708-718.

Oldemeyer, J. L., A. W. Franzmann, A. L. Brundage, P. D. Arneson, and A. Flynn. 1977. Browse quality and the Kenai moose population. Journal of Wildlife Management **41**:533-542.

Pacala, S. and J. Roughgarden. 1982. Spatial heterogeneity and interspecific competition. Theoretical Population Biology **21**:92-113.

Paragi, T. F., C. T. Seaton, and K. A. Kellie. 2008. Identifying and evaluating techniques for wildlife habitat management in Interior Alaska: moose range assessment. Alaska Department of Fish and Game, Division of Wildlife Conservation. Final Research Technical Report, Juneau, Alaska, USA. 76 pp.

Peek, J. M., D. L. Urich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monographs **48**:3-65.

Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology **81**:1533-1543.

R Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Risenhoover, K. L. 1989. Composition and quality of moose winter diets in interior Alaska. The Journal of Wildlife Management **53**:568-577.

Robbins, C. T., T. A. Hanley, A. E. Hagerman, O. Hjeljord, D. L. Baker, C. C. Schwartz, and W. Mautz. 1987. Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology **68**:98-107.

Schwartz, C. and A. Franzmann. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces **25**:1-10.

Seaton, C. T., T. F. Paragi, R. D. Boertje, K. Kielland, S. DuBois, and C. L. Fleener. 2011. Browse biomass removal and nutritional condition of moose *Alces alces*. Wildlife Biology **17**:55-66.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management **261**:381-390.

Shenoy, A., K. Kielland, and J. F. Johnstone. 2013. Effects of fire severity on plant nutrient uptake reinforce alternate pathways of succession in boreal forests. Plant Ecology **214**:587-596.

Spencer, D. L. and J. B. Hakala. 1964. Moose and fire on the Kenai. In *Tall Timbers Fire Ecology Conference* 3:11-33.

Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (Alces alces). Pages 145-182 in R. Olson, R. Hastings, and F. Geddes, eds. Northern Ecology and Resource Management. University of Alberta Press, Edmonton, Alberta, Canada.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology, Evolution and Systems **20**:171-197.

Van Cleve, K. and L. A. Viereck. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska. Pages 185-21. Forest Succession. Springer.

Van de Vijver, C. A. D. M., P. Poot, and H. H. T. Prins. 1999. Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna. Plant and Soil **214**:173-185.

Van Soest, P. J., J. B. Robertson, and B. A. Lewis. 1991. Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. Journal of Dairy Science **74**:3583-3597.

Vander Wal, E. and A. Rodgers. 2012. An individual-based quantitative approach for delineating core areas of animal space use. Ecological Modeling **224**:48-53.

Vartanian, J. M. 2011. Habitat Condition and the Nutritional Quality of Seasonal Forage and Diets: Demographic Implications for a Declining Moose Population in Northwest Wyoming, USA, M.Sc. thesis. University of Wyoming.

Walter, W. D., D. P. Onorato, and J. W. Fischer. 2015. Is there a single best estimator? Selection of home range estimators using area-under-the-curve. Movement Ecology:3:10.

CHAPTER 4. CONNECTING MOOSE MOVEMENT AND HABITAT SELECTION TO SPATIO-TEMPORAL VARIATION IN RISK DURING THE HUNTING SEASON[1]

4.1. ABSTRACT

Understanding the effects of hunting and motorized recreation on wildlife behavior is crucial to effective management and conservation. However, the timing and magnitude of disturbances across the landscape may impact the level of behavioral response. We used telemetry data from 26 adult male moose (*Alces alces*) monitored from 2012-2014 to create fine-scale step-selection models to test whether habitat selection and movement patterns were affected by spatiotemporal variation in risk from hunting activity. From August-October, we collected field data on human activity using a camera trap array (off-road vehicles, automobiles, 4x4 trucks, dirt bikes, and hunters afoot) which we coupled with a machine learning algorithm to create high-resolution hunter distribution models. We found that while moose selected habitat closer to trails and roads, they also avoided areas with more hunting activity. That is, the moose selected habitat closer to trails that were used less by humans. Additionally, moose with more exposure to roads and trails chose habitat that offered high-quality cover. Our models provide an innovative approach to examining the spatial variation of risk across a landscape and may serve as a framework for managers to better understand the relationships between human disturbance and wildlife management and conservation.

---

[1] Formatted for Journal of Applied Ecology as Brown, C. L., K. Kielland, E. S. Euskirchen, T. J. Brinkman, and K. A. Kellie. Connecting moose movement and habitat selection to spatio-temporal variation in risk during hunting season (2016).

4.2. INTRODUCTION

Recognizing the effects of human disturbance on wildlife behavior is essential for successful management and conservation of a range of ungulate species (Stankowich 2008). Ungulates can be particularly sensitive to anthropogenic disturbance including human activities associated with recreation and transportation (e.g., Gavin and Komers 2006, Bolger et al. 2008, Fahrig and Rytwinski 2009, St. Clair and Forrest 2009). The frequency and type of human activities also impacts the magnitude of their response (Shannon et al. 2014). For example, hunting and off-road motorized recreation can elicit stronger behavioral responses in ungulates than other less conspicuous types of recreation (Stankowich 2008, Naylor et al. 2009, Grignolio et al. 2011). Hunting affects ungulate populations directly via mortality, and also indirectly by eliciting risk-avoidance behavior such as shifting patterns of habitat selection (Bender et al. 1999). Ungulates may respond to hunting pressure by selecting spatial refugia (e.g., vegetative cover) or areas farther from trails and roads (Swenson 1982, Millspaugh et al. 2000, Vieira et al. 2003). Therefore, the possibility of human-related mortality during hunting season can cause animals to adjust resource selection strategies to avoid risk.

Disturbance associated with transportation corridors, such as road and trails, can induce behavioral responses in ungulates, such as heightened levels of vigilance and increased flight distance (Gavin and Komers 2006; St. Clair and Forrest 2009; Rumble and Gamo 2011). However, in some cases, ungulates seem attracted to, or unaffected by, road activity (Berger 2007). Rural roads and trails that support off-road vehicles (ORVs) may produce a wide-range of behavioral responses. Ungulates may select habitat near rural roads and trails due to their proximity to productive habitat (e.g., low valleys with good drainage). Rural roads can also bisect large patches of relatively undisturbed habitat and may offer accessible travel corridors for wildlife (Whittington et al. 2005) and cover from predators (Shannon et al. 2014). Alternatively, roads and trails can diminish habitat connectivity and decrease patch size (Forman et al. 2003). Research has found ORV routes less than 3 m wide can disrupt the movement and dispersal of wildlife species (Ouren et al. 2007). In addition to fragmenting habitats, rural roads and trails can also increase the proportion of edge-to-core habitat by extending the anthropogenic footprint (e.g., road-effect zone) well past the physical boundary of roads (Shanley and Pyare 2011). Lastly, traffic along rural roads and trails is often infrequent, and habituation by wildlife is less likely to occur when exposure to noise and visual disturbances are intermittent (Stankowich 2008, Brown et al. 2012).

In contrast, high levels of off-road activity might be an especially pervasive disturbance. Technological advancements in equipment that allow ORVs to easily access lands previously unaffected by mechanized recreation now allow for greater dispersion across the landscape (Ewert and Shultis 1999). Thus, the distribution of ORV activity may not be uniform across a given landscape. The concentration of ORV activity can depend on the quality of the trail, an area's topographic and landscape features (e.g., terrain ruggedness, slope, and hydrology), and proximity to towns and major roads (Ouren et al. 2007). In addition to spatial variability, ORV use can change over time throughout a given day or season.

An increase in hunting activity along ORV trails and other travel corridors can introduce a concentrated, but brief, disturbance. Spatial variation in risk is often referred to as the "landscape of fear", with indirect impacts on animal distribution (Brown 1999).

These indirect impacts result from shifting resource allocation towards behaviors that minimize exposure to predation (Laundré et al. 2001). It is important to note that disturbances may result in a range of behaviors depending on resource availability, an animal's physiological or reproductive state, social structure and accessibility to escape terrain or cover. The strength of an individual's response further depends on the spatial and temporal predictability of risk (Ferrari et al. 2009). For example, when risk is predictable, prey may respond strongly by avoiding risky areas or times when wolves are more active while responding less when risk is low (Creel et al. 2005). If risk is infrequent or unpredictable, prey would have to show continuous risk avoidance behavior, which can eventually impact time spent foraging. Theory supporting the landscape of fear predicts the strongest, enduring, behavioral responses occur where risk is spatially predictable but temporally unpredictable (Creel et al. 2005, Ferrari et al. 2009). Thus, when studying the impacts of hunting, it is important to evaluate a suite of variables including how risk may change over space and time (Lima and Bednekoff 1999).

In Alaska, hunting remains an integral lifestyle component for many people. Many Alaskans depend on wildlife species for both subsistence harvest (i.e., seasonal harvest of wild game to maintain food security and cultural identity) and for recreation (Loring and Gerlach 2009). Additionally, ORVs are used as one of the primary means of transportation for subsistence hunting in many rural Alaskan communities (Brinkman et al. 2007). The networks of rural roads and trails throughout Alaska create opportunities for hunter access as well as challenges to the management and conservation of wildlife habitat. Wildlife and hunter distributions can become concentrated in specific areas when habitat quality and hunter access across the landscape are not uniform (McCullough 1996, Brøseth and Pedersen 2000). Analyzing the distribution of roads and trails alone, without accounting for concentrations of activity, may be insufficient for deciphering the effects of hunting on wildlife behavior. If hunter and wildlife distributions do not overlap, the link between wildlife abundance and hunting opportunities may weaken, resulting in hunter dissatisfaction (Heberlein 2002). Hunter dissatisfaction will increase if wildlife avoid or select habitat away from accessible travel corridors (Fryxell et al. 1988, Brinkman et al. 2007). In this situation, hunting opportunities may decline further, resulting in negative attitudes by hunters to management. Thus, it is important to quantify and communicate how spatial and temporal variation of hunting can affect wildlife habitat selection and activity patterns.

This study explored how variations in hunter activity affected moose habitat selection and activity patterns. We 1) examined temporal variation in habitat selection patterns (before and during hunting season) for moose in two areas that differed in road and trail density, 2) quantified the effects of hunter activity on moose habitat selection, and 3) tested for differences in moose activity before and during hunting season.

4.3. MATERIALS AND METHODS

4.3.1. Study Area

The study area is located approximately 90 km southeast of Delta Junction, Alaska, USA, in Game Management Unit (GMU) 20D. The Gerstle River naturally divides the study area into eastern and western regions (Figure 4.1). We defined study-region boundaries by mapping the summer/fall locations from 26 GPS-collared, male moose over 2 hunting seasons (2013-2014) and created minimum convex polygons from seasonal locations for each region. Moose with locations that fell on the eastern side of the Gerstle River were designated as Johnson River moose. Moose with locations on the western side of the Gerstle River were designated as Hajdukovich Creek moose.

The Hajdukovich Creek area is characterized by deciduous and needle-leaf canopy forest, agricultural fields near Delta Junction, and subalpine shrub communities. Additionally, in 1994 the Hajdukovich Creek Burn affected 89 km^2 of black spruce forest in a flat glacial outwash plain north of the Alaska Range. Vegetation within the burn perimeter now varies from deciduous trees and shrubs (found predominately in high-severity sites) to black spruce and willow (*Salix* spp.), found in low-severity sites. The Johnson River area also includes deciduous, coniferous and subalpine shrub communities. However, this area has experienced no recent fires (< 60 years). Both areas have large glacially-fed rivers including the Tanana and Johnson Rivers. Additionally, the terrain varies in both areas; in that, the Johnson River region has more high-elevation terrain including subalpine foothills and plateaus (Figure 4.1).

The overall density of trails and roads varies considerably between the Hajdukovich Creek and Johnson River study areas (Figure 4.1). The Hajdukovich Creek area has approximately 513 km of ATV trails, dirt and paved roads, and a major highway (Alaska Highway) that bisect the landscape. The Johnson River area has far fewer (139 km) ORV trails and roads. The Hajdukovich Creek area also contains popular hunting areas managed by the U.S. Army (Gerstle River Training Area) and the Alaska Department of Fish and Game (ADFG; Gerstle Fields). I will collectively refer to these two areas as the Gerstle. The Gerstle is located at the base of the Alaska Range on the south side of the Alaska Highway.

4.3.2. GPS Telemetry

In October 2012, 26 adult male moose were captured in the Hajdukovich Creek (n = 15) and Johnson River (n = 11) study areas. All captures were carried out with approval from the ADFG Institutional Animal Care Use and Committee (#2012-033). Moose were darted from a helicopter and fitted with GPS collars (TDW-4780, Telonics, Inc. Mesa, Arizona) equipped with ARGOS connectivity. Collars were programmed to collect one location every hour from 16 August to 15 October 2014 and every two hours throughout the rest of the year. Four animals died during the 2012-2013 winter (Hajdukovich Creek n = 3, Johnson River n = 1) and were excluded from the analyses.

4.3.3. Predictive Landscape Variables

Moose habitat characteristics were identified using the Alaska Natural Heritage Program's Interior Vegetation Map and the Salcha-Delta Soil and Water Conservation District's map of the Gerstle River Training Area. Both maps included a variation of Viereck et al.'s (1992) Alaska Vegetation Classification III and IV coding definitions. We reclassified vegetation types into three categories (high, medium, low) for both browse-quality and vegetation-cover (Kellie 2005, Brinkman and Kellie 2014). A total of 74 vegetation classes were grouped into vegetation-cover and browse-quality categories (Appendix 4.1). The minimum distance (km) to high-quality forage as well as cover type was calculated for each location.

To assess the relationship between moose and hunter access, separate road and trail layers were created for each study area. We used a state-wide road layer to identify major highways, paved roads, and secondary roads. Additionally, we digitized ORV trails in ArcGIS 10.1 (ESRI, Redlands, CA) using the Salcha-Delta Soil and Water Conservation District Map trail guide, aerial imagery, and hand-held GPS units. We also included major rivers (e.g., Tanana River, Gerstle River) that could be navigated by boat. Road and trail layers were checked for accuracy by local wildlife managers. The minimum distance (km) to hunter travel corridors was calculated for each location.

4.3.4. Hunter Activity Models

In 2013-2014, we deployed 16 infrared trail cameras (Reconyx, HyperFire 5.0) in the Gerstle from August 1st – October 31st (Figure 4.2). Cameras were placed on a stratified grid of ATV trails and roads in the Gerstle to maximize coverage and to ensure that we captured variation in vehicle activity. Cameras were placed within 3 m of roads and 1 m above the ground to maximize detection zones. Cameras were operational 24 h/d and were set to take 3 pictures per detection. For each picture, we recorded the entity (e.g., human activity type), location, date, and time. We followed techniques from Carter et al. (2012) to define entity detections. A detection was either a) consecutive pictures of *different* individuals, b) consecutive pictures of individuals >30 minutes apart, or c) nonconsecutive pictures of individuals. We summed the number of detections for each entity at every camera trap location (Appendix 4.2). Human activity included all ORV, automobile, 4x4 trucks, dirt bikes and hunters afoot.

We used the machine-learning software RandomForests (Salford Systems, Inc. San Diego, CA, USA) to create spatial distribution models of hunter activity for the

Gerstle. RandomForests is a non-parametric method that uses binary recursive decision trees to classify datasets. RandomForests is especially useful for analyzing large spatial datasets and has been used in wildlife biology to map species distributions (e.g., Hegel et al. 2010, Booms et al. 2010, Evans et al. 2011, Baltensperger et al. 2013, Baltensperger and Huetmann 2015). Here, we used the average number of camera trap detections/day as a continuous response variable in a RandomForests regression analysis. We included a set of 240 pseudo-absences to represent the absence of hunting activity in areas away from roads and trails. To do this, we used ArcGIS 10.3 to create a 1 km buffer around all linear hunter access features to represent the area in which a hunter might travel off-trail (Johnson et al. 2016) and then randomly generated locations outside of buffered areas. We attributed camera and pseudo-absence locations with a set of 37 environmental predictor variables. The combined training dataset was modeled using 1,000 recursive decision trees and default RandomForests settings. RandomForests uses a bootstrapped sub-set of training locations to test the predictive performance of models and we assessed model performance using the root mean square area (RMSE) and R^2 values. We also used RandomForests to calculate the relative importance of individual variables in the construction of models and variables that did not contribute to the performance of models, which were removed from analyses. The best performing model (lowest RMSE and highest R^2 value) was applied to a lattice of points distributed at 25 m intervals across the Gerstle, generating predictions of average numbers of hunters for each point in the lattice. Points were then rasterized in ArcGIS 10.3 to create a final, continuous, predictive surface of average daily hunter activity for the Gerstle.

4.3.5. Moose Resource Selection Models

For 2013 to 2014, we modeled fine scale selection patterns for 22 moose before (August 1th-August 30th) and during (August 31st-September 16th) the hunting season. Step selection functions (SSFs) were used to identify habitat, landscape, and anthropogenic variables that influenced moose movement (Fortin et al. 2005). A step is a straight-line path between two consecutive GPS locations taken at regular intervals (Turchin 1998). Steps can be characterized by the line segments between locations, the average continuous habitat variables along the step, the proportion of habitat along each step, or by the environmental characteristics at the endpoint of each step. We analyzed the used and available locations at step endpoints (Figure 4.3). Matched sets of used and available steps are compared using conditional logistic regression, taking the same generalized exponential form as a resource selection function with a log-link function.

$$\widehat{w}(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n) \qquad \text{[Eq. 4.1]}$$

Where $\widehat{w}(x)$ is the relative probability of selecting a step, x_1 to x_n are environmental variables and $\beta_1$to β_n are the respective coefficients using conditional logistic regression. Steps with higher $\widehat{w}(x)$ have higher odds of being chosen.

Five available steps were generated for each used point by randomly drawing step length and turn angles from two distributions established from observations of monitored individuals. Separate step-length and turn-angle distributions were generated for each time period (pre-hunting and hunting). Because step length and turning angle may not be independent (Morales et al. 2004) and high fix-rates increase the correlation between step length and turning angle (Thurfjell et al. 2014), we used linear regressions to test for differences between distributions.

Next, we used a two-stage modeling approach that fits models separately for each individual animal and then averages regression parameters across individuals to quantify population-level patterns for both the Hajdukovich Creek and Johnson River areas (Sawyer et al. 2006). We fit conditional logistic regression models for each individual moose (i.e., cluster) with matched sets of used and available locations (i.e., strata) using the coxph package in R 3.2.0 (R Core Team 2016). We fit all models for each individual moose resulting in AIC (Akaike Information Criteria for small sample sizes) values and weights (Burnham and Anderson 2002). We then calculated an average AIC weight ($\bar{w}_i$) for each model across individuals.

$$\bar{w}_i = \frac{1}{n}\sum_{N=1}^{N}\left[\frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{i=1}^{R}\exp(-\frac{1}{2}\Delta_r)}\right] \qquad \text{[Eq.4.2]}$$

Where N is the number of individuals, R is the number of models in the candidate set, and Δ_i represents the change in AIC score of model *i* from the best (i.e., lowest AIC score) model

To estimate coefficients and standard errors at the population level, we fit mixed effects conditional logistic regression models (random coefficients designated individual moose) in R with the TwoStepCLogit package. Here, a global two-step approach estimates the cluster-specific parameters first and then uses the EM-algorithm in conjunction with conditional restricted maximum likelihood to estimate the population parameters for both the Hajdukovich Creek and Johnson River areas. Full model averaging was used to account for model uncertainty (Symonds and Moussali 2011). Because the TwoStepCLogit package currently provides restricted maximum likelihood estimates, we used the $\bar{w}_i$ from individual-level models to weight each coefficient estimate (Gilbert et al. 2016). The averaged parameter estimates were calculated using the following equation:

$$\tilde{\tilde{\beta}} = \sum_{i=1}^{R} \bar{w}_i \hat{\beta}_i \qquad \text{[Eq. 4.3]}$$

Here, the estimator is denoted as $\tilde{\tilde{\beta}}$, parameter estimates for all variables of the global model are averaged, and all models are considered. Additionally, we calculated standard errors for $\tilde{\tilde{\beta}}$ based on the variance of averaged parameter estimates (Burnham and Anderson 2002). The variance was calculated by the following equation:

$$\widehat{var}\left(\tilde{\tilde{\beta}}\right) = \sum \bar{w}_i \left[\widehat{var}(\hat{\beta}_i) + \left(\beta_i - \tilde{\tilde{\beta}}\right)^2\right] \qquad \text{[Eq. 4.4]}$$

4.3.6. Temporal Patterns of Moose Habitat Selection

To determine if moose responded to human activity during the hunting season, we evaluated temporal changes in selection patterns by dividing GPS data into locations obtained before the hunting season and during hunting season. Because we were concerned about confounding behavioral factors (i.e., heightened rut and loss of vegetative cover) during the post-hunting season, we did not examine moose habitat selection after September 16th. We also divided moose up into groups based on exposure to hunter travel corridors (Hajdukovich Creek = 12, Johnson River = 10). We evaluated the same set of candidate models for both groups before and during the hunting season. We excluded highly correlated predictive variables ($|r| > 0.7$) in the same model. Among highly correlated variables, we used variables based on average AIC scores of univariate models. Our 31 candidate models included combinations of five habitat and landscape predictor variables (cover type, distance to high-quality forage, terrain ruggedness, elevation, and distance to travel corridor).

4.3.7. Effects of Hunter Activity on Moose Habitat Selection

To examine how moose responded to varying levels of hunter activity on the landscape, we included a relative hunter occurrence variable generated from our RandomForests model output for the Gerstle region. Because SSF-model fitting is not possible if a covariate is not available to an individual (Thurfjell et al. 2014), we used a subset of individuals (n = 8) that used the Gerstle throughout the hunting season. In addition to hunter occurrence, we evaluated the same set of landscape variables for moose in the Gerstle. Thus, our 15 candidate models included combinations of five predictor variables including: cover type, distance to high quality forage, terrain ruggedness, DEM, distance to travel corridor and hunter occurrence.

4.3.8. Moose Activity Levels

In addition to examining how landscape and hunter-activity variables affected step selection, we examined whether moose activity levels were different during hunting season relative to before the hunting season and compared among groups of moose within the Hajdukovich Creek and Johnson River areas. Step lengths can also be used to characterize animal movement with longer steps, indicating increased travel or displacement (Franke et al. 2006, Roever et al. 2010). For each individual, we averaged daily distance moved (i.e., step length) for the two time periods (before hunting season: August 1-August 30th, and during hunting season: August 31-September 16th). We used paired t-tests to assess differences between groups (Hajdukovich Creek and Johnson River) and seasons (before and during hunting season).

4.4. RESULTS

4.4.1. Moose Habitat Selection Before and During Hunting Season

Step length and turn angle distributions were not highly correlated (mean adjusted $r^2 < 0.06$). Thus, random steps for each individual were chosen from the two distributions of individuals in the Hajdukovich Creek and Johnson River areas. During model building, we found that categorical measures of forage quality and cover types were highly correlated ($|r| = 0.8$). However, variables representing a minimum distance to high quality forage and cover type were not highly correlated ($|r| = 0.39$) and were included in our model combinations.

Among pre-hunting season model combinations, the Hajdukovich Creek moose were more likely to select habitats that were closer to hunter travel corridors and high-quality forage (Table 4.1 & Table 4.2). Additionally, Hajdukovich Creek moose selected for medium cover at lower elevations. The Johnson River moose selected for locations closer to high-quality forage, but unlike Hajdukovich Creek moose, they selected for higher elevations and avoided more rugged terrain (Table 4.1 & Table 4.2).

During hunting season, the top-ranked model ($\overline{w}_i = 0.07$) for Hajdukovich Creek moose only included elevation (Table 4.1). Similar to the pre-hunting model, moose were more likely to select areas at lower elevations. The Johnson River moose selected for habitat closer to travel corridors and at higher elevations during the hunting season (Table 4.1 & Table 4.2).

4.4.2. Hunter Activity Patterns and Moose Habitat Selection

Over the course of two years, we identified over 5,000 camera trap detections of automobiles, ORV's, dirt bikes, and hunters afoot in the Gerstle (Appendix 4.2). The number of detections varied strikingly between the pre-hunting (2013=389, 2014=246) and hunting season (2013=3,491; 2014=2,090). The distribution model created with RandomForests showed a high-degree of accuracy (RMSE = 3.18; $R^2 = 0.64$). Hunters were predicted to occur more often along trails and near roads in the eastern portion of the study area, and in the area near the Gerstle River (Figure 4.4). Hunters were predicted to avoid burned areas away from trails, especially in the western portion of the study area (Figure 4.4). The best-fit model predicting hunter activity included contributions from 9 of the 37 variables, but was based predominantly on the *distance to trail* and *fire severity* variables (Table 4.3, Appendix 4.3).

When accounting for human activity (based on the model predictions) during hunting season, our top step-selection model ($\overline{w}_i = 0.10$) found that moose in the Gerstle selected habitat closer to roads and trails (Table 4.4), but also selected areas further from more human activity. Additionally, moose selected for medium-quality cover (e.g., closed-broadleaf forest) at lower elevations. Terrain ruggedness and distance to forage were not important predictors.

4.4.3. Moose Activity

Across the entire two-week period before hunting season, we found that Hajdukovich Creek moose had significantly greater daily movement rates than Johnson River moose ($p = 0.020$). However, there was some variation in this pattern. For example, there were a number of days before hunting season where the average daily activity levels were higher for Johnson River moose than Hajdukovich Creek moose (Figure 4.5). Throughout the hunting season, we found that the average hourly step lengths for Hajdukovich Creek moose (186 ± 15 m) were significantly greater than Johnson River moose (153 ± 18).

4.5. DISCUSSION

Currently, there is a need in wildlife management to better understand how species respond to risk associated with hunting (Cromsigt et al. 2013). Our results suggest that moose are responding to an increase in human activity during hunting season by avoiding areas with more hunters. Analyzing the distance to roads and trails alone would suggest that moose select for habitat closer to these travel corridors. However, combining a spatial model of hunter occurrence with the distance to road/trail variable indicated that moose selected for habitat closer to trails that are used less by humans. This relationship suggests that hunting opportunities may decrease in areas that experience frequent exposure to human activity during hunting season.

There are several reasons why moose in the Gerstle would select habitat closer to trails and roads during the hunting season. The disturbance from ORV trails to the landscape can facilitate growth of highly desirable forage (e.g., willows; Child 1998). Rural roads and trails can also provide long-distance travel corridors for animals (Whittintgon et al. 2005). In contrast, research in southeast Alaska found a negative association between moose and roads (Shanley and Pyare 2011).

Our results indicated that the level of human activity along roads and trails indeed was not uniform across the landscape (Figure 4.4). Hunter occurrence was dictated by several landscape variables including distance to travel corridor, fire severity, and vegetation type. Predictably, our models predict that hunters are more likely distributed in areas closer to roads. Additionally, fire severity, especially non-burned and high-severity sites, can intensify hunter activity. Fire severity may increase the ease of travel within burned areas due to an abundance of downed logs. Severity-driven succession may also decrease the ability of hunters to see moose. Fire severity in Alaska's boreal forests is predicted to increase under a changing climate regime (Duffy 2007). It will be important for managers to consider the effects of fire severity on access to natural resources in regenerating burned areas. Finally, the magnitude of anthropogenic activity can also affect moose distribution and selection patterns. For example, moose occurrence has a greater probability when ORV route activity was < 0.25 km of vehicle travel/day according to Shanley and Pyare (2011), and may decrease significantly (50%) after a sharp increase in human activity (Burson et al. 2000). Thus, an increasing body of evidence indicates that analyzing road and trail distribution alone may underestimate the effects of motorized recreation on wildlife.

We also found that moose with more exposure to human activity along hunter travel corridors (such as Hajdukovich Creek) responded by shifting patterns of habitat selection following the onset of hunting season. Our top step-selection model results for moose in the Hajdukovich Creek indicated that individuals prior to hunting season are selecting areas closer to hunter travel corridors with medium cover. However, during hunting season, the distance to trail variable dropped out of the top model. Alternatively, top model results for Johnson River moose indicated that individuals selected habitat closer to trails during the hunting season but not before the onset of hunting. The Johnson

River region had fewer ORV trails than the Hajdukovich Creek region (Figure 4.1). Additionally, several trails in the Johnson River were located in rugged, mountainous terrain and are likely less accessible to hunters than those in the Hajdukovich Creek. Because moose in the Johnson River consistently selected habitat at higher elevations before and during hunting season, it does not appear that they are staying to higher elevations to reduce their exposure to human hunters. Lastly, moose in the Johnson River avoided high-quality cover both before and during hunting season.

Our step-selection model also exposed shifting habitat selection patterns associated with habitat and landscape features. We found that moose in both regions selected locations closer to high-quality forage before hunting season, but not after. This could be due to rut-induced behavioral changes in foraging patterns. Reduced forage intake by males typically coincides with the beginning of rut (late-September-early-October; Miquelle 1990). Therefore, finding high quality forage is likely less important for moose as the season nears peak rut. Moose in the Hajdukovich Creek selected terrain at low elevations, whereas moose in the Johnson River selected terrain at higher elevations. The overall availability of high elevation terrain was greater for moose in the Johnson River. Furthermore, moose may select habitat at high elevations because of the availability of shrub communities (Telfer 1984) and aggregations of cow-calf groups (Peek et al. 1974).

In addition to habitat selection patterns, step lengths for Hajdukovich Creek moose were significantly longer, indicating straighter, more rapid movements consistent with increased travel distances (Roever et al. 2010). In contrast, shorter steps denote foraging and resting behavior (Turchin 1998). Increased step lengths during hunting season point towards risk avoidance behavior (i.e., increased flight) in response to the increased activity on trails and roads during hunting season. Moreover, topographic variables (e.g., terrain ruggedness, slope, elevation), vegetation composition and rut may also be contributing to the difference in step length between the two areas. We believe the pronounced increase in step length after hunting season may be due to environmental conditions (e.g., leaf senescence) or rut behavior. Future research should compare moose movement behavior (e.g., step length) as a function of landscape variables that individuals encounter along steps during hunting season to help decipher habitat displacement during hunting season.

In Alaska, moose are a highly important food resource for many residents and most hunters utilize motorized transportation to gain access to moose populations because of the remoteness of terrain and the large body size of moose. An increasing number of studies suggest that hunter success is not only based on the abundance of wildlife, but is also contingent upon the seasonal distribution of wildlife and the abilities of hunters to access those locations during hunting season (Brinkman et al. 2013, Hansen et al. 2013, Johnson et al. 2016). In rural communities, the ability to access wildlife populations can be a critical driver of hunting opportunities (Berman and Kofinas 2004, Brinkman et al. 2014, Kofinas et al. 2010, Johnson et al. 2016). Both environmental conditions (e.g., topography, vegetation, and weather) and socio-economic variables (e.g., hunter income, mode of transportation available, the cost of fuel) can influence hunter access (Brinkman et al. 2013, Hansen et al. 2013). However, it is important to consider that if hunters focus their effort on habitats that provide the best access (e.g., close to roads or areas with high visibility), they may not overlap with high-densities of the species they are hunting. Additionally, hunting can elicit risk avoidance behavior if hunting effort is highly concentrated. In our study, we examined an index of hunter occurrence averaged across the entire hunting season. Based on this, future studies may want to examine fine-scale temporal dependence of daily hunter effort on moose habitat use including the effects of hunting on diurnal, crepuscular, and nocturnal selection patterns.

With overall greater moose movement away from highly used hunting trails during the hunting season, our results suggest that concentrated hunter activity has created a ‘landscape of fear’ where moose are responding to spatial patterns of human disturbance. Although relative hunter occurrence was highest along travel corridors, the distribution of activity extended past roads and trails in the eastern portion of our study area (Figure 4). Additionally, hunters seemed to avoid more remote areas and burned patches in our study area. Therefore, managers should incorporate planning that accounts for high-concentrations of use (e.g., extending the hunting season to account or limiting the number of hunting permits). As wildlife management issues become more challenging in human-dominated landscapes, managers will need to proactively quantify the effects of disturbances on wildlife. In doing so, managers will foster better communication with the public in an effort to minimize conflict over wildlife resources and potentially minimize wildlife behavioral responses to human activity.

4.6. ACKNOWLEDGEMENTS

Our research was supported by National Science Foundation grant "Integrative Graduate Education and Research Traineeship: Global-Local Interactions: Resilience and Adaption of Social-Ecological Systems in a Rapidly Changing North" (grant #0654441). Funding to support this research was provided by grants from the Joint Fire Science Program Graduate Research Innovation Award, the American Association of University Women "American Fellowship". We gratefully acknowledge the Alaska Department of Fish and Game, specifically the Delta Junction Area Office, for providing valuable assistance in the field with data collection. We thank S. DuBois, T. Paragi, T. Seaton, D. Bruning, S. Gilbert, and A. Baltensperger for consultation and advice on the project. We thank D. Bruning J. Staker, D. Feierabend, and B. Schmidt for field assistance. Lastly, we thank M. Spangler for photo compilation.

4.7. FIGURES

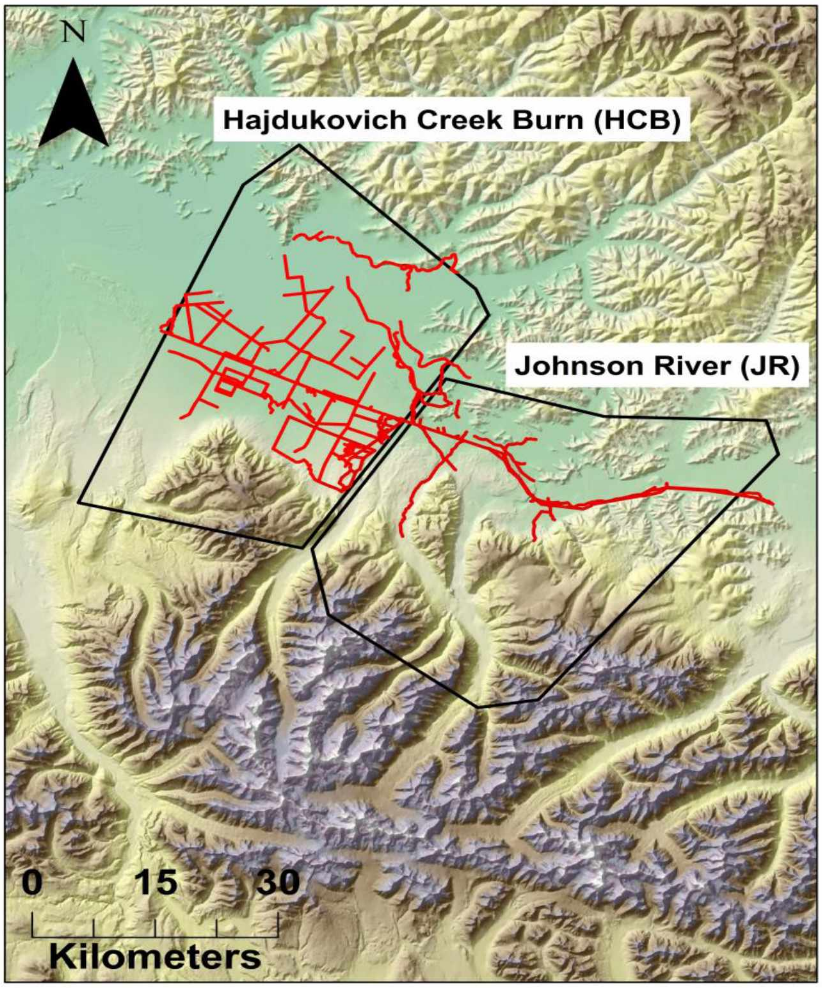


Figure 4.1. Map of Project Study Area

The Gerstle River naturally divided the study area into eastern (Hajdukovich Creek) and western (Johnson River) regions. The Hajdukovich Creek area has approximately 513 km of ORV trails, dirt and paved roads, and a major highway (denoted in red) bisecting the landscape, whereas the Johnson River area has far fewer (139 km) ORV trails and roads.

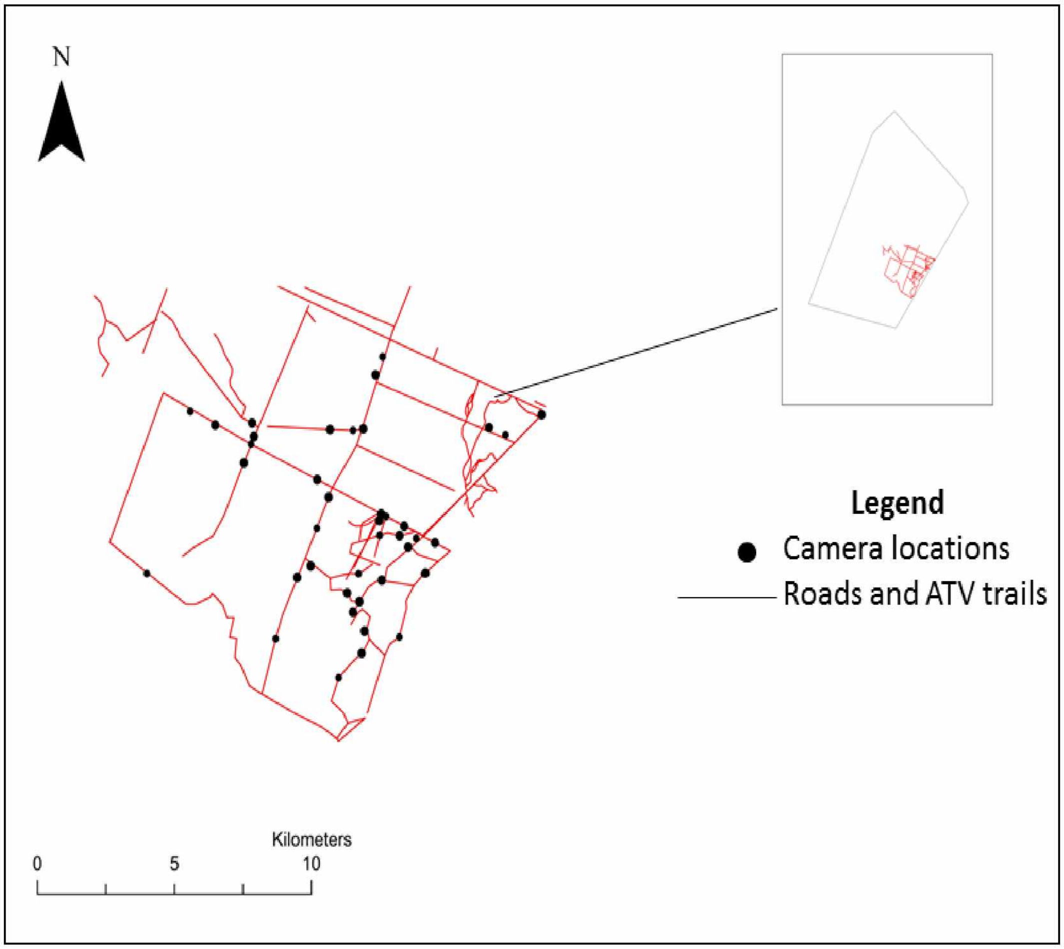


Figure 4.2. Camera Trap Grid

The Hajdukovich Creek study region contains several popular hunting trails. We used a camera trapping grid during the 2013 and 2014 hunting seasons to capture hunting activity.

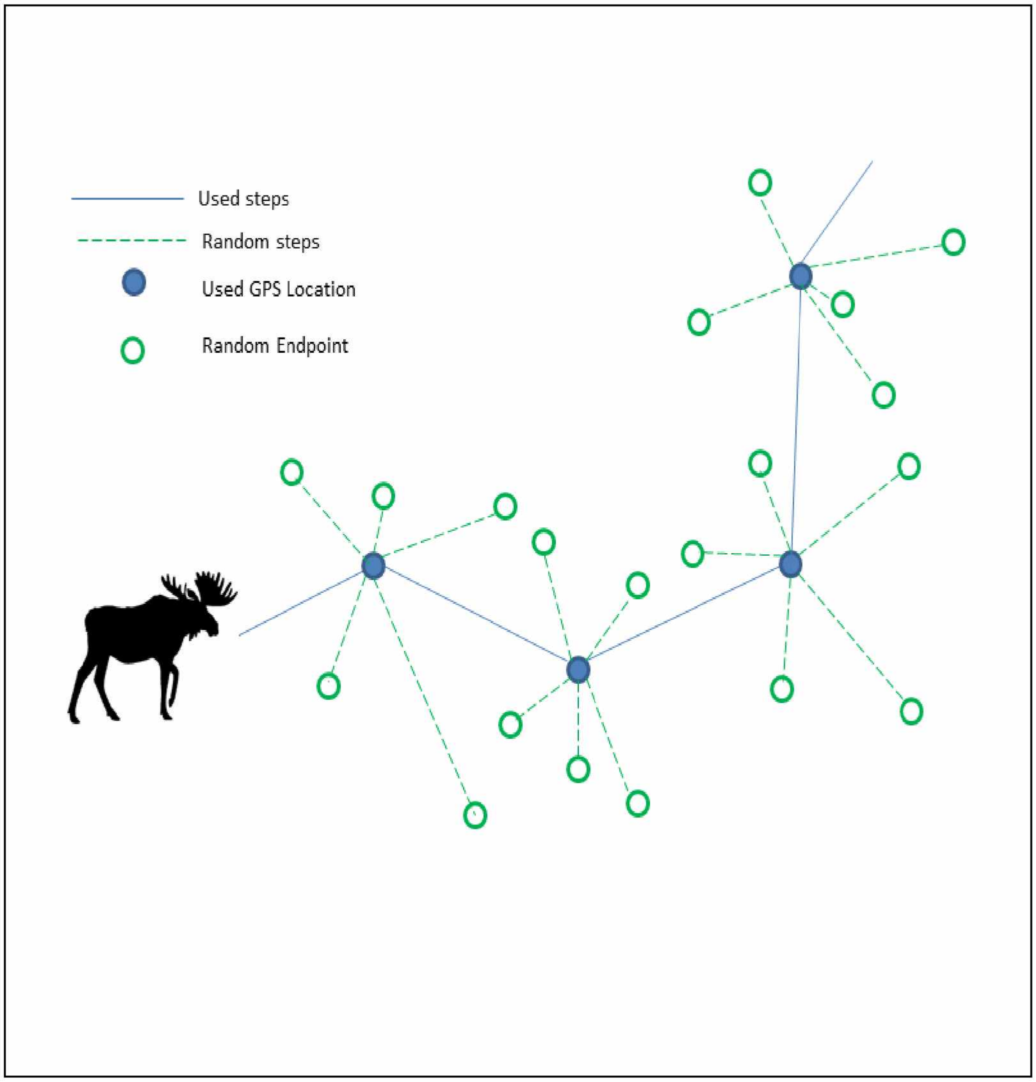


Figure 4.3. Illustration of Step Selection Function (SSF)

Illustration of movement pattern generated from SSFs that compared the environmental features at the endpoint of each used step to the endpoints of 5 random steps for each GPS location.

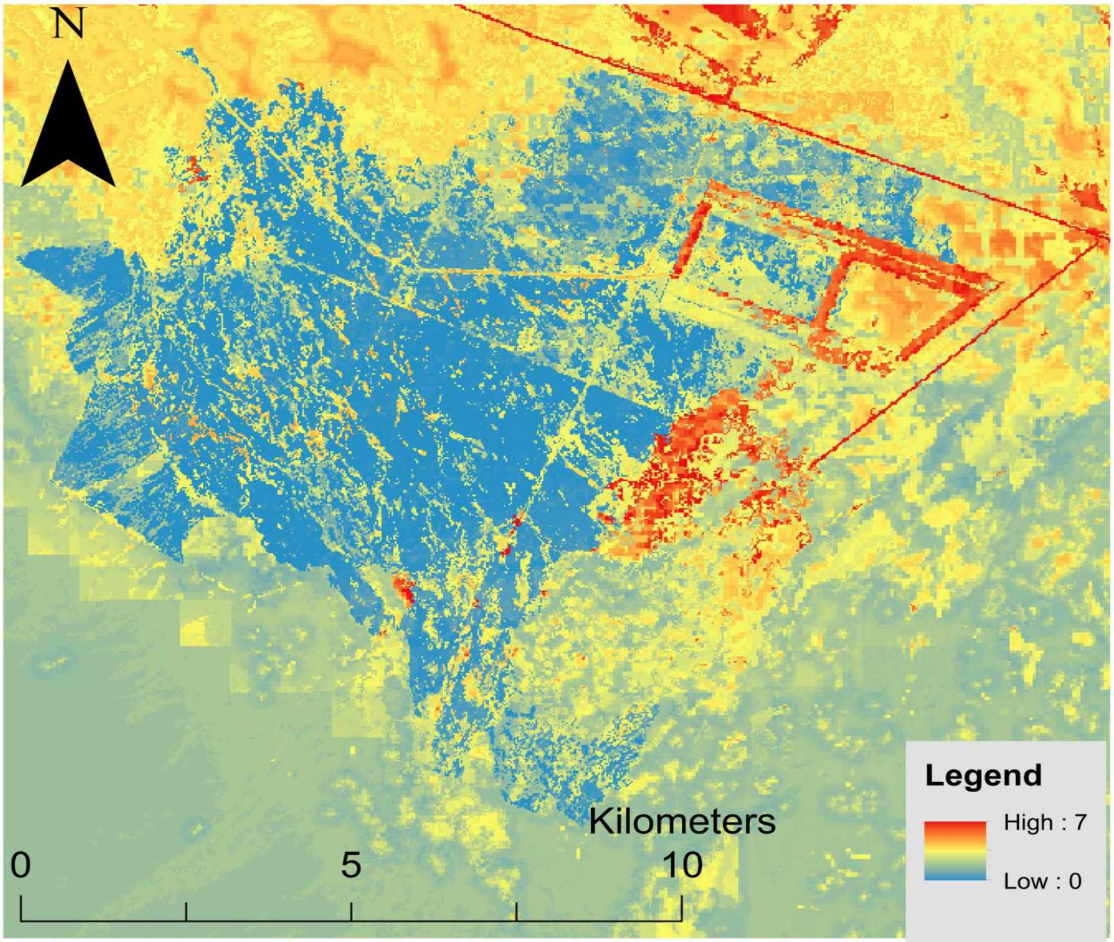


Figure 4.4. Hunter Distribution Map

Continuous, predictive spatial distribution of hunter occurrence in the Gerstle. Warm colors indicate higher average number of hunters and cool colors designate areas of lower average numbers of hunters.

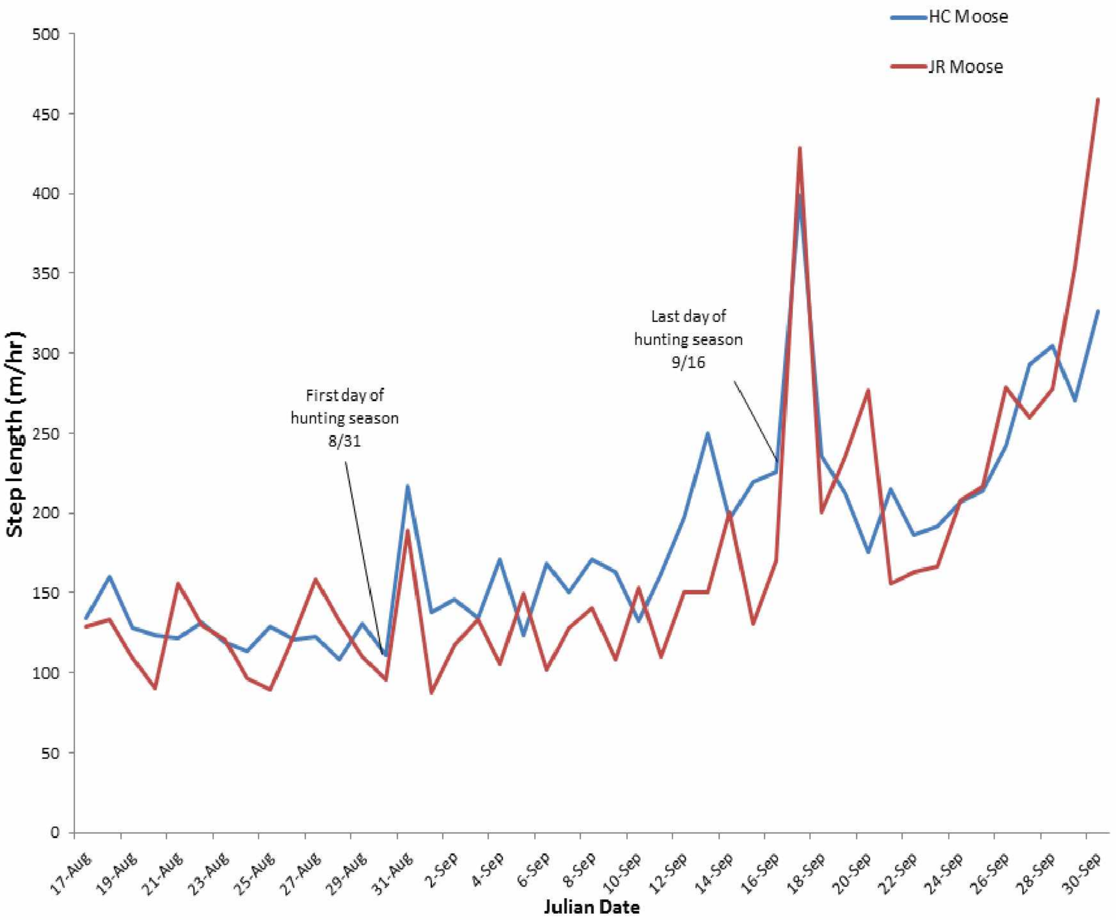


Figure 4.5. Moose Activity Patterns During Hunting Season

Mean hourly step length for moose in the Hajdukovich Creek and Johnson River (2013-2014).

4.8. TABLES

Table 4.1. Top Candidate Models

Top ranked candidate model and the associated model weight for Hajdukovich Creek (HC) and Johnson River (JR) moose for two different periods (pre-hunting and hunting). Trail distance represents distance to all hunter travel corridor (trails, roads, navigable rivers).

Study Region	**Season**	**Model**	**w_t**
HC	Pre-Hunting	Trail Distance + Elevation + Cover + Distance to Forage	0.07
HC	Hunting	Elevation	0.07
JR	Pre-Hunting	Elevation + Rugged + Distance to Forage	0.16
JR	Hunting	Trail Distance + Elevation	0.06

Table 4.2. Full Model Averaged and Top-ranked Model Regression Coefficients

Coefficients summarize the Hajdukovich Creek (HC) and Johnson River (JR) moose. Models results are across two time periods: Pre-hunting season (August 1-August 29th) and Hunting Season (August 30th-September 16th).

	HC Moose **Model Averaged**	**HC Moose** **Top Model**	**JR Moose** **Model Averaged**	**JR Moose** **Top Model**
	β (SE)	**β (SE)**	**β(SE)**	**β(SE)**
Pre-Hunting Season				
Trail Distance	-0.03 (0.1)	-0.02 (0.1)	-0.01 (0.1)	NA
Elevation	-0.48 (0.4)	-0.88 (0.3)	0.26 (0.2)	0.30 (0.2)
Rugged	0.03 (0.02)	NA	-0.07 (0.006)	-0.09 (0.05)
Cover	0.001 (0.002)	0.002 (0.003)	-0.005 (0.001)	NA
Distance to forage	-0.04 (0.05)	-0.08 (0.05)	-0.16 (0.1)	-0.21 (0.07)
Hunting Season				
Trail Distance	-0.01 (0.06)	NA	-0.36 (0.4)	-0.86 (0.27)
Elevation	-0.28 (0.2)	-0.50 (0.15)	0.25(0.3)	0.36 (0.2)
Rugged	0.003 (0.02)	NA	-0.01(0.02)	NA
Cover	0.001(0.002)	NA	-0.003(0.005)	NA
Distance to forage	-0.06 (0.02)	NA	-0.03(0.003)	NA

Table 4.3. Variable Importance Rankings for Hunter Distribution Model

Variable importance rankings of the nine most important variables used in hunter activity model construction. Scores are on a scale of 0-100 (top variable always receives the maximum value).

Variable	Score
Trail Distance	100.0
Fire Severity	15.8
Vegetation	8.6
Elevation	5.5
Slope	4.7
Winter Precipitation	3.9
Cliome	2.6
Spring Precipitation	2.0
Distance to Wet vegetation	1.1

Table 4.4. Gerstle Moose Regression Coefficients

Full-model averaged regression coefficients (standard errors) and the top-ranked model coefficients (standard errors) for a subset of moose used the Gerstle during the hunting season (August 30-September 16th). An additional hunter activity variable was included in this model.

	Model Averaged	**Best Model**
Hunting Season	**β (SE)**	**β (SE)**
Trail Distance	-0.004 (0.7)	-0.005 (0.1)
Elevation	-0.51 (0.4)	-0.6 (0.3)
Rugged	0.004 (0.02)	NA
Cover	0.004 (0.004)	0.007 (0.003)
Distance to forage	0.017 (0.04)	NA
Hunter Activity (ROI)	-0.4 (0.03)	-0.7 (0.02)

4.9. REFERENCES

Baltensperger, A. P. and F. Huettmann. 2015. Predictive spatial niche and biodiversity hotspot models for small mammal communities in Alaska: Applying machine-learning to conservation planning. Landscape Ecology **30:** 681–697.

Baltensperger, A. P., T. C. Mullet, M. S. Schmid, G. W. Humphries, L. Kövér, and F. Huettmann. 2013. Time series and machine learning-based niche model predictions for the common raven (*Corvus corax*) in the urban, subarctic environment of Fairbanks, Alaska. Polar Biology, **36**:1587-1599.

Bender, L. C., D. E. Beyer Jr, and J. B. Haufler. 1999. Effects of short-duration, high-intensity hunting on elk wariness in Michigan. Wildlife Society Bulletin **27**:441-445.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters **3**:620-623.

Berman, M. and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. Ecological Economics **49**:31-46.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters **11**:63-77.

Booms, T. L., F. Huettmann, and P. F. Schempf. 2010. Gyrfalcon nest distribution in Alaska based on a predictiveGIS model. Polar Biology **33**: 347–358.

Brinkman, T. J., G. P. Kofinas, F. S. Chapin III, and D. K. Person. 2007. Influence of hunter adaptability on resilience of subsistence hunting systems. Journal of Ecological Anthropology **11**:58.

Brinkman, T., G. Kofinas, W. Hansen, F. Chapin III, and S. Rupp. 2013. A New Framework to Manage Hunting. The Wildlife Professional **7**:38-43.

Brinkman, T., K. T. B. Maracle, J. Kelly, M. Vandyke, A. Firmin, and A. Springsteen. 2014. Impact of fuel costs on high-latitude subsistence activities. Ecology and Society **19**:18.

Brinkman, T. J. and K. A. Kellie. 2014. Tanana Flats Training Area Moose Calving Site Study. Final Report to the Military in Fulfillment of US Army Contract W912DY-09-2-011.

Brøseth, H. and H. C. Pedersen. 2000. Hunting effort and game vulnerability studies on a small scale: a new technique combining radio-telemetry, GPS and GIS. Journal of Applied Ecology **37**:182-190.

Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. PloS one 7:e40505.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research **1**:49-71.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

Burson III, S., J. Belant, K. Fortier, and W. C. Tomkiewicz III. 2000. The effect of vehicle traffic on wildlife in Denali National Park. Arctic **53**:146-151.

Carter, N. H., B. K. Shrestha, J. B. Karki, N. M. B. Pradhan, and J. Liu. 2012. Coexistence between wildlife and humans at fine spatial scales. Proceedings of the National Academy of Sciences **109**:15360-15365.

Child, K. 1998. Incidental mortality. Ecology and management of the North American moose. Smithsonian Institution, Washington, DC:275-301.

Creel, S., J. Winnie Jr, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology **86**:3387-3397.

Cromsigt, J. P., D. P. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology **50**:544-549.

Duffy, P. A. 2007. Analysis of Alaskan burn severity patterns using remotely sensed data. Int. Journal of Wildland Fire **16**:277-284.

Evans J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using Random Forest. In: Y. F. W. C. Drew Ashton, Huettmann Falk, editor editors. Predictive Species and Habitat Modeling in Landscape Ecology. Berlin: Springer. pp. 139–160.

Ewert, A. and J. Shultis. 1999. Technology and backcountry recreation: boon to recreation or bust for management? Journal of Physical Education, Recreation & Dance **70**:23-28.

Fahrig, L. and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and society **14**:21.

Ferrari, M. C., A. Sih, and D. P. Chivers. 2009. The paradox of risk allocation: a review and prospectus. Animal Behaviour **78**:579-585.

Forman, R., D. Sperling, J. Bissonette, A. Clevenger, C. Cutshall, V. Dale, L. Fahrig, R. France, C. Goldman, and K. Heanue. 2003. Road Ecology: Science ans Solutions. Washington: Island Press.

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

Franke, A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (Canis lupus) kill-sites using hidden Markov models. Ecological modelling **197**:237-246.

Fryxell, J. M., J. Greever, and A. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist **131**:781-798.

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

Gilbert, S., K. Hundertmark, D. Person, M. Lindberg, and M. Boyce. 2016. Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. Journal of Mammalogy *in press.*

Grignolio, S., E. Merli, P. Bongi, S. Ciuti, and M. Apollonio. 2011. Effects of hunting with hounds on a non-target species living on the edge of a protected area. Biological Conservation **144**:641-649.

Hansen, W. D., T. J. Brinkman, M. Leonawicz, F. S. Chapin III, and G. P. Kofinas. 2013. Changing Daily Wind Speeds on Alaska's North Slope: Implications for Rural Hunting Opportunities. Arctic **66**:448-458.

Heberlein, T. A. 2002. Peer-Reviewed Articles Too Many Hunters or Not Enough Deer? Human and Biological Determinants of Hunter Satisfaction and Quality. Human Dimensions of Wildlife **7**:229-250.

Hegel T. M., S. A. Cushman, J. S. Evans, and F. Huettmann. 2010. Current state of the art for statistical modelling of species distributions. In: Cushman S. A. and Huettmann F., editors. Spatial Complexity, Informatics, and Wildlife Conservation. New York: Springer. pp. 273–311.

Johnson, I., T. Brinkman, K. Britton, J. Kelly, K. Hundertmark, B. Lake, and D. Verbyla. 2016. Quantifying Rural Hunter Access in Alaska. Human Dimensions of Wildlife:1-14.

Kellie, K. A. 2005. Summer movements of female moose at high density. M. S. Thesis, University of Alaska Fairbanks. Fairbanks, Alaska.

Kofinas, G. P., F. S. Chapin III, S. Burnsilver, J. I. Schmidt, N. L. Fresco, K. Kielland, S. Martin, A. Springsteen, and T. S. Rupp. 2010. Resilience of Athabascan subsistence systems to interior Alaska's changing climate. Canadian Journal of Forest Research **40**:1347-1359.

Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the" landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology **79**:1401-1409.

Lima, S. L. and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. The American Naturalist **153**:649-659.

Loring, P. A. and S. C. Gerlach. 2009. Food, culture, and human health in Alaska: an integrative health approach to food security. Environmental Science & Policy **12**:466-478.

McCullough, D. R. 1996. Spatially structured populations and harvest theory. The Journal of Wildlife Management **60**:1-9.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. The Journal of Wildlife Management **64**:994-1003.

Miquelle, D. G. 1990. Why don't bull moose eat during the rut? Behavioral Ecology and Sociobiology **27**:145-151.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology **85**:2436-2445.

Naylor, L. M., M. J. Wisdom, and R. G. Anthony. 2009. Behavioral responses of North American elk to recreational activity. The Journal of Wildlife Management **73**:328-338.

Ouren, D. S., C. Haas, C. P. Melcher, S. C. Stewart, P. D. Ponds, N. R. Sexton, L. Burris, T. Fancher, and Z. H. Bowen. 2007. Environmental effects of off-highway vehicles on Bureau of Land Management lands: A literature synthesis, annotated bibliographies, extensive bibliographies, and internet resources. US Department of the Interior, US Geological Survey.

Peek, J. M., R. E. LeResche, and D. R. Stevens. 1974. Dynamics of moose aggregations in Alaska, Minnesota, and Montana. Journal of Mammalogy **55**:126-137.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography **33**:1113-1122.

Rumble, M. A. and R. S. Gamo. 2011. Habitat use by elk (cervus elaphus) within structural stages of a managed forest of the northcentral United States. Forest Ecology and Management **261**:958-964.

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

Shanley, C. S. and S. Pyare. 2011. Evaluating the road-effect zone on wildlife distribution in a rural landscape. Ecosphere **2**:1-16.

Shannon, G., L. S. Cordes, A. R. Hardy, L. M. Angeloni, and K. R. Crooks. 2014. Behavioral responses associated with a human-mediated predator shelter. PloS one **9**:e94630.

St. Clair, C. C. and A. Forrest. 2009. Impacts of vehicle traffic on the distribution and behaviour of rutting elk, Cervus elaphus. Behaviour **146**:393-413.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation **141**:2159-2173.

Swenson, J. E. 1982. Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. Wildlife Society Bulletin **10**:115-120.

Symonds, M. R. and A. Moussalli. 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology **65**:13-21.

Telfer, E. S. 1984. Circumpolar distribution and habitat requirements of moose (Alces alces). Pages 145-182 in R. Olson, R. Hastings, and F. Geddes, eds. Northern Ecology and Resource Management. University of Alberta Press, Edmonton, Alberta, Canada.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology **2**.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates Sunderland.

Vieira, M. E., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. The Journal of Wildlife Management:717-728.

Viereck, L. A., C. Dyrness, A. Batten, and K. Wenzlick. 1992. The Alaska vegetation classification. US Department of Agriculture, Forest Service, Pacific Northwest Research Station Portland, OR, USA.

Whittington, J., C. C. St. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications **15**:543-553.

4.10. APPENDICES

Appendix 4.1. Cover and Forage Classification

Reclassification of vegetation types into three cover and forage quality classes: (High, Medium, and Low). Viereck et al. 1992 used tree canopy closure (≥ 3 m from the ground) and shrub canopy cover (0.2-3 m from the ground) to describe cover for forest/shrub classes. I used Kellie's (2005) classifications of forest canopy cover for vegetation (1.5 and 3m). Here, forest classes with >25% canopy cover ≥ 3m from the ground were high-quality cover, and canopy copy 10-25% ≥ 3 m from the ground were defined as medium cover. Shrub classes that were 1.3 to 3 m above ground with >75% canopy cover were defined as dense cover, 25-75% as moderate cover and < 25% as open cover. All herbaceous classes had a canopy height < 1.5 m and were defined as low vegetative cover. Additionally, I used Brinkman and Kellie's (2014) forage quality classifications.

Vegetation Description	***Forage Quality***	***Vegetation Cover***
Barren Alluvial Deposits: Fluvial deposits	Low	Low
Barren Other: Agricultural lands	Low	Low
Barren Other: Urban (roads, paved areas, buildings)	Low	Low
Barren Rock: Scree; talus slopes	Low	Low
Barren Rock: (<20% vegetation): Rock, gravel	Low	Low
Closed Broadleaf Forest (60-100%): Paper Birch	Medium	High
Closed Broadleaf Forest (60-100%): Quaking Aspen	Medium	High
Closed Dwarf Tree Forest (60-100% Canopy, Trees<=3 m): Black Spruce	Low	High
Closed Low Scrub (76%-100% Cover, 0.2 m <=Shrubs<=1.5 m tall): Low alder/willow	High	High
Closed Low Scrub (76%-100% Cover, 0.2 m <=Shrubs<=1.5 m tall): Low willow	High	High
Closed Low Scrub (76%-100% Cover, 0.2 m <=Shrubs<=1.5 m tall): Shrub birch-ericacious shrub	High	High
Closed Low Scrub (76%-100% Cover, 0.2 m <=Shrubs<=1.5 m tall): Mixed shrub -tundra tussock	High	High
Closed Mixed Forest (60-100% Canopy): Balsam poplar - white spruce	Medium	High
Closed Mixed Forest (60-100% Canopy): Quaking aspen - spruce	Medium	High
Closed Mixed Forest (60-100% Canopy): Spruce - paper birch	Medium	High
Closed Mixed Forest (60-100% Canopy): Spruce - paper birch - aspen	Medium	High
Closed Needleleaf Forest (60-100% Canopy): Black spruce	Low	High

Closed Needleleaf Forest (60-100% Canopy): Black spruce - white spruce	Low	High
Closed Needleleaf Forest (60-100% Canopy): White spruce	Low	High
Closed Tall Scrub (76-100% Cover, Shrubs>1.5 m Tall): Alder - willow	High	High
Closed Tall Scrub (76-100% Cover, Shrubs>1.5 m Tall): Shrub birch	High	High
Closed Tall Scrub (76-100% Cover, Shrubs>1.5 m Tall): Shrub birch - willow	High	High
Closed Tall Scrub (76-100% Cover, Shrubs>1.5 m Tall): Willow	High	High
Dry Graminoid Herbaceous: Midgrass-shrub	High	Low
Dryas Dwarf Scrub (Shrubs <0.2 m Tall): Dryas - lichen or moss	Medium	Low
Ericaceous Dwarf Scrub (Shrubs ,0.2 M Tall); Mixed Shrub Community	High	Low
Freshwater Aquatic Herbaceous: Pond lily	High	Low
Mesic Graminoid Herbaceous: Bluejoint meadow	High	Low
Mesic Graminoid Herbaceous: Tussock tundra	Medium	Low
Open Broadleaf Forest (25-59% Canopy): Balsam Poplar	Medium	Medium
Open Broadleaf Forest (25-59% Canopy): Paper birch	Medium	Medium
Open Broadleaf Forest (25-59% Canopy): Paper birch-aspen	Medium	Medium
Open Broadleaf Forest (25-59% Canopy): Quaking aspen	Medium	Medium
Open Dwarf Tree Forest (25-59% Canopy, Trees <= 3m): Black spruce	Medium	Medium
Open Low Scrub (25-75% Cover, 0.2m<=Shrubs<=1.5 m Tall): Low alder - willow	High	Medium
Open Low Scrub (25-75% Cover, 0.2 m <= Shrubs<=1.5 m Tall): Mixed shrub -sedge tussock bog	High	Medium
Open Low Scrub (25-75% Cover, 0.2 m <= Shrubs<=1.5 m Tall): Mixed shrub -sedge tussock tundra	High	Medium
Open Low Scrub (25-75% Cover, 0.2 m <= Shrubs<=1.5 m Tall): Shrub birch	High	Medium
Open Low Scrub (25-75% Cover, 0.2 m <= Shrubs<=1.5 m Tall): Willow	High	Medium
Open Low Scrub (25-75% Cover, 0.2 m <= Shrubs<=1.5 m Tall): Willow - sedge -shrub tundra	High	Medium
Open Mixed forest (25-59% Canopy): Paper birch-balsam poplar-spruce	Medium	Medium
Open Mixed forest (25-59% Canopy): Quaking aspen - spruce	Medium	Medium
Open Mixed forest (25-59% Canopy): Spruce-balsam poplar	Medium	Medium
Open Mixed forest (25-59% Canopy): Spruce-paper birch	Medium	Medium
Open Mixed forest (25-59% Canopy): Spruce-paper birch-aspen	Medium	Medium
Open Needleleaf Forest (25-59% Canopy): Black spruce	Low	Medium
Open Needleleaf Forest (25-59% Canopy): Black spruce - white spruce	Low	Medium
Open Needleleaf Forest (25-59% Canopy): White spruce	Low	Medium

Open Tall Scrub (25-75% Cover, Shrubs>1.5 m Tall): Alder	Low	Medium
Open Tall Scrub (25-75% Cover, Shrubs>1.5 m Tall): Alder - willow	High	Medium
Open Tall Scrub (25-75% Cover, Shrubs>1.5 m Tall): Shrub birch	High	Medium
Open Tall Scrub (25-75% Cover, Shrubs>1.5 m Tall): Shrub birch - willow	High	Medium
Open Tall Scrub (25-75% Cover, Shrubs>1.5 m Tall): Willow	High	Medium
Snow/Ice	Low	Low
Water Lakes/Ponds	High	Low
Water streams/Rivers/Canals	High	Low
Wet Graminoid Herbaceous: Marsh or bog meadow	High	Low
Wet Graminoid Herbaceous: Fresh grass marsh	High	Low
Wet Graminoid Herbaceous: Wet sedge-grass meadow tundra	High	Low
Wet Graminoid Herbaceous: Moss (wet)	Medium	Low
Wet Graminoid Herbaceous: >20% Wet sedge - grass meadow tundra, Bareground>50%	Medium	Low
Woodleaf Broadleaf Forest (10-24% Canopy): Balsam Poplar	Medium	Medium
Woodleaf Broadleaf Forest (10-24% Canopy): Paper birch	Medium	Medium
Woodleaf Broadleaf Forest (10-24% Canopy): Paper birch - aspen	Medium	Medium
Woodleaf Broadleaf Forest (10-24% Canopy): Paper birch - balsam poplar	Medium	Medium
Woodleaf Broadleaf Forest (10-24% Canopy): Quaking aspen	Medium	Medium
Woodleaf Mixed Forest (10-24% Canopy): Balsam poplar - spruce	Medium	Medium
Woodleaf Mixed Forest (10-24% Canopy): Quaking aspen - spruce	Medium	Medium
Woodleaf Mixed Forest (10-24% Canopy): Spruce - paper birch	Medium	Medium
Woodleaf Mixed Forest (10-24% Canopy): Spruce - paper birch-aspen	Medium	Medium
Woodleaf Needleleaf Forest (10-24% Canopy): Black spruce	Low	Medium
Woodleaf Needleleaf Forest (10-24% Canopy): Black spruce - white spruce	Low	Medium
Woodleaf Needleleaf Forest (10-24% Canopy): Black spruce - white spruce-lichen	Low	Medium
Woodleaf Needleleaf Forest (10-24% Canopy): White spruce	Low	Medium

Appendix 4.2. Camera Trap Detections

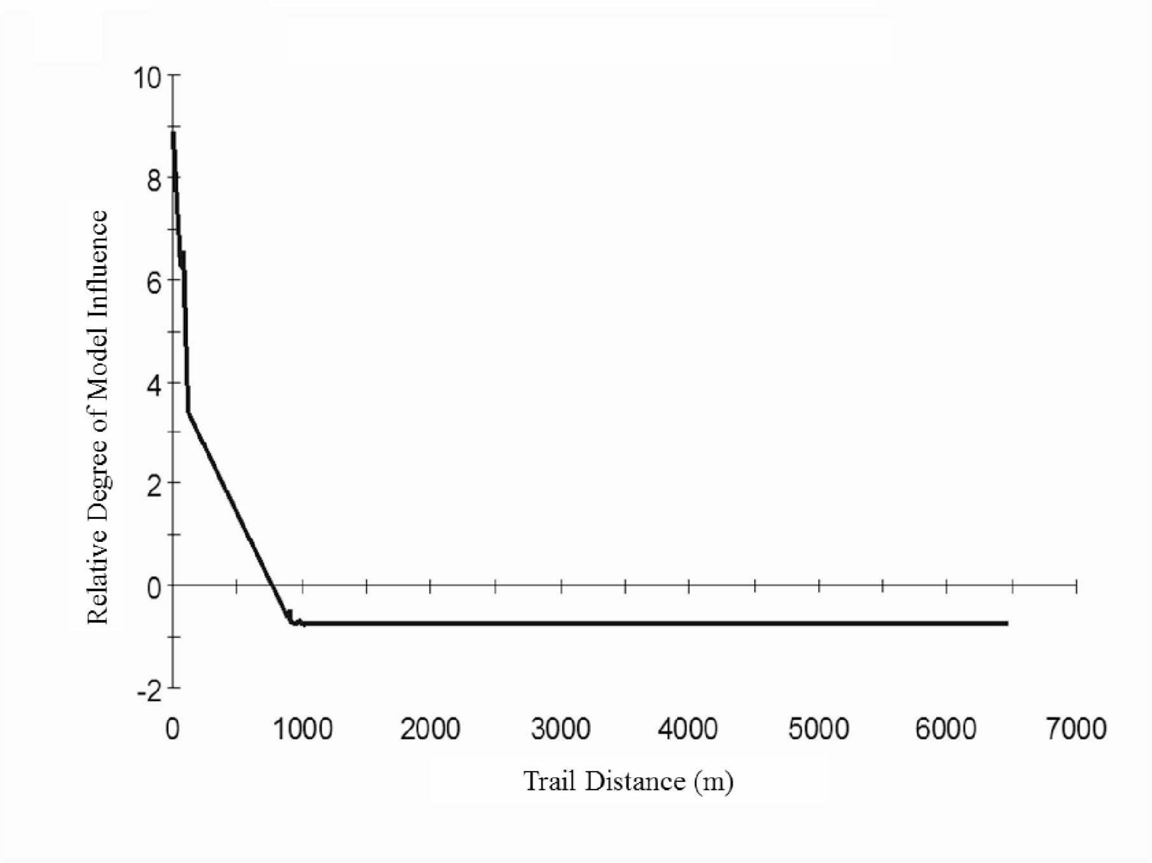
Total camera detections (2013-2014) from the Gerstle camera trap grid.

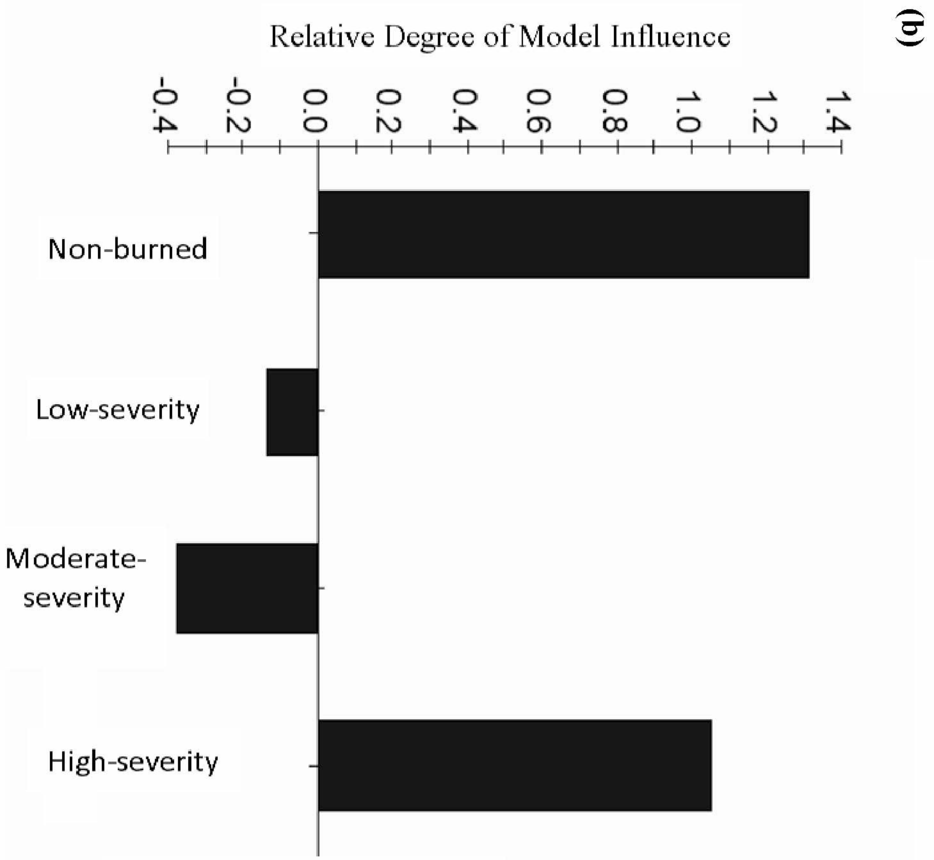
SEASON	YEAR	Human Activity	Female Moose	Moose Bull	Moose Unknown	Brown Bear	Black Bear	Lynx	Wolf	Coyote	Bison	Fox
PRE-HUNTING	2013	389	57	29	12	5	1	5	5	2	213	0
	2014	246	11	4	1	7	1	2	1	0	11	0
HUNTING	2013	3491	21	12	2	9	1	4	1	0	20	0
	2014	2090	20	9	1	6	1	17	2	0	0	0
POST-HUNTING	2013	17	32	22	3	17	3	4	5	3	0	1
	2014	209	52	19	5	8	0	11	11	2	0	3

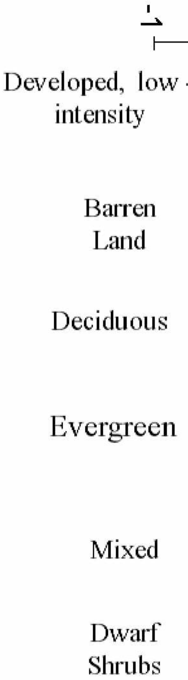
Appendix 4.3. Partial Dependence Plots

Partial dependence plots for the top three variables used in RandomForest algorithms. Plots demonstrate the relative degree of influence for models predicting hunter occurrence in relation to **a)** distance to trails, **b)** fire severity, and **c)** vegetation.

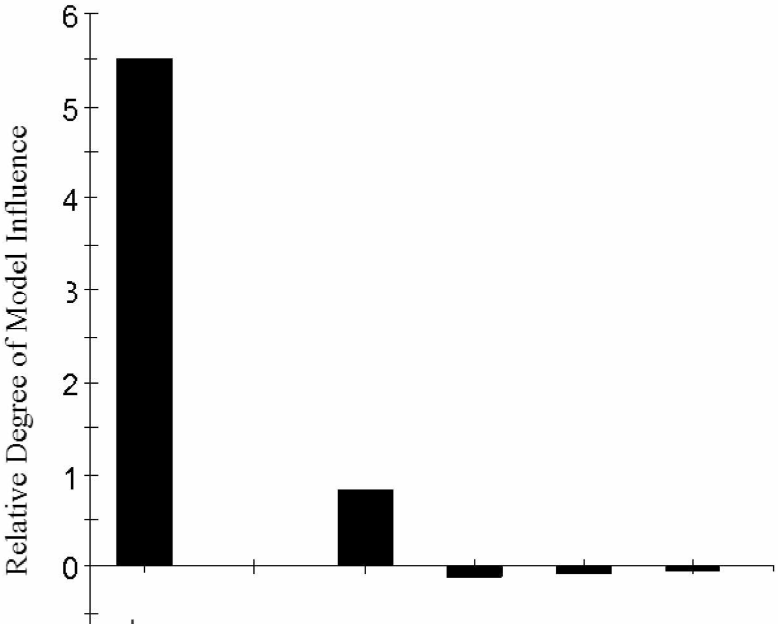
(a)



(b)
Relative Degree of Model Influence
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Non-burned
Low-severity
Moderate-severity
High-severity


-1
Developed, low intensity
Barren Land
Deciduous
Evergreen
Mixed
Dwarf Shrubs

(c)



CHAPTER 5. CONCLUSIONS

Interdisciplinary methods are often necessary to understand the broad spectrum of effects associated with changing habitat conditions on wildlife. Applying a framework that incorporates social-ecological variables is becoming increasingly important for research that focuses on the management of game species. In Interior Alaska, moose are especially important to consider because they constitute the largest non-fish subsistence resource for many communities. My dissertation demonstrated the utility of using a variety of methods to describe and evaluate the dynamic effects of a natural (wildfire) disturbance and an anthropogenic disturbance (hunting activity) on moose habitat use patterns and management scenarios. These methods include browse assessment surveys, landscape modeling, habitat selection modeling, and machine learning techniques. Additionally, the research presented here demonstrates that hunter-wildlife systems are particularly strong social-ecological systems to study because of direct interactions between humans and game species. The results from this project will provide an opportunity for both wildlife and fire managers to incorporate information into future management strategies that maximize the positive effect of natural wildfire for both moose nutrition and harvest.

5.1. INCORPORATING RESILIENCE THEORY INTO MOOSE MANAGEMENT DECISIONS

Using a social-ecological systems framework, I showed that fire severity can have important consequences for slow and fast social-ecological variables in an Alaskan hunter-wildlife system (Chapter 2). Post-fire conditions, such as the depth of organic soil, can promote deciduous forage production (slow variable) translating into more food for moose. As moose move into burns, the rate of forage removal also increases (fast variable). Additionally, the proximity of wildfires to human developments can influence the availability of hunter travel corridors (slow variable). Finally, as hunters gain access to burned areas, annual hunter opportunities should increase (fast variable).

The management scenarios discussed in Chapter 2 provide a framework for monitoring social-ecological variables for moose harvest following a wildfire (Figure 5.1). This framework can be applied to management of other human-wildlife systems. Before this can happen, managers first need to develop a thorough understanding of the various socio-ecological components and their interaction when choosing which variables to monitor. I recommend that wildlife managers continue monitoring fast variables (e.g., forage production and offtake) on a recurrent basis (e.g., annually) in order to adapt and keep their management responsive as resource availability fluctuates. Fast variables typically can be highly variable throughout a given year and are more sensitive to daily, monthly, or seasonal changes (e.g., annual crop production or abundance of a game species). Slow variables can be strong drivers of these systems, but remain more stable overtime because they are buffered by feedbacks which prevent rapid change (Carpenter and Turner 2000). Slow variables might include the presence of functional types of plants/animals, disturbance regimes (e.g., fire frequency), and the capacity of soils to cycle nutrients (Walker and Salt 2006). Slow variables may require less monitoring effort (2-5 years), however, it is highly recommended that managers understand the broader ecological consequences that can occur if these variables do change.

By identifying and monitoring key slow and fast variables, managers can adapt goals and actions to changing dynamics that might affect wildlife-hunter systems. Additionally, management scenarios can help forecast changing habitat conditions following a disturbance. These scenarios will prepare managers to communicate their strategies to the public. In doing so, managers are improving decision-making transparency and minimizing potential conflict.

5.2. EFFECTS OF WILDFIRE ON RESOURCE SELECTION BY MOOSE

In Chapter 3 I showed that adult male moose made extensive use of post-fire burn habitats throughout the year. I found that the Hajdukovich Creek burn was the most abundant habitat class across individual moose home range and core use areas. Browse assessment surveys indicated that willow biomass production has more than doubled since 2007 in low-severity patches, and currently is exceeding willow production in high-severity patches. Results from dynamic Brownian bridge models indicate that moose preferentially selected low-severity patches more than high-severity sites during the winter season. This suggests that moose are responding to changes in vegetation composition, especially increased forage availability, related to differences in burn severity during the winter season. Additionally, winter selection does not appear to be driven by the nutritional quality of winter browse. Finally, fine-scale habitat use patterns changed seasonally. In summer, moose selected for high-severity sites more than low-severities. The increase in selection for high-severity sites in summer may be due to thermal and structural cover provided by deciduous tree and shrub species.

Over the past 15 years, forest regeneration in the Hajdukovich burn has been studied extensively: fire severity classes were identified by Michalek et al. (2000), vegetation composition and regeneration post fire have been documented (Shenoy et al. 2011), and moose-browse dynamics have been quantified (Lord and Kielland 2015). My results from Chapter 3 build upon these studies and demonstrate that variability of wildfire severity across a landscape can create a dynamic mosaic of habitat patches that may extend the value of burns over time for moose. It is projected that fires will increase in both frequency and severity in Alaska as a result of rapid warming (Calef et al. 2015). If the relationship between fire-severity, forage production, and habitat heterogeneity persists across northern latitudes, moose populations in the short term (i.e., 10-30 years post-fire) should benefit from changing habitat conditions that follow forest disturbance. The results from this study indicate that the Hajdukovich Creek burn produced a dynamic, spatially heterogeneous landscape that can influence a range of habitat requirements for moose

5.3. EFFECTS OF HUNTER ACTIVITY ON HABITAT USE AND MOVEMENT PATTERNS OF MOOSE

Applying machine learning techniques along with step selection functions, I found that moose responded negatively to spatial variation in risk associated with human activity along roads and trails during hunting season (Chapter 4). Moose selected habitats closer to trails and roads, but also avoided those areas if hunting activity was high. Additionally, movement rates in areas with higher road/trail densities were significantly greater during hunting season. Our results align with others that have found that moose respond negatively to an increase in human activity at fine scales (Burson et al. 2000, Shanley and Pyare 2011).

For the research described in Chapter 4, I also used camera trap technology to generate an innovative spatial model that depicts hunter occurrence on the landscape. Moose responded to risk associated with human activity during hunting season by avoiding areas with more hunters. However, this also suggests that hunter concentrations are not overlapping with the moose they are seeking. This relationship suggests that hunting opportunities may decrease in areas that experience frequent exposure to anthropogenic activity during hunting season.

In Alaska, research has found that hunter success is not only based on the abundance of game, but is also highly dependent upon the seasonal distribution of wildlife on the landscape during hunting season and the abilities of hunters to access those locations (Brinkman et al. 2013, Hansen et al. 2013). In rural communities, the ability to access game can be a critical driver of hunting opportunities (Berman and Kofinas 2004, Johnson et al. 2016). However, it is important to consider the effects of hunting on risk avoidance behavior especially when hunting effort is highly concentrated on the landscape.

If managers want to incorporate natural wildfires into management plans to increase harvest rates, I propose using a hunter accessibility metric that accounts for the proximity of regenerating burns to human communities as well as an index of hunter activity levels (Figure 5.2). If hunting activity is concentrated along popular roads and trails, managers may need to consider spreading hunting effort over a larger area. To do so, local wildlife agencies will need to actively communicate this objective to the hunting public. Additionally, roads and other access points may need to be improved in alternative areas to reduce hunter concentrations along popular roads and trails. Second, managers may need to reduce the temporal predictability of hunting risk (e.g., extending hunting season) so that ungulates can return to areas where they have been displaced. As wildlife management issues become more challenging in human-dominated landscapes in Alaska, managers should consider incorporating the effects of hunting disturbance on wildlife displacement. In doing so, managers would be taking steps to reduce conflict over wildlife resources and foster better communication with the public.

5.4. FIGURE

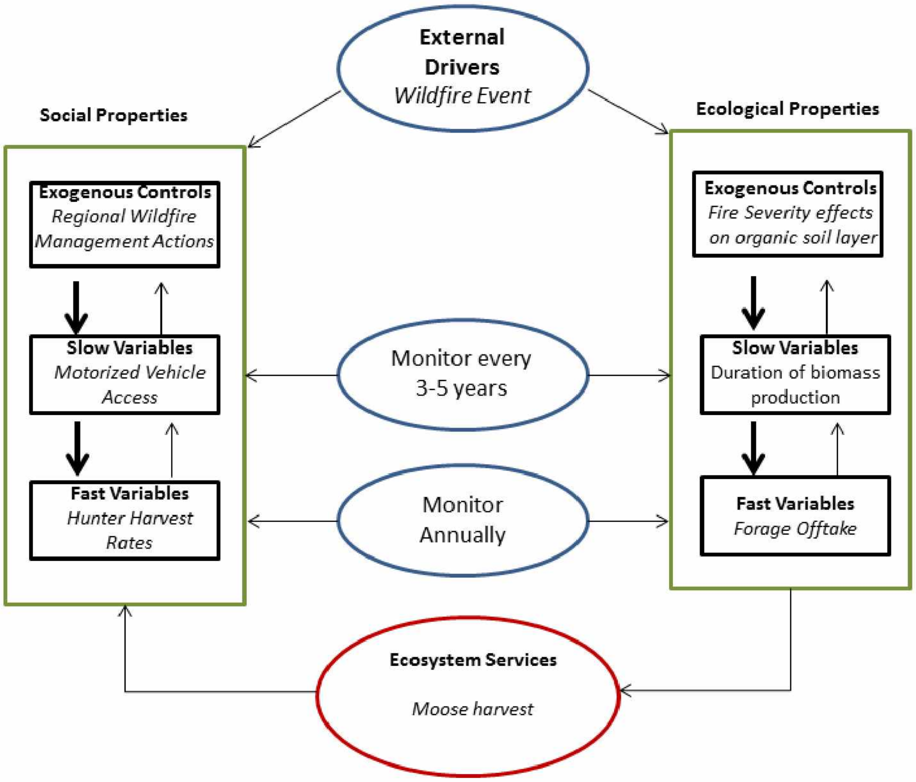


Figure 5.1. Integrated Social-ecological System Framework.

Exogenous controls affect slow variables, which, in turn can impact fast variables that change quickly. If transitions to fast variables persist over time, these effects can propagate upward to impact slow variables. Post-fire conditions, such as the depth of organic soil, can promote deciduous forage production (slow variable) translating into more food for moose. As moose move into burns, the rate of forage removal also increases (fast variable). Additionally, the proximity of wildfires to human developments can influence the availability of hunter travel corridors (slow variable). Finally, as hunters gain access to burned areas, annual hunter opportunities should increase (fast variable). Adapted from Chapin et al. (2009) and Collins et al. (2010).

5.5. REFERENCES

Berman, M. and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. Ecological Economics **49**:31-46.

Brinkman, T., G. Kofinas, W. Hansen, F. Chapin III, and S. Rupp. 2013. A New Framework to Manage Hunting. The Wildlife Professional 7:38-43.

Burson III, S., J. Belant, K. Fortier, and W. C. Tomkiewicz III. 2000. The effect of vehicle traffic on wildlife in Denali National Park. Arctic **53**:146-151.

Calef, M., A. Varvak, A. McGuire, F. Chapin III, and K. Reinhold. 2015. Recent changes in annual area burned in Interior Alaska: the impact of fire management. Earth Interactions **19**:1-17.

Carpenter, S. R. and M. G. Turner. 2000. Hares and tortoises: interactions of fast and slow variables in ecosystems. Ecosystems **3**:495-497.

Chapin III, F. S., G. P. Kofinas, C. Folke, S. R. Carpenter, P. Olsson, N. Abel, R. Biggs, R. L. Naylor, E. Pinkerton, and D. M. S. Smith. 2009. Resilience-based stewardship: strategies for navigating sustainable pathways in a changing world. Pages 319-337 Principles of ecosystem stewardship. Springer.

Collins, S. L., S. R. Carpenter, S. M. Swinton, D. E. Orenstein, D. L. Childers, T. L. Gragson, N. B. Grimm, J. M. Grove, S. L. Harlan, and J. P. Kaye. 2010. An integrated conceptual framework for long-term social-ecological research. Frontiers in Ecology and the Environment **9**:351-357.

Hansen, W. D., T. J. Brinkman, M. Leonawicz, F. S. Chapin III, and G. P. Kofinas. 2013. Changing Daily Wind Speeds on Alaska's North Slope: Implications for Rural Hunting Opportunities. Arctic **66**:448-458.

Johnson, I., T. Brinkman, K. Britton, J. Kelly, K. Hundertmark, B. Lake, and D. Verbyla. 2016. Quantifying Rural Hunter Access in Alaska. Human Dimensions of Wildlife **21**:1-10.

Lord, R. and K. Kielland. 2015. Effects of variable fire severity on forage production and foraging behavior of moose in winter. Alces: A Journal Devoted to the Biology and Management of Moose **51**:23-34.

Michalek, J., N. French, E. Kasischke, R. Johnson, and J. Colwell. 2000. Using Landsat TM data to estimate carbon release from burned biomass in an Alaskan spruce forest complex. International Journal of Remote Sensing **21**:323-338.

Shanley, C. S. and S. Pyare. 2011. Evaluating the road effect zone on wildlife distribution in a rural landscape. Ecosphere **2**:1-16.

Shenoy, A., J. F. Johnstone, E. S. Kasischke, and K. Kielland. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management **261**:381-390.

Walker, B. and D. Salt. 2006. Resilience thinking: sustaining ecosystems and people in a changing world. Island Press.