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13. ABSTRACT *(Maximum 200 Words)*

Beginning in 2010 through 2012 JBER adult cow moose were outfitted with Global Positioning System (GPS) collars and a variety of body condition measures were recorded from each animal. A JBER nutritional landscape map was developed based upon seasonal metabolic requirements of moose and the JBER landscape. Resource Selection Function (RSF) analyses of moose habitat use were inconclusive, though provided support for the nutritional landscape model. JBER moose habitat can be highly fragmented and resident moose have individualistic movements. RSF work showed that shrub habitat is important and that moose tend to seasonally avoid open grassy areas that may have deep snow. Distance to buildings was negatively correlated to habitat selection. Travel between habitat patches is highly individualistic; however large structures such as the Glenn highway are somewhat resistant barriers to moose movement. Gene frequencies among JBER moose show a developing division into two distinct groups separated by the Glenn highway. This report contains multiple appendices which contain individual project descriptions and results. Resident JBER wolf packs were extirpated due to dangerous behavior relative to people and no research was conducted. Black bears were also collared with GPS collars on JBER and location data are reported.

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Introduction

Beginning in 2010 through 2012 JBER adult cow moose were outfitted with Global Positioning System (GPS) collars and a variety of body condition measures recorded from each animal. Black bears were also collared with GPS collars on JBER and location data collected. A metabolic model of moose requirements was constructed as a nutritional landscape map with important moose habitat. Resource Selection Function (RSF) analyses of moose habitat use were inconclusive, though provided support for the nutritional landscape model. JBER moose habitat can be highly fragmented and resident moose have individualistic movements. RSF work showed that shrub habitat is important and moose tend to avoid open grassy areas that may have deep snow. Distance to buildings was negatively correlated to habitat selection. Travel between habitat patches is highly individualistic; however large structures such as the Glenn highway are barriers to movement. Long-term effects will be to develop two distinct moose populations. Current gene frequencies among JBER moose show a division into two distinct groups separated by the highway. There are multiple reports appended to this report as stand-alone appendices. Resident JBER wolf packs were extirpated due to dangerous behavior relative to people and no research was conducted.

Body

This report summarizes work that investigated biological attributes associated with habitat use by moose (*Alces alces*) and black bear (*Ursus americanus*) on Joint Base Elmendorf Fort Richardson (JBER). Beginning in 2010 and continuing until 2012 adult cow moose on JBER were captured, outfitted with Global Positioning System (GPS) collars, and a variety of body condition measures recorded from each animal. Black bears were captured on JBER as well and collared with GPS radio-collars. Location data were collected on bear movements as well as areas of high bear problem calls to JBER wildlife game wardens

Habitat use by moose was examined by constructing a nutritional landscape map of JBER, identifying important moose diet items, and then combining the results from a metabolic model of moose requirements with the habitat map to generate a map outlining potential moose production for all areas. Managers will be able to take the ArcMap files of this nutritional landscape and use them to predict the effect on moose populations from proposed developments and to generate plans to improve habitat to support the moose population. This work is presented in the Master's thesis by Joe Welch and is found in Chapter 1.

We employed Resource Selection Function (RSF) analyses to identify habitat used by moose according to degree and type of use (encamped or traveling). Whereas the nutritional landscape maps show the metabolic values of habitat types, the RSF work was intended to identify habitat use that was not nutritionally explicit (i.e., cover, distance to buildings). The RSF work was somewhat inconclusive, though overall provided additional support for the nutritional landscape models. JBER moose habitat that was part of this study is a highly fragmented landscape and the resident moose are individualistic in their movements. The fragmentation apparently drives moose to adopt highly individualistic movements at a scale less than 100m. Overall RSF work showed that shrub habitat is important to moose, which is a conclusion shared by the nutritional landscape model. The RSF model also showed that moose tend to avoid open grassy areas (likely due to snow depth) and that distance to buildings was negatively correlated to habitat selection.

Travel between habitat patches is highly individualistic as well, however it became clear that large structures such as the Glenn highway are barriers to movement and that the long-term effects will be to drive the development of two distinct moose populations. While the GPS collars show some travel across the highway, location data are a very limited level of analysis. When relative gene frequencies shared between JBER moose were determined the results clearly showed a division of the overall moose population into two distinct groups separated by the highway.

Overall the utility of this research is to provide JBER wildlife managers with guidelines as they are requested to rank development projects. The JBER moose population is highly adapted to the urban landscape, but maintaining this will require providing enough high quality, nutritionally dense forage as well as with areas for cover. The shapefile provided in the Master's thesis by J. Welch will enable managers to visually assess development impacts.

The travel paths used by moose in this study are identified in the Master's thesis proposal of D. Battle. While his degree work is not complete at the time of this writing, he has calculated potential path areas (PPAs) for all moose in the study.

There are multiple reports that resulted from this research. They are appended to this executive summary as stand-alone appendices; however each has an abstract identified in the table of contents. By sectioning the information into discrete appendices it allows the reader to focus quickly on the on the area(s) of interest.

This project involved assistance from biologists from the Alaska Department of Fish and Game, from JBER, and from several graduate students and one post-doctoral appointment. The disparate theses, manuscripts, and raw data are included in this document.

The wolf component of the project was stopped early in the process. The resident wolf packs on JBER had exhibited dangerous behavior relative to people recreating on base and there had been numerous incidents of wolves trailing people, attacking dogs, and in one case, actually driving people up trees. Consequently authorities instituted a control program and effectively removed wolves from JBER lands, which also removed wolves from this research program.

Acknowledgements

The funding for this work was provided by Elmendorf Air Base and Fort Richardson Army Post when separate institutions. During the study the bases were combined into Joint Base Elmendorf Fort Richardson (JBER). The Elmendorf Wildlife Agents program, including multiple airmen volunteering their time, assisted with captures and radio tracking. Numerous biological technicians from JBER, especially Richard Graham, assisted with captures and radio tracking, and recovered collars from all areas on and off the base. Alaska Department of Fish and Game biologists Rick Sinnott, Jesse Coltrane, and Tony Carnahan provided invaluable local knowledge and capture assistance. Graduate students Joe Welch and Dave Battle were able to incorporate section of the study into their Master's theses and thereby help produce a quality research product.

Key Research Accomplishments

Nutritional ecology of moose.

Master's thesis by J. Welch. Joint Base Elmendorf-Richardson (JBER), Alaska supports a large population of moose that lives in and around the urban and industrial development of Anchorage. This study evaluates the body condition of adult female moose on JBER and calculates the relative nutritional value of habitat for planning development and for mitigating the effects of development on this population. Body condition of moose on JBER was similar to that of other populations of moose in Alaska. Our nutritional model predicted that shrublands could support 11-81 times more moose than any other habitat on JBER. Activity patterns of JBER moose were similar to those published for non-urban moose, indicating habituation to human activity. Activity levels increased as moose moved through higher quality habitats. Sustained production of this heavily utilized population requires maintaining shrublands in undeveloped portions of the base where moose-vehicle collisions can be minimized. See Appendix A

Resource Selection function analysis by West, inc.

Moose habitat selection patterns within the study area varied among individuals. The level of fragmentation that exists within the study area may have limited our ability to identify covariates that were most influential to the average moose. However, we did develop predictive maps that provide managers with information that details the varying degrees of use within the study area. These areas can be incorporated in future development plans to limit negative impacts on moose habitat. Although the barren landcover type was the most common landcover class within the study area, moose appear to strongly avoid barren areas. In addition, moose appear to avoid areas of grass landcover classes within the study area. On the other hand, moose appeared to select for habitats with a high density of shrub cover.

The movement model accurately assessed moose states (traveling or encamped) during the winter and summer periods, but had difficulty assigning state to movements with large leg lengths. While some states with large leg lengths could have miss-categorized, the overall effect of these miss-categorized movements on the overall habitat selection patterns is likely very small.

We assessed habitat selection at a very fine scale (meters and hourly intervals), while the habitat covariates that we considered were derived at a larger landscape scale. This difference in scale may have limited our ability to detect consistent habitat selection patterns among individuals. Because the study area is a highly fragmented landscape, moose are likely selecting specific habitats at a very small scale (i.e., a very small shrub patch that is surrounded by buildings or forest) and the habitat covariates we considered may not have captured these potential features. Overlaying the nutritional predictive model with the estimates from the habitat selection model might provide further insight into the selection patterns of moose within the study area. See Appendix B

Investigation of the genetic health of JBER moose

The two manuscripts presented here have been submitted for publication in peer-reviewed journals. They are the result of investigations by post-doctoral associate, Dr. R. Wilson.

The over-riding question for his work was to assess the effect (if any) of anthropogenic structures such as the Glenn highway on the population structure of JBER moose and the degree of relatedness between JBER moose and other populations. Kenai Peninsula moose were chosen as a comparative population. The work reflects consideration of moose population genetics at the fine scale of local populations (JBER alone) and at the landscape scale spanning from the Kenai Peninsula to moose in the Anchorage bowl (which includes JBER east of the Glenn highway.

JBER moose population genetics show evidence of subdivision between east and west of the Glenn highway, indicating that over time the numbers of animals on each side likely will not be augmented by immigration, but sustained by internal population demographics. This is more likely for the west side which is more isolated than the eastern portion of JBER in communication with the Anchorage bowl.

The degree of structure found on JBER is not a management problem at present, and may not become one. However the amount of subdivision identified is significantly greater than that measured in a contiguous moose population on the Kenai Peninsula. See Appendix C

Movement characteristics and potential path area (PPA) of JBER moose and black bear.

The objectives of this work are related to movements of moose and black bear on JBER. The final product will provide managers with a ranking of moose habitat by behavior patterns and movement characteristics. Each moose GPS collar was built with a tri-axial accelerometer collecting vector data on movements, in addition to location. Habitat types will be ranked by behaviors and movement characteristics to identify those habitat types important to moose. The potential path areas identified for each moose will be used to identify possible movement corridors which likely maintain habitat connectivity.

These data on moose behaviors, movement characteristics, and potential connectivity will assist JBER wildlife managers if they need to direct moose movements through habitat and landscape modifications.

Potential Path Area analysis of black bear locations is complete and representative maps are attached below. A resource selection function analysis of the black bear data, shaped by the location data of known JBER bear conflict zones, is being conducted. The final result will enable managers to focus on eliminating discrete pockets of attraction to black bears.

Taken together, the moose movement data will allow researchers to identify the following:

1. Can tri-axial accelerometers distinguish between the behaviors of browsing, grazing, walking, standing, and lying? Captive animals were used for this portion of the work and the results are summarized in appendix D. As constructed, the Telonics, the tri-axial accelerometers are not capable of distinguishing behavior other than walking, running, and remaining still. The clearest behavioral distinction is between active and inactive. The results of the captive animal trials are summarized in Appendix D, page10-21.

2. Moose movement data and characteristics of travel (i.e., turning angle, speed, density of locations) have been calculated and are being ranked by presence across moose habitat. The student will characterize each habitat type by behavioral value.

3. The winter (Dec.-Feb) and summer (June-Aug) home ranges of moose have been calculated using the Potential Path Areas. The student is using the PPA data to look for travel corridors on JBER. Preliminary maps are below. See Appendix D

Reportable Outcomes

Battle, D. Movement patterns and use of the landscape by female moose on Joint Base Elmendorf-Richardson, AK. MS thesis, Colorado State University, Fort Collins, Colorado, In progress.

Battle, D., T. Carnahan, and S. Farley. 3013. Moose Research and Management. Poster presented at the 2013 national meeting of the Ecological Society of America.

Carnahan, T. ,D. Battle, S. Farley, and J. Coltrane. 2013. Brown and Black Bear Movement and Behavior Studies. Poster presented at the 2013 national meeting of the Ecological Society of America.

LaBeau, C., T. McDonald, and B. Augustine. 2014. Moose Habitat selection within Joint Base Elmendorf-Richardson, Anchorage, Alaska. 36 pp. Report prepared for Sean Farley, Alaska Dept. Fish and Game.

Welch, J.W. Nutritional ecology of moose in an urban landscape. MS. Thesis. University of Fairbanks, Fairbanks, Alaska. 117pp. completed

Wilson, R.E., S. D. Farley, T. J. McDonough, S. L. Talbot, and P. S. Barboza. (Accepted). A Genetic Discontinuity in Moose (Alces alces) in Alaska corresponds with fenced transportation infrastructure. Conservation Genetics.

Wilson, R.E., T. J. McDonough, P.S. Barboza, S. L. Talbot, and S.D. Farley. (submitted) Population Genetic Structure of Moose (*Alces alces*) of south-central Alaska. Alces.

Conclusion

The nutritional model has provided the means to construct shapefiles that enable mangers to identify potential habitat changes by effect on moose numbers. The landscape on JBER is (in places) highly fragmented and it appears the moose in those habitats have been able to specialize on very small, discrete patches. The high degree of fragmentation makes the use of resource selection functions problematic and difficult for identifying important habitat. The fragmentation, coupled with the presence of a large highway bisecting JBER moose habitat, has effectively created barrier to the migration of moose, which in turn is leading to the development of genetically separate moose populations. At the time of this writing this schism does not appear to have ecological ramification for the health of the moose, however there are differences in the degree of relatedness which are not evident is moose populations without a highway bisection.

Black bears are an ongoing problem animal for JBER authorities and over the course of this study intensive effort was applied to remove attractants on JBER. Additional research on the JBER black bear dataset will include application of resource selection functions to identify further attractant sites that existed during the time of collaring. Similarly to moose, the highly fragmented landscape, coupled with a black bear's ability to easily exist in urban or wild areas, implies that most of JBER is acceptable black bear habitat if food attractants are present. Once those attractants are removed the bears will likely be present in low densities only.

Appendix A

NUTRITIONAL ECOLOGY OF MOOSE IN AN URBAN LANDSCAPE

By

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NUTRITIONAL ECOLOGY OF MOOSE IN AN URBAN LANDSCAPE

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements
for the Degree of

MASTER OF SCIENCE

By

Joseph H. Welch, B.S.

Fairbanks, Alaska

August 2012

Abstract

Joint Base Elmendorf-Richardson (JBER), Alaska supports a large population of moose that lives in and around the urban and industrial development of Anchorage. This study evaluates the body condition of adult female moose on JBER and calculates the relative nutritional value of habitat for planning development and for mitigating the effects of development on this population. Body condition of moose on JBER was similar to that of other populations of moose in Alaska. Our nutritional model predicted that shrublands could support 11-81 times more moose than any other habitat on JBER. Activity patterns of JBER moose were similar to those published for non-urban moose, indicating habituation to human activity. Activity levels increased as moose moved through higher quality habitats. Sustained production of this heavily utilized population requires maintaining shrublands in undeveloped portions of the base where moose-vehicle collisions can be minimized.

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Acknowledgments

Completion of my thesis would not have been possible without the help and guidance of many people. Most importantly, I would like to thank my adviser, Dr. Perry Barboza. The knowledge I have gained from him and the lessons he has taught me are invaluable. I truly learned from the best, and know I'm a better scientist because of his guidance. I also thank Dr. Sean Farley at the Alaska Department of Fish and Game, who essentially worked as a co-adviser on this project. My other two committee members, Dr. Don Spalinger and Dr. Kris Hundertmark gave critical input for the development of my study, and data analysis. Their expertise in moose nutrition and ecology was an irreplaceable asset to me. I thank you all for your guidance and assistance.

I would also like to give a big acknowledgement to Dave Battle. We both studied the same moose population for our Master's programs. I've really enjoyed working alongside him, and my thesis wouldn't be what it is today without his help.

Many thanks go out to all the employees at Fish and Game that have helped me along the way, namely Jessy Coltrane and Rick Sinnott, who were a formidable moose darting duo, Liz Solomon, who helped a lot with GIS and databases, and Bill Collins, who ran all of my digestion trials.

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At the University of Alaska-Fairbanks, I must acknowledge all of my professors that have taught me so much during these last few years. I must also thank all of the support staff at the Department of Biology and Wildlife and the Institute of Arctic Biology for helping me blunder through paperwork, payroll, travel, pro-cards, and any other miscellaneous things I needed help with. During my years in Alaska, I have also met many wonderful people that have provided great support for, or a good excuse to get away from, my thesis. I'm sure some of us will be lifelong friends.

And last, but not least, I would like to thank my family. I really appreciate how understanding you all have been about my spotty communications and infrequent trips back home (I'm planning on turning that around now that this thesis is completed). However, I was fortunate enough to move to Alaska and still have close relatives up here to spend holidays and weekend adventures with, and even share a house for 12 months with.

CHAPTER 1: INTRODUCTION

1.1 Why Study Nutrition of Moose?

Moose (*Alces alces*) in Alaska are managed for many user groups including recreational hunters, subsistence hunters, and wildlife viewers. Moose are a valuable game species in Alaska, with an estimated net worth of $28 million in 2005 (consumptive and non-consumptive value, minus the cost of property damage and bodily injury) (Northern Economics Inc. 2006). However, increasing human encroachment and development of habitat may reduce and alter the distribution of resources for moose. Human activities also alter moose behavior and movements (Andersen et al. 1996, Neumann et al. 2009, Støen et al. 2010). Ultimately, changes in food availability and moose behavior could decrease nutritional condition and fitness of individuals and reduce the number of moose on the landscape. Therefore, understanding the ability of the landscape to support the nutritional needs of moose is critical for effective management of moose populations.

1.2 Nutritional Requirements of Moose

Moose are the largest members of the Family Cervidae. Large body size is accompanied by large absolute demands for energy and nutrients in the diet. Demands include the nutrients and energy needed for basal metabolism, thermoregulation, activity, growth, and reproduction (Barboza et al. 2009). At a minimum, moose must meet requirements for basal metabolism to sustain body function for survival. In winter, the cost of locomotion through snow can be high (Parker et al. 1984) and food is scarce and low in quality (Crête and Jordan 1982, Oldemeyer et al. 1977, Renecker and Hudson

1985, 1988). To reduce costs, moose decrease basal metabolic rate (BMR; Regelin et al. 1985, Renecker and Hudson 1986), but must burn fat and protein stores to provide the additional energy needed to survive winter (Schwartz et al. 1988). Moose build stores of fat and protein in summer and autumn when forage is abundant and relatively high in quality to increase body mass by 25% to 43% at the start of winter (Schwartz et al 1987). To reproduce, female moose must have adequate stores to support the added 3% cost of gestation over BMR in winter (Keech et al. 2000, Testa and Adams 1998). Females that give birth must support the added energy and protein demands of lactation during summer, which may reduce their ability to build body stores before the following breeding season. Therefore, moose that lactate in summer can have reduced pregnancy and twinning rates the following year (Testa and Adams 1998). Energy and nutrient intakes necessary to meet requirements can be calculated as sum of costs for maintenance of the body and for reproduction. Given nutrient availability in habitats, the theoretical number of moose for which requirements can be met can also be calculated from a nutritional model.

1.3 Nutrient Availability on the Landscape

Nutrient availability is a function of forage abundance and quality. Greater than 60% of the diet of a moose is usually composed of fewer than 6 items across their range (Shipley 2010). Diets are of substantially higher quality in summer than in winter (Renecker and Hudson 1985). Protein and energy are generally considered to be the most limiting nutrients for moose (Barboza et al. 2009, Wallmo et al. 1977). Forage dry matter contains 6% to 7% protein in winter and 12% to 21% protein in summer (Renecker and

Hudson 1985). Similarly, digestible dry matter (DDM), and therefore digestible energy (Barboza et al. 2009), is typically lower in winter (44% to 52% DDM) than in summer (64% to 65% DDM; Renecker and Hudson 1985). Forage quantity is also much greater in summer when leaves and forbs are abundant. Forage abundance varies among habitats to provide a wide distribution of available energy and protein for the daily demands of moose across the landscape.

1.4 The Effect of Food on Movements of Moose

Food distribution also affects how moose move on the landscape. There are many conflicting results in the literature regarding the response of moose to variable habitat and diet quality. High browse density has been correlated not only with increased activity and increased diet selectivity (Vivas and Saether 1987), but also with decreased activity (Dussault et al. 2005). Low browse density has been shown to decrease distance travelled and decrease diet selection (Saether and Andersen 1990), but low browse density may also increase search time and distance travelled (Risenhoover 1987). Foraging patch shape and distribution also alter the foraging behavior of ungulates (Etzenhouser et al. 1998). These variable responses to food resources by moose are not likely due to sampling design issues, but rather reflect responses specific to each population.

1.5 Effects of Urbanization on Moose

Populations of urban moose must meet their nutritional requirements for survival and reproduction in fragmented landscapes with many forms of disturbance. Development such as roads, buildings, parking lots, and agricultural fields, has the negative effects of removing, altering, and fragmenting habitat. Development may also have positive effects. Clearing land sets back succession, creating preferred high-quality shrubby areas along roads, power lines, railroads, backyards, and abandoned lots (Rea et al. 2010, Weixelman et al. 1998). Because of the dynamic nature of the landscape, it is of utmost importance to understand how moose populations in these conditions will respond to changes in food resources.

Urban areas that include shrublands can attract moose and lead to conflicts with humans. Urban communities must contend with threats to life and property from collisions between moose and vehicles, aggressive encounters with moose, and damage to cultivated plants by moose (Child et al. 1991, Dussault et al. 2007, Garrett and Conway 1999, Sinnott 2008, Young 2008). Human activities can affect the behavior of moose especially when humans approach moose on foot, skis, and recreational vehicles (Andersen et al. 1996, Neumann et al. 2009, Støen et al. 2010). Human disturbances may therefore alter foraging times and locations to reduce nutrient intakes while increasing the cost of movement to potentially reduce the energy and protein available for survival or reproduction.

1.6 Study Objectives

Over 300,000 people live on Joint Base Elmendorf-Richardson (JBER) and Anchorage, Alaska (U.S. Department of Defense 2012, U.S. Census Bureau 2010). The moose population in Anchorage area has increased over the past 70 years (Sinnott 2008) even though the human population has grown exponentially from 3,495 people to over 226,338 people during the same period (Gibson and Jung 2005). Currently, moose are common in urban areas and in the adjacent public forests. However, as development increases on JBER and more habitat is developed, the condition of individual moose and the size or productivity of the population may decline. For instance, how will developing an early successional shrubland located in an undeveloped portion of the base impact the number of moose the area can support? Also, how might moose change their movements to access other food resources? My objectives for this study were to determine: 1) the relative nutritional value of habitats; 2) the relative nutritional condition of this moose population compared to others in Alaska; and 3) the potential effects of habitat and diet quality on moose movements in this fragmented, urban landscape.

In chapter 2, I will address the question: what is the relative nutritional value of habitats found on Joint Base Elmendorf-Richardson? To accomplish this, I measured animal body condition, reproduction, plant and diet quality, and available biomass of forages in different habitats. These results were used to build a model comparing nutrient requirements of adult female reproductive moose, to nutrient availabilities in habitats. Results from chapter 1 can be used for land management plans and mitigating adverse effects of development on the population. Results from chapter 1 will also provide baseline data on the body condition of females in this population to monitor productivity and manage harvests.

In chapter 3, I examine the relationship between movement of individual moose and the quality of their diet and habitat. Chapter 2 also compares activity patterns of urban moose in Anchorage and JBER with those of non-urban populations of moose. This thesis examines how moose move and forage through a mosaic of habitats of varying quality. My results can be used to modify and increase the accuracy of foraging models or help remediate conflicts between moose and humans.

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CHAPTER 2: BODY CONDITION AND THE NUTRITIONAL VALUE OF HABITAT FOR URBAN MOOSE[1]

2.1 Abstract: We studied adult female moose (*Alces alces*) on Joint Base Elmendorf - Richardson near Anchorage, Alaska. This population of moose lives in and around both urban and industrial development and is exposed to natural predation and an annual hunter harvest of 7-16%. Rump fat depths in November ($\bar{x}$ = 3.0 cm, SE = 0.3, n = 24) and March ($\bar{x}$ = 1.1 cm, SE = 0.1, n = 31) were consistent with pregnancy rates that ranged between 85 and 100%. Microhistology of composite fecal samples indicated that willows (*Salix* spp.) dominated the summer diet, whereas the winter diet was divided among willows, birch (*Betula* spp.), and cottonwood (*Populus balsamifera*). We modeled energy and nitrogen demands to project the relative value of habitats in units of moose-days. Low concentrations of available nitrogen in stems limited the number of moose-days in winter whereas energy and digestible dry matter of leaves were more limiting than nitrogen in summer. The shrubland habitat type was the most valuable habitat for moose because it could theoretically support 11– 81 times more moose per hectare. Therefore, sustained production of this population is dependent upon maintaining shrublands.

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2.2 Introduction

Urban and industrial developments of habitats alter the behavior and distribution of ungulates (Cameron et al. 2005, Chetkiewicz and Boyce 2009, Laurian et al. 2008). Populations of ungulates may increase and become densely populated near urban areas that provide foraging opportunities and refuge from predators (Berger 2007, Côté et al. 2004, Harveson et al. 2007, Hebblewhite and Merrill 2009, McCullough et al. 1997). For moose (*Alces alces*), increasing foraging pressure on the landscape has negative effects on body condition, reproduction, and ultimately the number of animals the landscape can support (Ferguson et al. 2000, Franzmann and Schwartz 1985, Keech et al. 2000, Seaton et al. 2011, Testa and Adams 1998).

Although Anchorage is the largest city in Alaska, moose as well as their predators (black bears, *Ursus americanus*; brown bears, *Ursus arctos*; and wolves, *Canis lupu*s) use the adjacent public lands, as well as the greenbelts, parks, and yards within the urban areas. Moose are also common on Joint Base Elmendorf-Richardson (JBER; Fig. 2.1), a military base adjacent to Anchorage that has a long history of land development and military operations. The number of moose in Game Management Unit 14C (GMU 14C), which encompasses JBER and Anchorage, has increased since the 1940's as urban and industrial development increased in both area and intensity (Sinnott 2008). Moose densities in GMU 14C were 0.31 to 0.44 moose/ km^2 from 1998—2007 (Sinnott 2004, 2006, 2008). However, intensively developed land and alpine habitats concentrate moose in more suitable habitat. The physiography of the Anchorage bowl also concentrates moose in habitats at low elevations and in urban areas when animals attempt to avoid the deep snows at higher elevations in winter. Sinnott (2008) hypothesized the convergence of moose in these developed areas may exacerbate winter mortality due to vehicle collisions. He also proposed that moose overabundance may increase winter starvation especially in years when snow depths are high.

The military lands on JBER and the adjacent Ship Creek drainage contain only 27% of moose in GMU 14C, but provide 57% of the total harvest from this unit. Between 1998 and 2006, harvest rates on JBER and Ship Creek lands were high (7% to 16% of the population; Gasaway et al. 1992, 1983), and included a liberal antlerless harvest of 2% to 6% (Boertje et al. 2006) of the population (Sinnott 2004, 2006, 2008).

Managers on JBER desired to know more about the overall nutritional condition of this heavily harvested moose population and what the potential effects of JBER land development would be on the number of moose that could be supported. Our first objective was to determine body fat content, blood chemistry values, and reproductive rates for comparison with other populations in Alaska. Our second objective was to determine the nutritional value of habitats in this area. We modeled energy and nitrogen demands for reproductive female moose to project seasonal rates of food intake. We assessed the relative nutritional value of habitats as reflected by the hypothetical number of animal units (AU; moose-days per hectare) the habitats could support in three seasons. Our model was used to develop a map of the distribution of AU on military land and to model impacts of potential land planning decisions in this large area with multiple users.

2.3 Study Area

JBER is a 30,400 ha military installation adjacent to Anchorage, AK, U.S.A (61.25°N, 149.75°W) with a climate transitional between the maritime Gulf of Alaska and the continental interior. Average daily air temperatures were mild for Alaska at +16°C and +14ºC in July 2009 and 2010, respectively, and -7.5°C in January 2010 (Alaska Climate Research Center 2012). Average annual precipitation was 40.1 cm, of which 58% is rainfall between July and October (Western Regional Climate Center 2011). Compared to the mean precipitation from 1971 to 2000, rain was 28% below normal for May—Aug 2009, snowfall was 1% below normal for November 2009–March 2010, and rain was 12% above normal for May to August 2010 (Natural Resources Conservation Service 2012).

Approximately 40% of the study area consisted of undeveloped lands more than 0.5 km from a road. Development was localized in the central part of the base. This central developed area (Fig. 2.1) was 28% of the study area and consisted of housing, office buildings, warehouses, storage lots, runways, golf courses, and firing ranges that were interspersed with greenbelts and small (< 0.25 ha) to large (> 25 ha) woodlands. These woodlands were comprised of birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and black cottonwood (*Populus trichocarpa*). Shrubs included willow (*Salix* spp.), alder (*Alnus* spp), and high-bush cranberry (*Viburnum edule*).

Most of the study area (66% or 19,900 ha) was woodland (mixed, deciduous, coniferous, and shrub) that ranged from recent (< 5 yr) burns or clearings to climax communities without signs of recent logging or fire (Fig. 2.2A). Communities of birch and spruce dominated the mixed forests (91% of 9,083 ha) whereas birch stands dominated deciduous forests (66% of 5,341 ha). Conifer forests were 44% (835 ha) white spruce, 24% (454 ha) black spruce, and 32% mixed black and white spruce or mountain hemlock (*Tsuga mertensiana*). Shrublands were nearly equally dominated by alder or willow (45% and 55% of 3,580 ha respectively). The majority of willow shrublands were early successional hardwoods (55% of 1,969 ha) that were created by fire and clearing. Grasslands (2,509 ha) included developed areas such as sports fields and golf courses as well as recent burns and clearings. Alpine tundra along the eastern boundary of the study area accounted for most of the barren habitat (63% of 5,312 ha). Wetlands colonized by low growing shrubs were a minor proportion of the total wetland habitat (36% of 905 ha).

2.4 Methods

2.4.1 Animal Capture, Measurements, and Sample Collection

We studied animals under approved protocols for animal care and assurance from Alaska Department of Fish and Game (#90-05) and from the University of Alaska Fairbanks (#148885, 182744). We captured adult female moose in March 2009 (*n* = 7) and Nov 2009 (*n* = 12) within 0.5 km of roads, often in or adjacent to the central developed area. We darted all moose from the ground with a 3 cc dart containing a mixture of 3.0 to 3.9 mg carfentanil (carfentanil-citrate, Wildlife Pharmaceuticals, Fort Collins, CO) and 100 mg xylazine (xylazine-hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO). We cleaned dart wounds with a 0.1% providone-iodine solution and filled the wound with antibiotic ointment (0.2% nitrofurazone, Squire Laboratories, Inc., Revere, MA) to reduce risk of infection. A prophylactic dose of 600 to 5,000 mg oxytetracycline (Oxytet, Norbrook, Lenexa, NJ) was also administered intramuscularly at the rump. We placed moose in sternal recumbency to monitor anesthesia and collect samples. A single intravenous dose of 20 to 60 mg Dopram (doxapram hydrochloride, Baxter Healthcare Corporation, Deerfield, IL) was administered when poor perfusion was apparent as discoloration of gums and lips. Anesthesia was reversed within 30 minutes of darting by intravenous injection of 400 mg Naltrexone (naltrexone-hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO) and 800 mg Tolazoline (tolazoline-hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO).

Maximum depth of subcutaneous rump fat was measured by ultrasound using a Tringa Linear portable ultrasound (Esaote Group, Genova, Italy) along a transect from the spine, at the closest point to the coxal tuber (hip bone), to the ischial tuber (pin bone) (Stephenson et al. 1993, 1998). Shoulder muscle depth was measured via ultrasound from a point 5 cm cranial of the posterior process of the scapula. Jaw length was the linear distance from base of the gum line of the incisors to the posterior angle of the mandible. Leg length was the linear distance from tip to base of the metatarsus when the limb was retracted and aligned with the torso. Blood was collected from the jugular vein into glass tubes without additive (serum) and with lithium heparin (plasma) (Vacutainer, Becton Dickinson, Franklin Lakes, NJ). We insulated blood samples to prevent freezing in the field for up to 8 h from collection. Blood was centrifuged at 3000 x g and stored at -20° C for analysis. We collected fecal pellets directly from the rectum or sampled from a pellet pile defecated during the capture.

We equipped moose with Global Positioning System (GPS) store-on-board collars (Telonics, Inc. Mesa, AZ) programmed to record a location every 30 or 60 min. GPS collars were equipped with very high frequency (VHF) transmitters. During the annual calving period (May 15 - 30), we attempted to relocate females each day to determine if a parturition event occurred. We estimated twinning rates as the proportion of calving females observed with twins. We attempted to monitor calves twice a month through August for survival. We recaptured animals in March and November of 2009, 2010, and 2011 to recover location data stored on collars and to record body condition and pregnancy status.

2.4.2 Blood Analysis

We analyzed blood serum with Heska Fujifilm DRI-CHEM® Analyzer (Heska Corporation, Loveland, CO) to determine concentrations of blood urea nitrogen (BUN), creatinine, phosphorus, calcium, total protein, albumin, globulin, glucose, cholesterol, gamma glutamyltransferase (GGT), alanine aminotransferase (ALT), alkaline phosphatase (ALP), and total bilirubin. We evaluated pregnancy rates with Pregnancy Specific Protein B (PSPB; Bio-Tracking, Moscow ID) and progesterone (ELISA kit; Cayman, Ann Arbor MI).

2.4.3 Habitat Types

We used 1:20,000 high-resolution (~10 m) ecotype shapefiles to determine moose habitat types in ArcGIS 10 (ESRI Inc, Redlands, CA). Ecotype shapefiles were delineated by hand in GIS with the aid of orthorectified aerial photography, false color infrared (CIR) photography, a Landsat Thematic Mapper (TM) image, and 1:12,000 CIR hardcopies (Jorgenson et al. 2003). Vegetation data from 231 survey plots were used to classify ecotypes (Jorgenson et al. 2003). The study originally delineated 54 vegetation classes that we grouped into 7 habitats based on the original vegetation class descriptions (Appendix 2.1; Jorgenson et al. 2003). We grouped forested (>25% tree cover) classes as: deciduous forests (dominated by only deciduous trees), mixed forests (co-dominated by deciduous and conifer trees), and conifer forests (dominated by only conifer trees). We grouped non-forested habitats as: barrens (alpine tundra, pavement, floodplains, mudflats, landscaping, sites with <30% ground cover, open water); shrublands (willow, alder, and seral scrub communities); shrubby wetlands (bogs and wetlands commonly containing an understory of sweetgale (*Myrica gale*), *Salix* spp., and *Betula* spp.); and grasslands (wetland and upland graminoid vegetation classes lacking a shrub understory. Open black spruce vegetation classes were classified as either shrubby wetlands or conifer forests depending on habitat characteristics: stands with a boggy substrate with intermixed shrubs were classified as shrubby wetlands, and stands with a non-boggy substrate in more upland zones were classified as conifer forests. We verified habitat units near roads and development on the ground to confirm or update the classification.

2.4.4 Biomass Estimation

Plants identified a-priori as probable moose browse included *Betula papyrifera*, *Populus tremuloides, Populus balsamifera/trichorcarpa* (hereafter simplified as *P. balsamifera*), *Viburnum edule, Salix barclayi*, *Salix bebbiana, Salix pulchra*, *Salix glauca, and Salix scouleriana.* We estimated total available current annual growth (CAG) stems and leaves for moose browse at the end of the growing season in August 2009 and 2010. Biomass was estimated in five randomly selected plots in conifer forests, deciduous forests, grasslands, mixed forests, shrublands, and shrubby wetlands (total $n = 30$). We assumed that barrens had no available biomass. GPS coordinates of plot centers were randomly generated in GIS. Plot radius was 15 m for most sites; however, we used a smaller survey radius of 5 or 10 m when biomass of a forage species was very high and evenly distributed across the plot.

Similar to Seaton et al. (2011), we used a random sample of 30 stems per species to estimate average stem basal diameter. We randomly selected at least 3 individual plants and no more than 10 CAG stems per plant for measures of basal diameter, until 30 stems were sampled for each species per plot. We used the 30 basal diameter measurements for each species to calculate the average basal diameter of stems in each plot. We counted the total number of CAG stems and leaf clusters (any leaves or leaf groups not originating from a CAG stem) 0.5 - 3.0 m above ground for each species in each plot. This range corresponds to the normal browsing height of Alaskan moose (Seaton et al. 2011, Weixelman et al. 1998).

Sample stems with leaves, as well as leaf clusters were brought back to the lab for measurements. We measured stem basal diameter and then dried stems and leaves at 100° C for 24 h to determine dry biomass. Data were used to establish relationships of dry stem and leaf biomass to basal diameter and to determine mean leaf cluster biomass (Appendix 2.2; Oldemeyer 1982, Seaton et al. 2011). Stem biomass was square-root transformed (Zar 1999) to meet assumptions of normality and homogeneity of variance for linear regression. We estimated the average total available CAG biomass of moose browse in each habitat from our stem and leaf cluster count and our estimated biomass from the stem diameter-biomass relationships and the mean stem diameter of each species in each plot. We assumed that CAG leaf and stem biomass reflected availability of summer forage and that CAG stem biomass indicated winter forage availability.

2.4.5 Forage Collections

We used two approaches to collect representative samples of forages used by moose. In 2009, we selected a random sample of 20 forage sampling sites, stratified by total area of each habitat type (Fig. 2.3). In 2010 and 2011, we collected forage samples based upon locations of individual collared animals (Fig. 2.3). We located moose from a road or trail via radio-telemetry. If radio signal strength indicated the animal was more than 250 m away then a straight line transect to the animal was walked and we collected forage samples along the transect until the moose was sighted, at which time we collected samples in a 100m radius around the animal. If radio signal strength indicated the animal was within 250 m of a road or trail, we collected samples only in a 100 m radius around the animal.

We collected up to 200 g of each forage species in 4 seasons: spring (20 May), early summer (20 June), late summer (15 August), and winter (1 January). During the growing season, we tried to mimic leaf stripping by moose to collect both leaves and new growth stems. Winter samples were only collected in 2010 while spring and summer samples were collected in 2009, 2010, and 2011. Samples were frozen on dry ice in the field and stored at -20º C until analysis.

2.4.6 Forage Nutritional Composition Analysis

Forage samples were freeze dried, ground through a Wiley mill (Thomas Scientific, Swedesboro, N.J.) with a 20 mesh (1.2 mm) screen, and stored at room temperature until analysis. Only plant species commonly found in our moose diets were analyzed. We determined total nitrogen with a LECO TruSpec CN analyzer (LECO Corporation, St. Joseph, MI). We sequentially extracted detergent fiber fractions by methods of Van Soest et al. (1991) as described by Peltier et al. (2003). We extracted neutral detergent fiber (NDF) from 1.0 g of sample sealed in polyester bags (F57 25µm pore size, Ankom Technology, Macedon, New York, USA). We extracted acid detergent fiber (ADF) from the NDF residue. We conducted extractions in Ankom^{200} Fiber Analyzers (Ankom Technology, Macedon, New York, USA). We determined the N concentration of the ADF (ADFN) by analyzing a subsample of the ADF for total N.

We measured *in sacco* digestibility with two adult female fistulated moose housed at the University of Alaska Fairbanks Experimental Farm in Palmer, Alaska, USA (Spalinger et al. 2010, Tilley and Terry 1963). We sealed ground samples of 0.50 — 0.75 g in 5 cm x 15 cm polyester bags (50 µm pore size, Ankom Technology, Macedon, New York, USA) and suspended the bags in the rumen for 30 h (summer forage) or 45 h (winter forage). We rinsed bags and gently massaged under cold water to remove debris then dried to constant mass at 55° C. The proportional loss of dry mass from the sample was the apparent digestibility. We assumed digestible dry matter (DDM) to be equivalent to apparent digestibility. We extracted i*n sacco* residues in neutral detergent to determine digestible NDF (DNDF) content (Goering and Van Soest 1970, Spalinger et al. 2010). We used the same ground *Betula* mixture as Spalinger et al. (2010) for comparison of NDF digestibility between our study and theirs.

We measured phenols according to Singleton et al. (1999) by extracting 0.1 g of ground sample in 5 ml of acetone at 25° C for 30 min in a sonic bath. We reacted extracts with Folin—Ciocalteu Reagent (Fischer Scientific, CAT NO 195186, MP) to measure absorbance at 765 nm against standard solutions of gallic acid in acetone. We expressed phenol concentrations of samples as mg gallic acid equivalents on a dry matter basis.

2.4.7 Diet Determination

Sample collection and initial forage identification.—We collected fresh fecal samples during moose captures (n = 39), and while conducting other field work (n = 90) from January 2009 through March 2010. We prepared composite fecal samples by combining an equal number and mass of fecal samples from each habitat. We used 2 random samples per habitat in winter (n = 10) and 1 random sample in the growing seasons (n = 5) per composite. We used fewer samples in the growing season because of a smaller pool of available samples. We used the composite fecal samples to estimate diet in spring, early summer, late summer and winter. We analyzed composite fecal samples by microhistology (200 views per sample) at the Wildlife Habitat and Nutrition Laboratory (Washington State University, Pullman, WA). Microhistology identifies plant fragments in the feces. Plant fragments were identified by comparing the physical properties of plant fragments to reference samples of plant species. Results were reported as the proportion (0% - 100%) of total plant fragments counted for each diet item. Microhistology identified fragments of stems and leaves of P. *balsamifera, P. tremuloides*, *B. papyrifera*, *V. edule* and *Chamerion angustifolium* (fireweed) to species. We identified leaves to species for *Salix barclayi, S. bebbiana, S. pulchra,* and *S. scouleriana*. *Salix* stems could only be identified to genus. We assumed that *Salix* stems would be browsed at the same rate as *Salix* leaves, so the proportion of *Salix* stems reported in a fecal sample was allocated to the respective proportion of leaves for each *Salix* spp. Forages identified to functional groups were fern, fern rhizome, and grass. *Equisetum* spp. (horsetail) was identified to genus. We classified all other forages as either other shrubs or other non-shrubs. Since animals consumed both stems and leaves during early and late summer, we combined proportions of stem and leaf fragments, by species, to provide diet estimates for *Betula papyrifera, Populus tremuloides*, *P. balsamifera*, and *Viburnum edule*.

Estimating diet proportions with differential digestibility corrections. — A more accurate estimation of the diet requires that each plant's contribution to the diet, as determined by microhistology, be corrected for digestibility (Boertje 1984). We divided each plant's microhistology proportion by its respective indigestibility (1-DDM), and then standardized the results across entire fecal samples on a scale of 0-100%. There were no estimates of digestibility for two forage classes (other shrubs and other non-shrubs). For each fecal sample, we corrected the microhistology proportion of the other shrub habitat type by using the mean DDM for all shrub species, and we corrected the proportion for other non-shrub type using the mean DDM for all herbaceous species. Finally, because *Salix* stems could not be resolved to species in winter, we corrected the winter proportions of *Salix* stems in the feces by the DDM of the most abundant JBER *Salix* species (*S. bebbiana*). We estimated NDF, ADF, DDM, DNDF, phenol concentration, %N, and fiber bound N (ADFN) of the whole diet for each season (spring, early summer, late summer, and winter) from the individual proportions of plants in the diets and the nutritional composition of each plant.

2.4.8 Modeling Energy and Nitrogen Demands of Moose

To calculate the number of adult reproductive female moose each habitat could support, we first estimated energy and nitrogen demands of a reproducing moose using a factorial approach (Fig. 2.4, Appendix 2.3; Barboza and Bowyer 2001, Barboza et al. 2009). Estimates were for four points of time in winter (1 January: early and mid-pregnancy), spring (20 May; last trimester of pregnancy), early summer (20 June: peak lactation) and late summer (15 August: late lactation). During each season, we used the following steps to calculate demands for energy and protein.

Non-reproductive energy demands.—Demands for maintenance (i.e., survival) without reproduction included basal metabolic rate (BMR), activity, thermoregulation, and fat production (Appendix 2.3). We modeled total energy demand across a realistic range of body masses, based on measurements of minimum (328 kg), average (428 kg), and maximum (510 kg) body mass of female moose on the Kenai Peninsula (Schwartz and Hundertmark 1993). We derived seasonal changes in total body mass from estimates of fat mass. We used the average November rump fat depth (Rump = 2.97 cm) of moose from this study to calculate peak body fat content (BFat = 44 kg) using the relationship of Stephenson et al. (1998). We assumed that moose were still at peak condition by 1 January (Schwartz et al 1987a), but rump fat was exhausted by spring and through early summer (Rump = 0.0 cm, BFat = 12.36 kg, BM = 400 kg) when females were nursing calves. We assumed that moose regained 10% of their peak fat store by late summer as calves were weaned (BFat = 15.52 kg, BM = 400 kg). We based seasonal energy requirements on basal metabolic rate (BMR) of 306 kJ/kg$^{0.75}$ in winter (Schwartz et al. 1988a). We increased BMR by 40% (428 kJ/kg$^{0.75}$) to account for seasonal changes in maintenance metabolism of moose in spring and summer (Regelin et al. 1985). We calculated the daily change in body fat (kg/d) as the total change in fat mass over a season (kg), divided by the length of the season (late summer: 60 d; winter: 180 d). We equated daily changes in body fat to net energy at 39.3 kJ/g with an efficiency of 80% (Barboza et al. 2009). We subtracted energy gained from fat catabolism from energy demands in winter. The additional demand of activity and thermoregulation in each season was equivalent to BMR, and hence, the estimated field metabolic rate was 2 x BMR at maintenance (Barboza et al. 2009, Moen and Moen 1998, Robbins 1993).

Reproductive energy demands.—We added energetic demands for reproduction to those for maintenance during gestation (spring) and lactation (early summer; Appendix

2.3). We assumed that 80% of the neonate and the associated uterine tissues were deposited in the last trimester of a 231 d gestation (Barboza and Bowyer 2000, Schwartz and Hundertmark 1993). We calculated the total mass of neonates from the average birth mass for singletons (16.2 kg) and twins (13.5 kg each) and the twinning rate of moose in south-central Alaska (27%; Schwartz and Hundertmark 1993). We assumed birth mass to be 82% of the mass of the conceptus (Oftedal 1985). We calculated fat and protein content of the conceptus from relationships with whole body mass for reindeer and caribou calves (Gerhart et al. 1996). We calculated the equivalent investment of energy on the basis of 39.3 kJ/g fat and 23.7 kJ/g protein (Blaxter 1989). We calculated daily milk production from the daily milk intake (1820 kJ/kg$^{0.75}$), the average birth mass and the daily mass gain (785 g/d) of calves averaged over the first 30 days of lactation (Reese and Robbins 1994). We assumed that the conversion efficiency of energy from maternal tissues to fetus and milk was 80% (Blaxter 1989).

Seasonal energy demand and biomass intakes.—The sum of non-reproductive and reproductive demands was the net energy (NE, kJ/day) demand (Appendix 2.3). We used NE demands to estimate dry matter intake (DMI). First, we calculated the metabolizable energy (ME, kJ/day) of food by assuming that food energy was metabolized at an efficiency equal to 1-DIT, where DIT is diet induced thermogenesis (Barboza et al. 2009). We assumed that DIT was 0.3 when animals were expected to lose body mass (negative energy balance) during winter, spring and early summer, and 0.5 when animals were regaining mass in late summer (Blaxter 1989). We calculated total dry matter digestibility of the diet in each season as the sum of dry matter digestibility weighted by the proportion of each species in the diet. We used each season's diet dry matter digestibility to convert the seasonal ME demand to gross energy (GE, kJ/day) demand, after correcting for the proportion of ME lost in urine (0.062) and methane (0.031; Barboza et al. 2009, Schwartz et al. 1988b).

We derived estimates of total dry matter intake (DMI, kg/day) from calculated GE demands by assuming an average gross energy content of 18.83 kJ/g for forage (Appendix 2.3; Hjeljord et al. 1982). We calculated the seasonal DMI of each species by multiplying the total seasonal DMI by the proportion of each species in the diet (Fig. 2.4). We did not have biomass estimates for non-shrub forages, so we calculated adjusted DMI as the sum of the species-specific intakes for only browse. We assumed that browses were the limiting forages. Adjusted DMIs of browses alone were 30%, 74%, 85%, and 98% of the total DMI in spring, early summer, late summer, and winter respectively. Due to the low proportion of browse in spring diets, the number of moose supported in spring was not calculated.

Seasonal nitrogen demand and intakes.— The daily N requirement was the sum of endogenous urinary N (EUN, 0.056 g N/ kgBM$^{0.75}$; Schwartz et al. 1987b), metabolic fecal nitrogen (MFN, 5.536 g N/ kg DMI; Robbins et al. 1987) adjusted for available metabolizable dietary N, and N required for reproduction. We considered the proportion of unbound N in each season's diet (total N – ADFN) to represent the available metabolizable dietary N for each season. We used the adjusted DMI to calculate the adjusted N intake from shrubs. Adjusted demands were 45%, 87%, 86%, and 98% of the requirements estimated with the unadjusted DMI. The added demand of N for gestation was the daily deposition of N in the conceptus, estimated as 0.16 g N/g protein deposited. The N demand of lactation was the average daily production of milk with a N content of 0.157 g N/g milk protein (Reese and Robbins 1994). We assumed that maternal N was deposited in fetal and milk proteins without any loss in conversion from tissue (Barboza and Bowyer 2000).

2.4.9 Estimating Available Energy and Nitrogen in Habitats

To estimate the number of adult female moose each habitat could support, we also estimated available food biomass, energy, and N only for the shrub component of the diets of moose on the study area. The biomass densities (kg/ha) of all *Salix* spp., *Betula* spp., *Populus* spp., *Viburnum edule*, and other shrubs in each habitat were multiplied by the corrected dietary proportions to represent the utilizable biomass of each forage. We assumed biomass density of the other shrub category to be 10% of the total biomass of identified browse species because other shrubs were never greater than 10% of the total diet and 10% seemed a reasonable estimate in the field. Early summer biomass density was assumed to be 50% of late summer. The utilizable N in each habitat was calculated as the product of N density and corrected dietary proportions.

2.4.10 Calculating Animal Units

We divided the utilizable biomass or N (kg DM/ha or g N/ha) for each habitat by the adjusted intakes calculated from energy and nitrogen requirements (kg DM/day or g N/day). The result represents the number of reproductive female moose that could be supported per hectare of habitat per day (daily animal units; AU; moose-days/ha). Thus, for any region of JBER, we can multiply AU by the area (ha) of each of the 7 habitat types to calculate the total AU supported by that habitat. Total AU of each habitat can then be summed for the region (Fig. 2.4). Total AU were divided by the number of days in early summer (30 days), late summer (60 days) and winter (180 days) to estimate the number of AU that could be supported by each season.

2.4.11 Statistical Analysis

We estimated forage biomass and diet diversity with the Shannon-Wiener index (Krebs 1999). We estimated diet selection for woody browse in late summer and winter with Ivlev's Electivity Index and Strauss' Linear Index (Ivlev 1961, Strauss 1979). We assessed variation in the quality of plants with the coefficient of variation, defined as the standard deviation divided by the mean. To test for differences in plant quality, body condition by season, and forage biomass by habitat, we used analysis of variance (ANOVA) with a Tukey test for multiple comparisons between groups ($\alpha = 0.05$). We conducted statistical analyses in JMP Statistical Packages (version 9.0.02, SAS Institute Inc. Cary NC). We used ArcMap10 (ESRI, Redlands CA) for GIS maps and habitat manipulations.

2.5 Results

2.5.1 Forage Biomass and Diet

Mean biomass density by habitat ranged from 2.7 kg/ha to 380.7 kg/ha in summer and 1.4 kg/ha to 126.5 kg/ha in winter (Fig. 2.2). Shrublands provided the greatest mean biomass density of leaves (381 ± 344 kg/ha) and stems (126 ± 126 kg/ha) among all the habitats ($P < 0.01$). Shrublands were only 12% of the total study area but provided 72% of forage biomass (Fig. 2.2). Leaf biomass in shrublands was dominated by *Betula* spp. (37%), *Salix bebbiana* (36%) and *Populus balsamifera* (23%).

In 2009, we collected 253 samples of 32 species of potential forage items and in 2010 and 2011 we collected 258 samples of 24 plant species and 18 samples of 4 plant species, respectively for chemical analysis. The seasonal pattern of forage nutritional composition in this study area was similar to those described for moose in other areas (Hjeljord et al. 1990, McArt et al. 2009, Oldemeyer et al. 1977, Regelin et al. 1987, Renecker and Hudson 1988). Willows decreased in N from 1.7 – 2.2% to 1.0 – 1.2% and increased in fiber from 35.6 – 45.8% to 47.9 – 56.5% NDF between late summer and winter in our study area (Appendices 2.5, 2.6). At other sites in south-central Alaska, willow leaves declined from 2.2 to 1.0 % N and increased from 32.4 to 51.1% NDF over a similar time period (Oldemeyer et al. 1977). Variation in plant nutritional composition between sites reflect differences in age of plant, age of forest stand, local growing condition (e.g. temperature, shade, soil conditions), insect damage, and browsing intensity by moose and other herbivores (Pastor and Danell 2003, Regelin et al. 1987, Schwenk and Strong 2011, Spaeth et al. 2002, Weixelman et al. 1998). The coefficient of variation within seasons for individual species of *Salix* was 2 – 24 % for N, 0.4 – 17 % for NDF, and 0.1 – 21% for DDM. High variation in N fiber content, and DDM likely reflected the diverse growing conditions across our study area (Appendices 2.5, 2.6).

Absolute values for the concentration of N and fiber from plants in this study were similar to those of other studies for the same species (Oldemeyer et al. 1977, Renecker and Hudson 1988, Schwartz et al. 1988b, Spalinger et al. 2010, Weixelman et al. 1998). Measures of digestibility *in sacco* were difficult to compare because these estimates vary with plant phenology (e.g., N content), method (e.g., pore size of bag, duration of incubation, washing method) and the animal (e.g., individual, season, diet). Our estimate of NDF digestibility for the *Betula* mixture was 28 ± 3% and significantly greater than the expected value of 25 ± 4% ($P < 0.05$) established by Spalinger et al. (2010). Our method therefore may have overestimated the DDM of forages for moose in this area by up to 12%.

Diets differed seasonally (Appendix 2.7; Table 2.1). Shrubs dominated the diet of moose through most of the year (> 70%) except during spring when forbs accounted for an equal proportion of the indigestible particles in the feces (Appendix 2.7). However, when the diet was adjusted for digestibility, we estimated that forbs accounted for 70% of the diet in spring (Table 2.1). Diets were most diverse when moose were foraging on many types of forbs in the spring (Table 2.1). Willows were the predominant shrub in the diet throughout the year. In summer, *S. barclayi* and *S. scouleriana* were selected over other willows (Table 2.2) and accounted for 74% of the willow intake. Moose also selected *S. pulchra* (Table 2.2), but low abundance of this willow resulted in low proportions in the diet (Appendix 2.4; Table 2.1). The winter diet was dominated by equally high proportions of *Salix* and *Betula* (Table 2.1) and these were apparently consumed in proportion to their availability (Table 2.2).

Changes in diets were related to forage quality. Dietary proportions of *Equisetum* spp. and grass were greater than those for *Salix* spp. in spring (Table 2.1). However, *Equisetum* and grass were similar to newly emerged willow leaves with respect to concentrations of DDM (87 to 91 %), DNDF (79 – 86 %) and N (3.8 – 4.2 %; Appendices 2.5, 2.6, 2.8). Fern rhizomes accounted for 34% of the spring diet. However, concentrations of fiber in the rhizomes were similar to those of emerging willow leaves (30 – 39 % NDF), but contained less N (2.1 vs. 4.0 %) and digestible dry matter (69 vs. 89%) than the preferred willows (Table 2.1; Appendices 2.5, 2.6, 2.8). In summer, preferred willows (*S. barclayi* and *S. scouleriana*) were higher in DDM (84 vs. 81%) than the most abundant species of willow (*S. bebbiana*). Concentrations of N decreased from early (2.6 – 2.9%) to late summer (2.1 – 2.2%) in both preferred species as well as *S. bebbiana*. Low summer intakes of *Betula* leaves were associated with lower DDM than preferred *Salix* spp. species in early summer (67 vs. 86%) and also in late summer (64 vs. 83%). However, N concentrations of *Betula* were similar to preferred *Salix* spp. in early summer (2.3 – 2.5%) and higher than the preferred willows in late summer (2.4 vs. 2.1%). In winter, *Betula* and *Salix* spp. accounted for similarly high proportions of the diet (Table 2.1). *Betula* stems were higher in N than *Salix* spp. (1.2 vs. 1.1%), but had lower DDM (72 vs. 89%) during winter.

The overall quality of the diet was shaped by seasonal phenological changes of forage plants (Table 2.3). The N content of forages declined from peak values in spring and early summer (emergent plants), to intermediate levels in late summer (mature plants) to low levels in winter (only stems were available). As the nitrogen content of forages decreased from early summer to winter, the availability of that nitrogen to the moose also decreased as seasonally increasing fiber levels bound more and more nitrogen to indigestible diet fractions (Table 2.3). These higher fiber concentrations were accompanied by increases in phenols and reduced fiber and dry matter digestibility (Table 2.3).

2.5.2 Body Condition and Reproduction

The narrow range of mandible length (56.7 ± 0.9 cm) and metatarsal length (47.5 ± 1.9 cm) indicated moose had reached asymptotic growth. Serum chemistries of captive moose were similar to those of healthy captive moose at the Moose Research Center, Alaska (Appendix 2.9; P. S. Barboza and J. Crouse, unpublished data). Muscle depths at the shoulder were not different between November (2.62 ± 0.53 cm), and March (2.22 ± 0.60 cm; $P > 0.05$) suggesting little loss of lean body mass over winter. Serum enzymes that are associated with degradation of muscle, liver and kidney were also similar between November and March and within the range of values for captive moose at the Moose Research Center (P. S. Barboza and J. Crouse, unpublished data). Serum urea concentrations of moose in our study area were consistently low in both November and March (9.56 ± 3.7 mg/dl), which is consistent with low intakes of N and conservation of body protein (Parker et al. 2005) and within the normal range observed for moose (Franzmann and Schwartz 1983).

Maximum rump fat depth decreased from November to March ($P < 0.01$; Fig. 2.5). The corresponding estimates of body fat declined from 11.8 % to 7.9 % of body mass (ingesta free basis) over the winter (Stephenson et al. 1998). Only 4 of the 24 measures (17 %) of fat depth in November were below 1.66 cm, which is the threshold for 50 % probability of pregnancy in moose from south-central Alaska (Testa and Adams 1998). In March, only 3 of the 31 (10 %) fat depth measures were below the mean depth for non-pregnant moose from interior Alaska (Keech et al. 2000), with 2 of the 3 animals also having rump fat depths below pregnancy thresholds the previous November. Pregnancy rates as determined by PSPB concentration in March and November were 85 % (11/13), 94 % (17/18), and 100 % (14/14) in 2009, 2010, and 2011 respectively. Of the animals with rump fat depths below threshold values for pregnancy, only 25 % (1/4) of moose in November and 33 % (1/3) of moose in March were not pregnant as determined by PSPB, with the same non-pregnant moose responsible for both accounts. Serum progesterone varied from 156 to 8,150 pg/mL but the distribution of values did not separate into two groups that would correspond to pregnancy status (Testa and Adams 1998). We observed twins for 0 % (0/5), 7 % (1/17), and 22 % (2/9) of all females that we saw with calves in 2009, 2010, and 2011 respectively. The proportion of females successfully rearing at least one calf through August was 40 % (2/5), 50 % (8/16), and 50 % (5/10) for 2009, 2010, and 2011, respectively.

2.5.3 Nutritional Value of Habitat

Projected AU were based on the seasonal changes in demands of energy and N for a reproductive female moose throughout the year. Forage intakes reflected both seasonal changes in energy demands as well as changes in the digestibility of the diet (Fig 2.4; Appendix 2.3; Table 2.3). Energy demands increased from gestation (17.1 MJ/d) to peak lactation (19.6 MJ/d) to project an increase in dry matter intake from spring (9.1 kg/d) to early summer (10.4 kg/d). Declines in digestibility in late summer increased the intake of energy (24 MJ/d) and dry matter (12.9 kg/d) required to restore body fat before winter. Dry matter intakes subsequently declined in winter (7.6 kg/d) because decline in energy demand after accounting for energy production from fat catabolism (14 MJ/d) was even greater than the decline in digestibility as animals shifted from mature leaves to stems (Appendix 2.3, Table 2.3). These patterns of metabolism and DMI were similar to other studies of moose (Hubbert 1987, Moen and Moen 1998, Renecker and Hudson 1985, Renecker and Hudson 1989, Schwartz et al. 1984). High biomass density of shrublands (Fig. 2.2) provided the greatest amount of dry forage to support the largest number of AU among all the habitats in both summer and winter (Fig. 2.6). Our method of adjusting available biomass by the dietary proportions of each species was reasonable as our estimates for utilized proportions were within 12 % of the proportions determined by microhistology of feces collected from moose in this area.

The corresponding supply of N from forage intake was affected by N availability, that is, the binding of protein to fiber or other compounds such as tannins. Intakes of N followed that of forage intake and the concentration of N in the plant from spring through summer (Table 2.3). Dietary concentrations of N were 2% of dry matter or greater from spring through summer when fiber bound less than 22% of the total N (Table 2.3). The concentration of available N in the diet exceeded the threshold to meet N demands of the animal from spring to summer: 2.1 vs. 0.7 % in spring, 2.2 vs. 1.1 % in early summer and 1.2 vs. 0.6 % in late summer (Table 2.3). Fiber bound N increased with decreasing N content in winter, that is, available N in the dry mass of forage declined to 0.8 %, which was near the threshold of 0.7% N required to meet N demands in winter. Projections of AU in all habitats are greater for N than for dry mass in late summer because energy and thus forage dry mass is most limiting (Fig. 2.6A). Conversely, low concentrations of available N limit the number of AU that can be supported in all the habitats during winter (Fig. 2.6B).

The distribution of AU across habitats was heavily biased towards shrublands for both dry mass and N. In equivalents of moose-days during winter, each hectare of shrubland was equivalent to 11 ha of shrubby wetlands, 17 ha of mixed forest, 19 ha of deciduous forest, 75 ha of coniferous forest and 81 ha of grasslands. Projections of the total number of moose that could be supported in JBER were therefore dependent on the distribution of shrublands (Fig. 2.7). Shrublands were most prevalent in the subalpine region on the southeast boundary of JBER and within the central developed area (Fig. 2.7). Although foraging habitats (i.e., excluding barrens and fenced areas) accounted for 77% of JBER, shrublands were only 15% of the habitat. Foraging habitats accounted for only 31% of the central developed area but shrublands were 21% of that habitat. Habitat in developed areas on JBER could therefore support a greater density of AU than the undeveloped areas.

Estimates of the number of moose that could be supported across the study area depend on the season and the length of the time frame considered (Fig. 2.8). High biomass in a short window (60 d) during late summer resulted in high estimates of the number of moose that can be supported on the available mass of dry matter and N (Fig. 2.8). Projection of the number of moose that can be supported on N from winter stems over 180 days were 13.5 times lower than those for the available dry forage in late summer (Fig. 2.8). The size of the moose used to calculate AU alters the projection of the number of animals that can be supported in the area: an increase in body mass by

42% from 360 to 510 kg decreased the estimates of the number of reproductive females by 24 % in later summer and by 27 % in winter (Fig. 2.8). Similarly, reducing the energy demands of the animal by projecting a young female without reproductive demands increases the projected number of small moose (360 kg) by 45% in early summer. Overestimation of the average DDM by 12% would likewise increase the quality of the diet and the estimated AU on JBER by 13% for forage N in winter and by 16% for dry forage mass in late summer.

2.6 Discussion

Our model projections supported the hypothesis that shrublands would provide the greatest amount of energy and N for moose (Fig. 2.6). The potential impact of habitat change on moose in the study area can be projected from the distribution of habitats within a region. For example, we used the model to project the change in winter AU for a 25 ha parcel of shrublands and mixed forest within the central developed area undergoing two development scenarios (Fig. 2.9). Excluding moose from a 10 ha section of shrublands (5.6 ha) and mixed forest (4.4 ha; Fig. 2.9A) had approximately the same effect on winter AU as converting the shrublands to mixed forests within the 10 ha section (Fig 2.9B). The importance of shrublands as forage areas for moose is well documented and reviewed by Thompson and Stewart (2007). Small areas of shrubs on the perimeter of developments and roads can mitigate some of the loss of forage, especially when low forage habitats such as conifer forests or grasslands are replaced with shrublands. However, shrub perimeters can attract moose to roads and urban development that can result in vehicle collisions and property damage (Danks and Porter

2010). Also, while the model predicts that a fragmented area could contain enough habitats to support a projected number of AU, the negative cumulative effect(s) of habitat fragmentation must be considered. Our results indicate the loss of shrublands through natural succession could reduce the number of AU an area can support as much as development. In south-central Alaska, the natural succession from willow to spruce forest has decreased the numbers of moose over 50 years (Stephenson et al. 2006). Active management of shrublands, such as hydro-axing, may be required to maintain the existing forage base and to offset continued JBER development.

Our projection of AU relies heavily upon the classification of habitats and the associated plant communities that provide forage. For example, a shrubland dominated by willows can support more moose than one dominated by alder. Conversely, succession from grasslands to shrublands after fire can provide an increase in forage biomass within 7-10 years and a peak in forage biomass within 20 - 30 years (Weixelman et al. 1998). Successional changes, as well as the aging of individual plants, are also associated with gradual declines in forage quality (Regelin et al. 1987, Spaeth et al. 2002, Weixelman et al. 1998). The size, shape, and distance to cover also affects forage utilization within shrublands. For instance, Hamilton et al. (1980) found that 95% of moose browsing in clear-cuts in Ontario occurred within 80 m of cover even when openings exceeded 500 ha. Only 8.0% of shrublands in our study area were > 80 m from the edge of the shrubland. Many of these shrublands are small patches created from human disturbances resulting in much of the biomass located close to shrubland edges.

Our projection of AU is also dependent on changes in diets that are associated with shifts in both the species of plants and the quality of the parts consumed. Our diets were dominated by just a few species of preferred forages throughout the year (Table 2.1). Species quality shifted seasonally resulting in the greatest diversity of the diet in the spring. Early and late summer diet diversity was slightly lower than the winter, contrary to other studies of moose (Hjeljord et al. 1990, Renecker and Hudson 1992, Risenhoover 1989, Wam and Hjeljord 2010, Wam et al. 2010). Changes in plant quality likewise influenced diet selection (Table 2.1, Appendices 2.5, 2.6, 2.8). Selection of *S. barclayi and S. scouleriana* in early summer and late summer were positively associated with digestibility, whereas selection of *Betula* spp. in winter was positively associated with available N. Changes in diet selection support our model predictions of energy limitation in summer and N limitation in winter (Fig. 2.6, 2.8). Avoidance of *Betula* spp. and *Populus balsamifera* in summer may also be a response to specific plant secondary metabolites. Preferred species of willows leaves were higher in total phenols than *Betula* and yet *Salix* was still preferred. The subsequent selection of *Betula* stems in winter suggests that moose may respond differently to a wide variety of plant secondary metabolites in both deciduous and coniferous trees (Stolter et al. 2009). Morphological attributes such as stem diameter may also contribute to diet selection by affecting foraging dynamics such as bite size and thus intake rate (Spalinger and Hobbs 1992; Searle and Shipley 2008). The preference for *S. scouleriana* may therefore reflect longer, less branched stems with larger leaves than the more abundant *S. bebbiana*.

Fiber content of the whole diet was similar in spring and summer even though forage fiber concentrations were lowest in spring (Table 2.3; Appendix 2.6). Forbs that emerge early in the spring may be very important for moose until emerging willow leaves increase in abundance. Fern rhizomes and newly emergent horsetails and grasses make up the majority of the diet in spring. However, in the summer, fern rhizomes are only minor components of, or are absent from the diet. This was an unexpected discovery. Fern rhizomes may be very important to moose right before the calving season. Fern rhizomes were of moderate quality, and were less digestible than emerging leaves and forbs in spring, but still more digestible than winter stems. Intakes of indigestible dry matter from our spring diets, which contained high proportions of fern rhizomes and highly digestible forbs, is projected at 3.2 kg/d. This intake of indigestible dry matter is intermediate to those for early summer (2.3 kg/d) and later summer (4.4 kg/d) when animals consumed predominantly willow leaves. Therefore, ingesting fern rhizomes instead of stems in spring appears to be a strategy for increasing N and digestible dry matter intakes while maintaining gut fill for optimal gut function until willow leaves become available (Barboza et al. 2009, Spalinger and Hobbs 1992). Plant morphology may also have affected the consumption of rhizomes of ostrich fern (*Matteuccia struthiopteris*), northwestern lady fern (*Athyrium filix-femina* ssp. *cyclosorum*) and shield fern (*Dryopteris expansa*). These ferns produce large, bite-sized balls of starch and fiber for moose. These rhizomes grow in the topsoil and are easily accessible to moose soon after the snow has melted. Moose may be able to maximize intakes of rhizomes because they grow in easily accessible patches when better quality foods are at low density

(Shipley et al. 1998, Spalinger and Hobbs 1992). The diversity of foraging areas for moose may be important in late winter and spring when females seek birth sites and foraging areas that will minimize predation risk and ameliorate mass loss before the onset of lactation (Bowyer et al. 1998, Poole et al. 2007).

Our estimate of AU was sensitive to the size of the model animal and its metabolic demands for reproduction (Fig. 2.8; Appendix 2.3). The model provides estimates of the relative value of habitat for a single animal type, which can be extended to estimate the demand of a local population if the population demographics were known (Miquelle et al. 1992). Measures of rump fat depth of captured female moose were used as inputs for the model. Continued monitoring of the population's fat stores, reproduction, and diet will allow managers to monitor the number of animals JBER can support over time.

Rump fat depths were above the thresholds for pregnancy defined by Testa and Adams (1998) and Keech et al. (2000) and likewise, pregnancy rates in our study area were high and similar to most populations of moose (Ballard et al. 1991, Bertram and Vivion 2002, Gasaway et al. 1992, Ouellet et al. 1997, Testa et al. 2000). Our small sample of observations indicate that twinning rates are low and below the rate of 72% observed in populations with abundant and high quality winter forage (Franzmann and Schwartz 1985). Our method of confirming calves on foot likely underestimated the true population twinning rate and we felt justified in using a slightly higher twinning rate for moose in an adjacent population as inputs for the model. The model also estimated that female moose were selecting a diet that removed a moderate proportion (31%) of the winter biomass. Direct evaluations of winter browse removal in this area are required to confirm this estimate because twinning rates have been shown to decline with increasing rates of browse removal in populations of moose from interior Alaska (Seaton et al. 2011). Calf survival was high compared to other studies across the state (Ballard et al. 1991, Bertram and Vivion 2002, Gasaway et al. 1992, Testa et al. 2000), but this estimate is also based on a small sample size that should be augmented by further monitoring.

Our data on body condition and reproductive output indicate that this urban population is in moderate condition. Further data and analysis are required to confirm parameters of recruitment (e.g. birth rate and survival of calves) and to assess the effect of movement of moose into JBER for sustaining the high harvest from GMU 14C. Continued monitoring of the condition of the population could be combined with hunter harvests by examining the reproductive tract and body fat depots to monitor fecundity of yearlings, two year-olds and prime aged females (Heard et al. 1997).

2.7 Management Implications

Shrublands are crucial to sustaining this heavily harvested population of moose that are also exposed to predators and urbanization. Our model provides relative values of shrublands and other habitats that can be further customized to the structure of the population and the plant communities to predict the impact of natural and human induced habitat change for harvest or for non-consumptive use of the moose population. We recommend that late winter browse surveys be conducted to estimate the proportion of winter browse removal. Because of the extensive road systems, this would minimize the time and cost of monitoring this population.

2.8 Figures

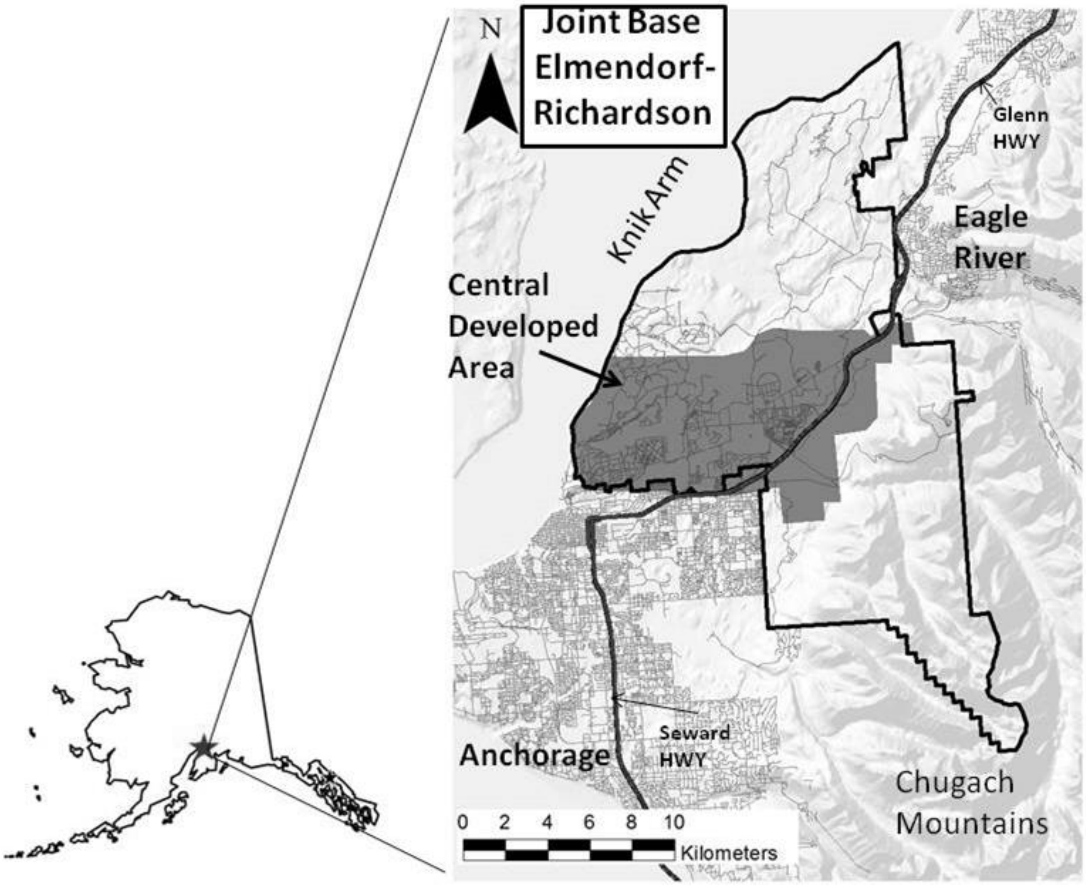

Figure 2.1. Study area for female moose on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

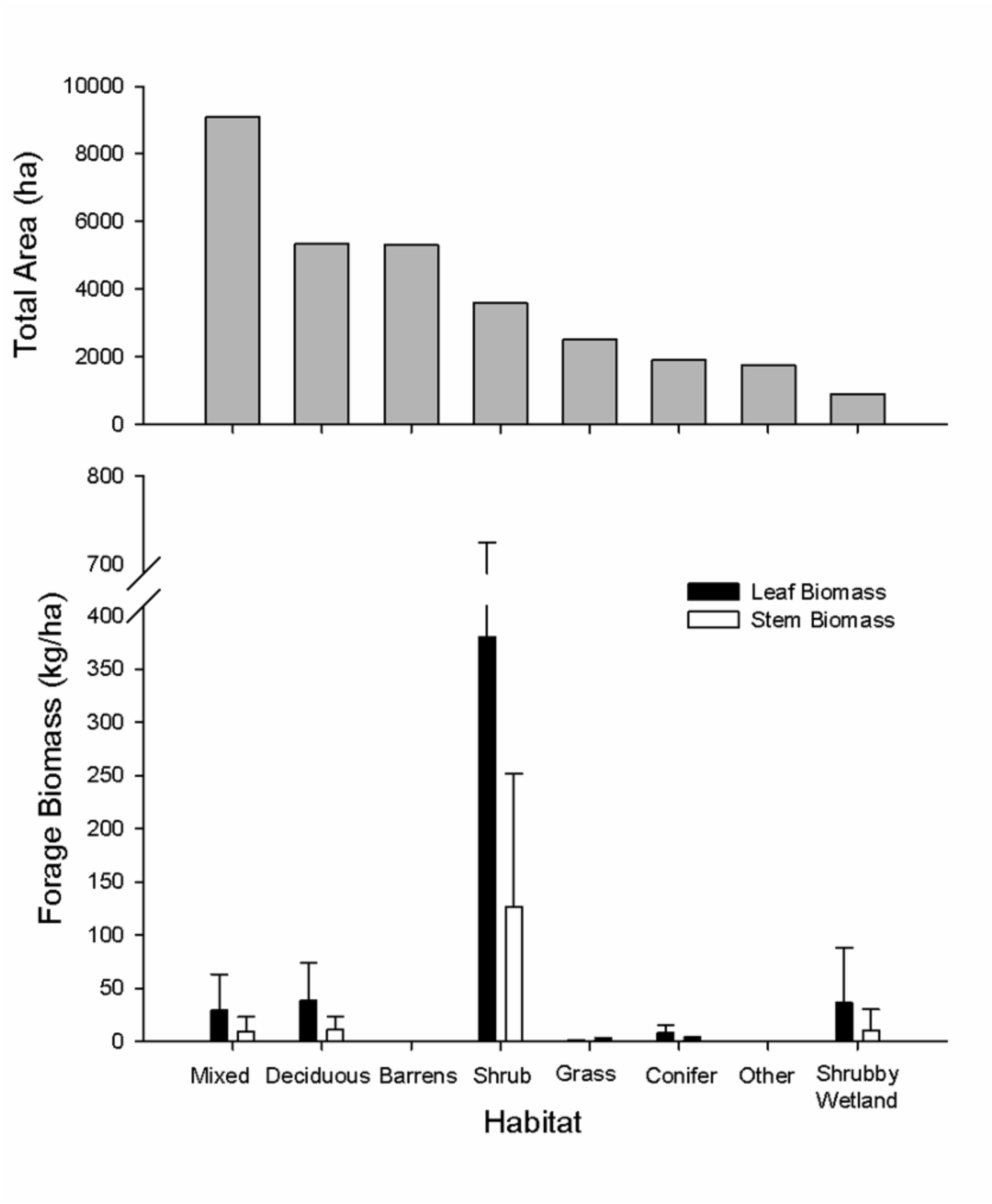

Figure 2.2. Metrics of habitat classes for moose on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA. Barrens include upland tundra as well as areas cleared for operations such as gravel pits and parking lots. “Other” areas include water bodies and fenced areas that exclude moose. A. Total area of each class of habitat in the study area. B. Density of dry forage mass (kg/ha) in each habitat in late summer (15 August).

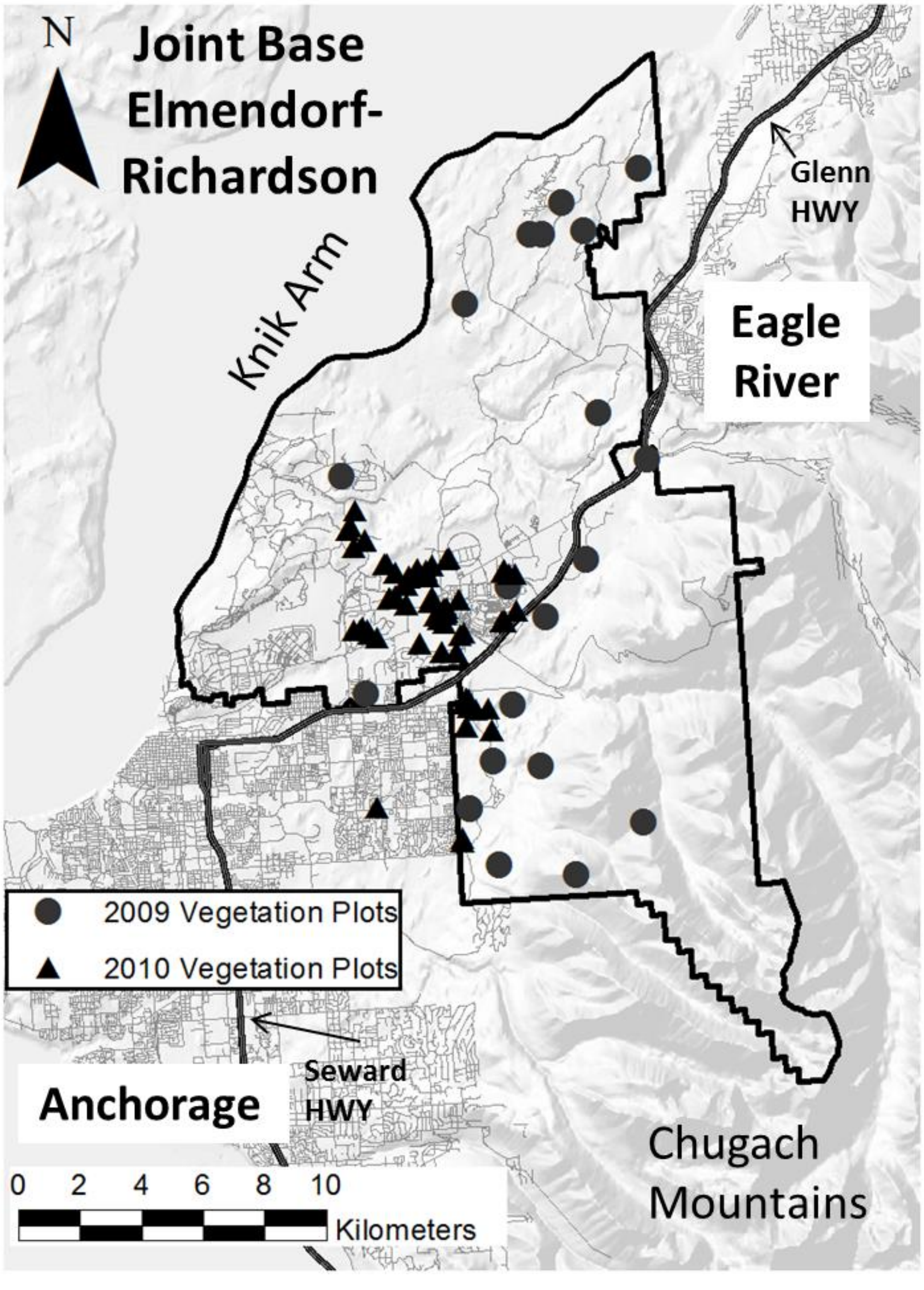

Figure 2.3. Vegetation plots for forage collections in 2009 and 2010 on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

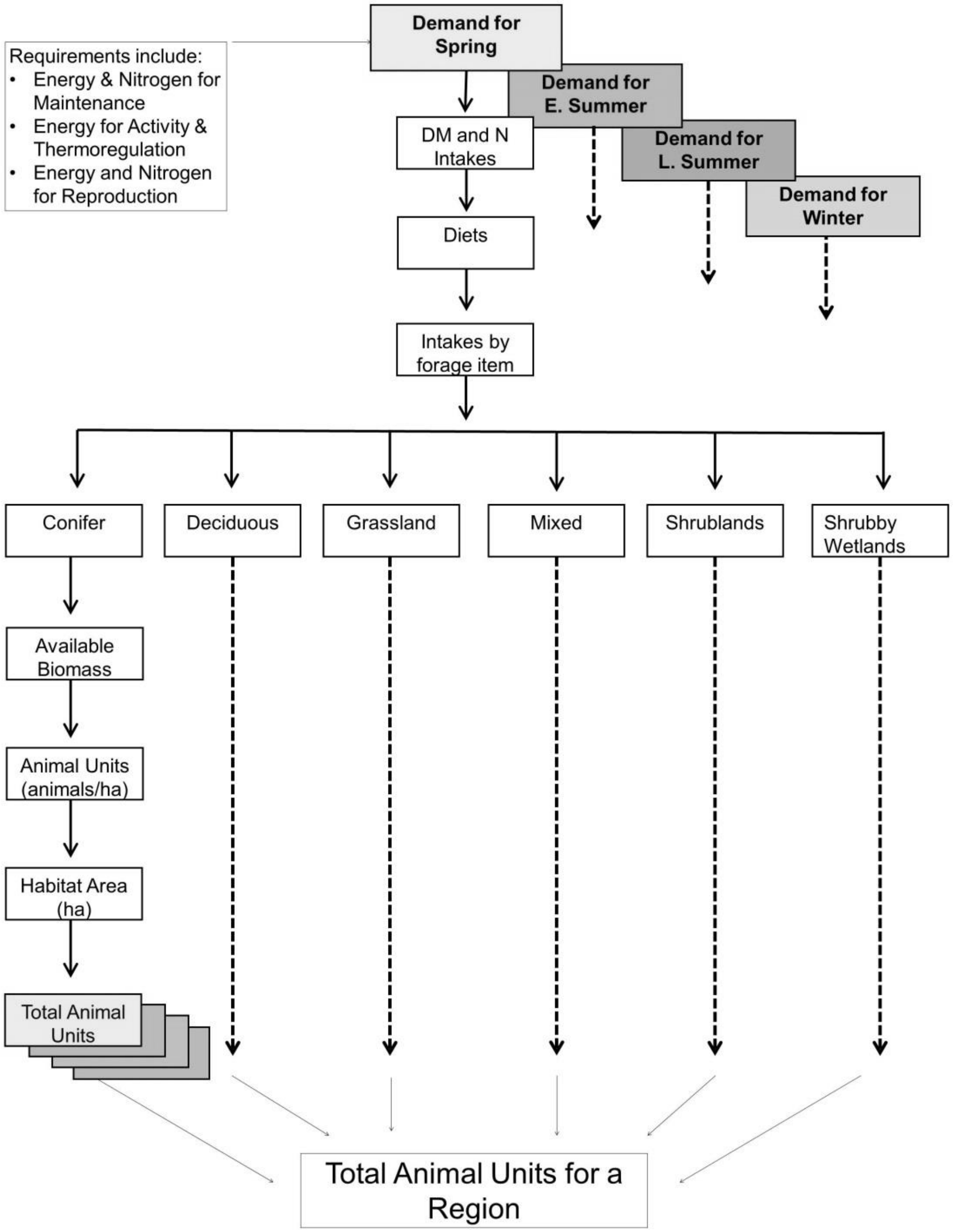

Figure 2.4. Scheme for modeling the nutritional demands of moose to project animal units for each habitat class and area on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

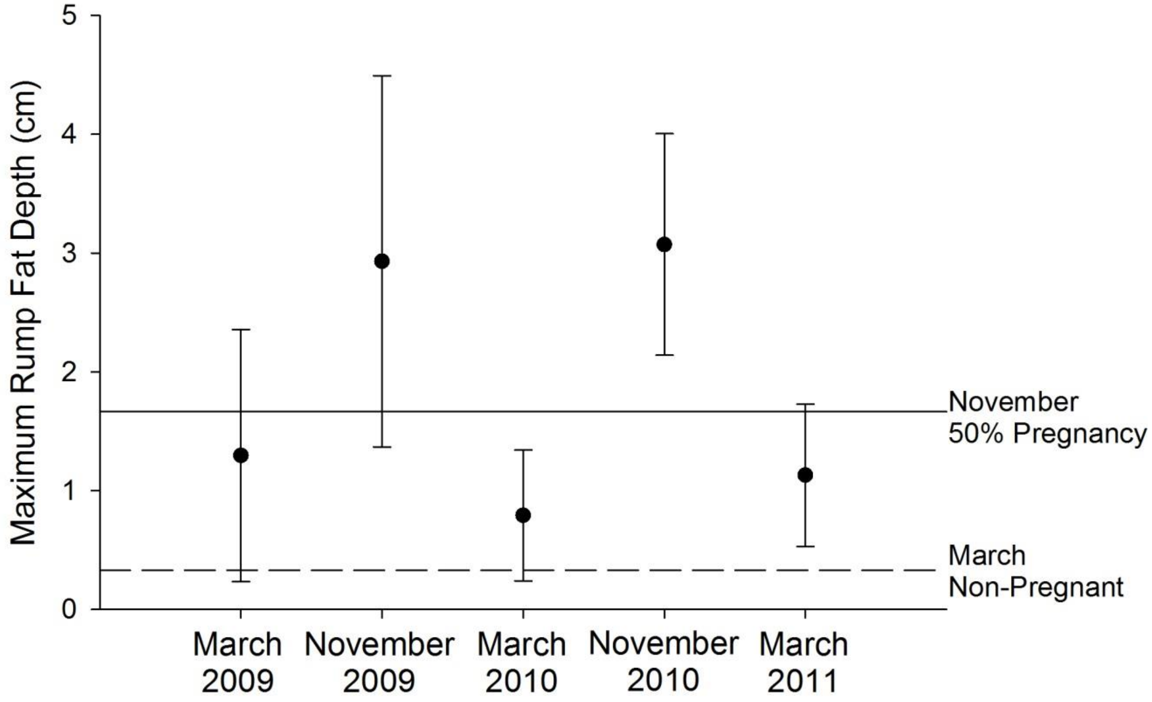

Figure 2.5. Subcutaneous fat stores measured by ultrasound of female moose captured on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA. Solid line indicates a fat depth (1.66 cm) that corresponds with a 50% probability of pregnancy in November (Testa and Adams 1998). Dashed line indicates the mean depth of fat (0.33 cm) for non-pregnant moose in March (Keech et al. 2000).

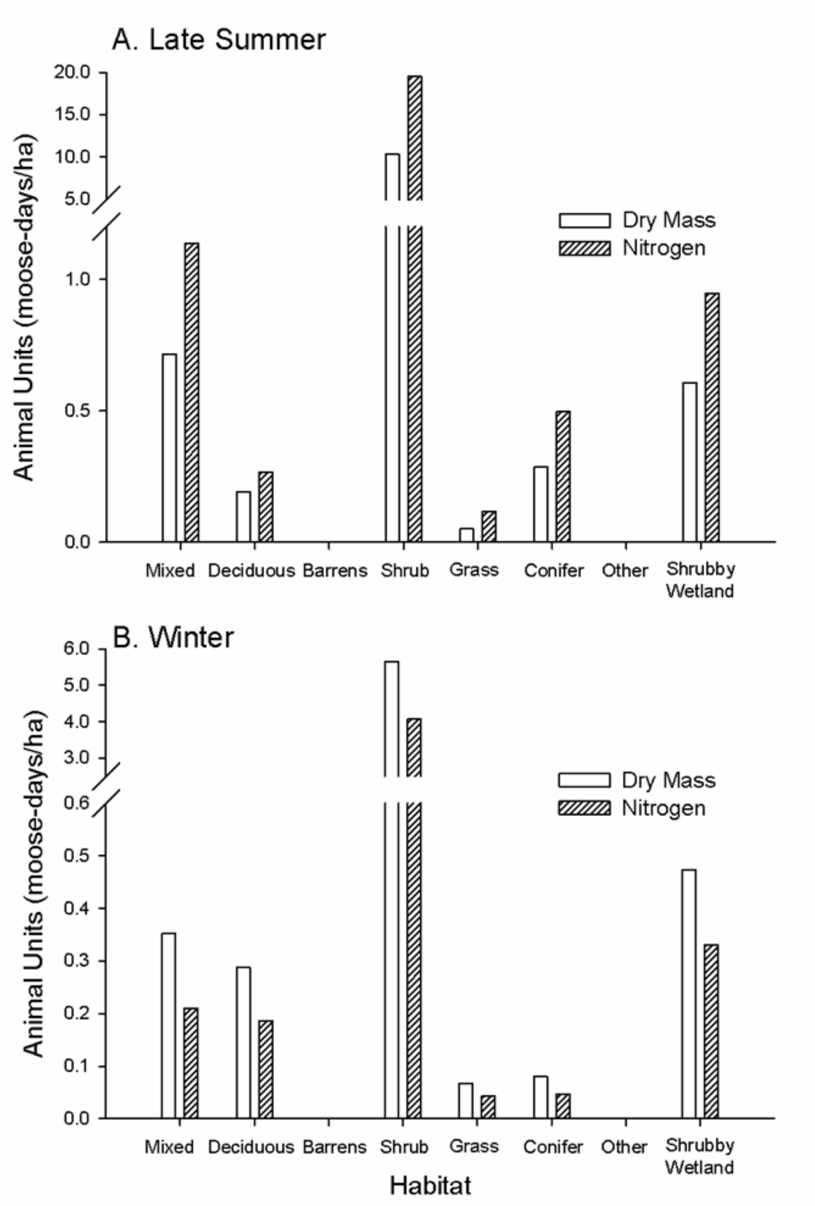

Figure 2.6. Seasonal estimates of animal units (moose – days/ha) for each class of habitat on Joint Base Elmendorf-Richardson near Anchorage, AK. Estimates are based on the utilizable dry mass (open bars) and Nitrogen of forages that were projected by a nutritional model for a reproductive female moose of 428 kg body mass on 1 January. A. Late summer (15 August) B. Winter (1 January)

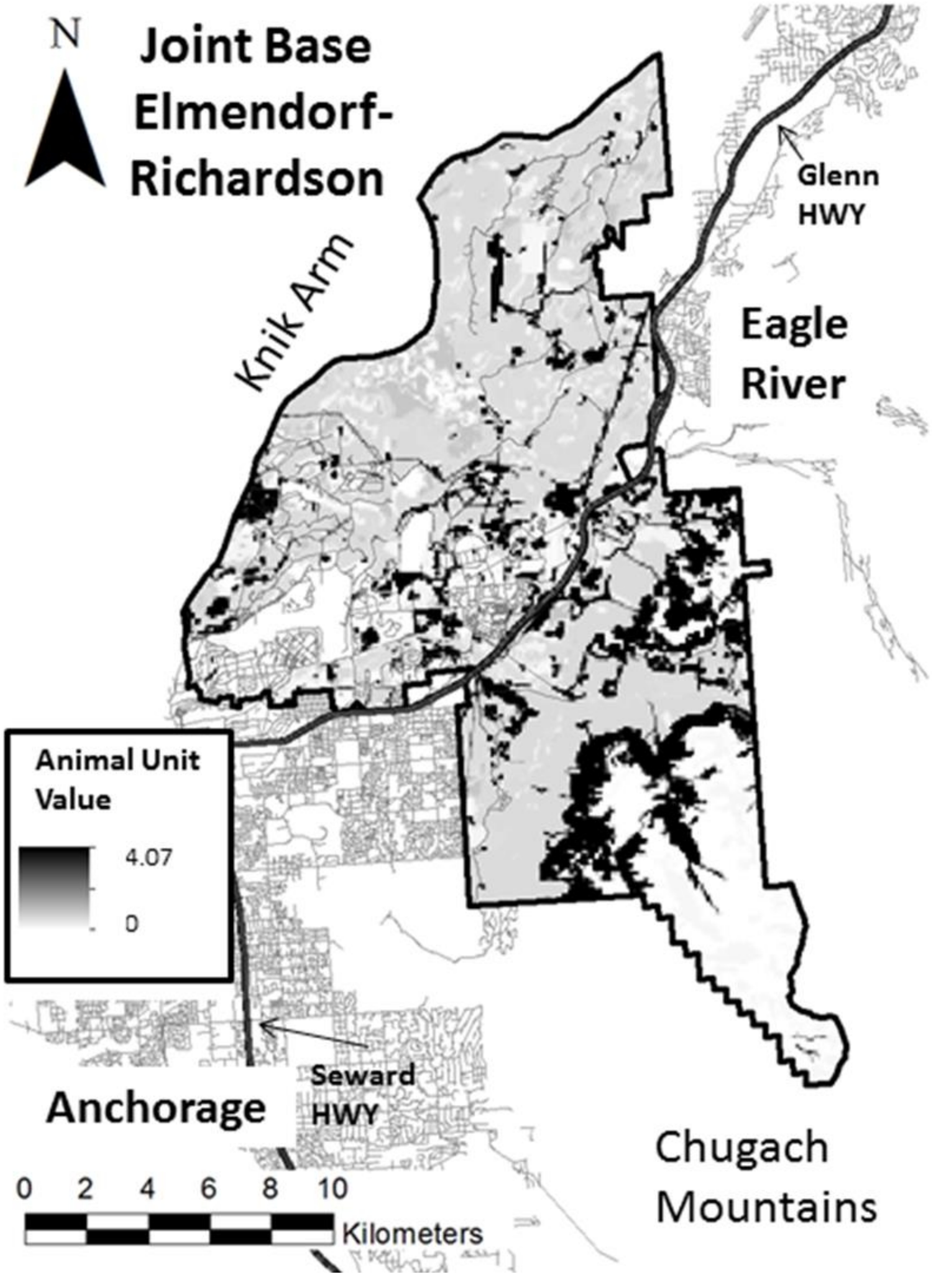

Figure 2.7. Winter distribution of animal units (AU; moose-days/ha) for Joint Base Elmendorf-Richardson near Anchorage, AK projected by the nutritional model for utilizable Nitrogen. Estimates are based on reproductive female moose of 428 kg in January.

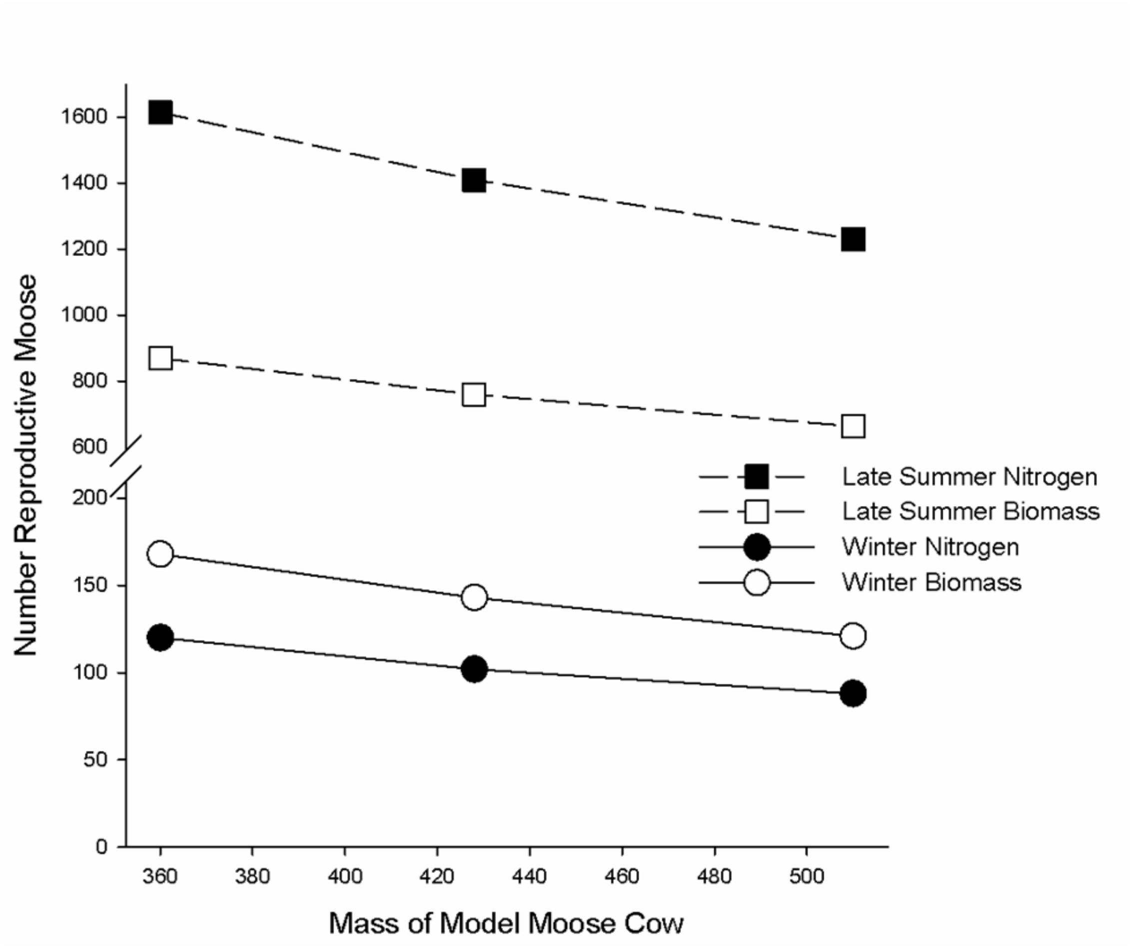

Figure 2.8. Number of reproductive female moose that can be supported by habitats on Joint Base Elmendorf-Richardson near Anchorage, AK. Numbers are projected by the nutritional model from the utilizable dry mass and Nitrogen in forage starting with a body mass of 360, 428 or 510 kg in January. Estimates for late summer are based on a 60 day window (midpoint at 15 August) when females have weaned their calves and are restoring body mass for winter. Estimates for winter are based on a 180 day window (midpoint 15 February) when females are losing body fat.

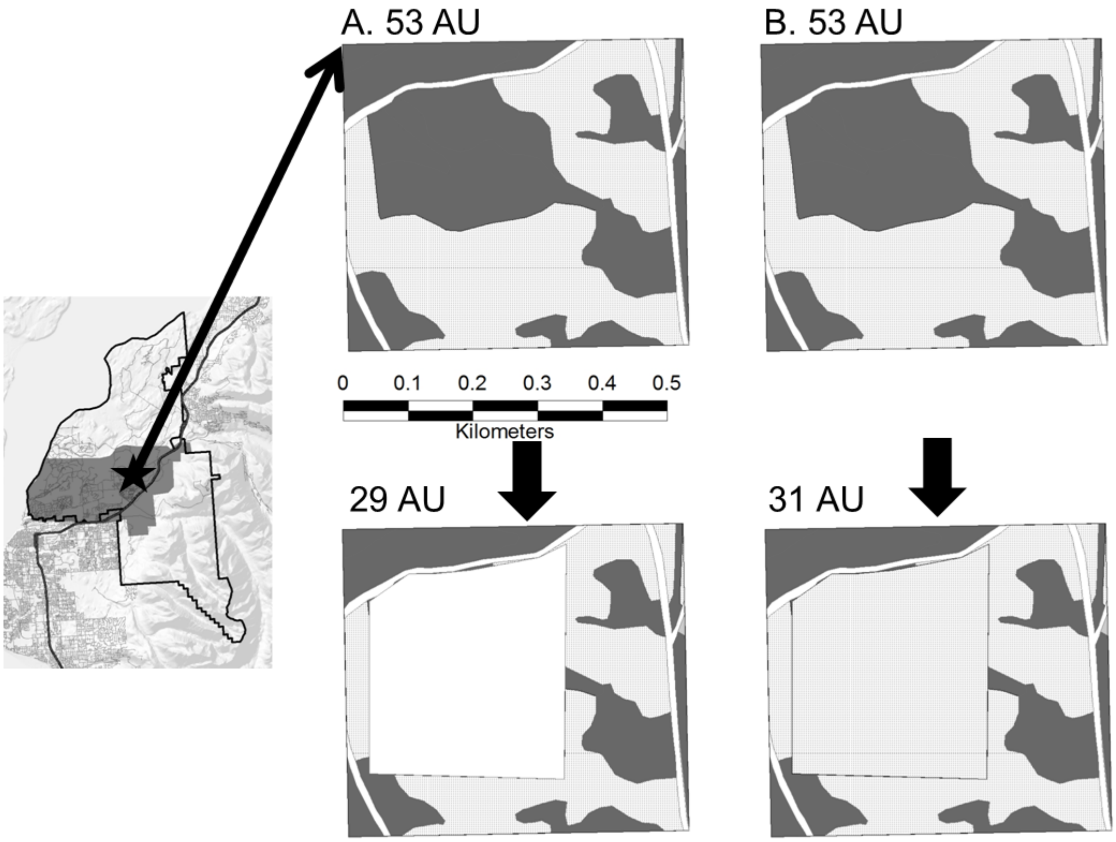

Figure 2.9. Projected winter animal units (AU; moose-days/ha) supported by a 25 ha parcel. Light shading indicates mixed forest (valued at 0.24 AU), dark shading indicates shrublands (valued at 4.07 AU), and white indicates barrens and roads (valued at 0 AU). If a 10 ha section is fenced (A), total AU of the 25 ha parcel is reduced by 45%. If the same 10 ha section is converted to mixed forest (B) but not fenced, total AU for the 25 ha parcel is reduced by 42%. All habitat outside 10 ha section is assumed unchanged.

2.9 Tables

Table 2.1. Percent (%) of plant fragments determined by microhistology and corrected for digestibility of pooled fecal samples (n = 5 except for winter where n = 10) from moose near Anchorage, Alaska, USA.

Species	Spring	Early Summer	Late Summer	Winter
Betula stem	5.5	0.0	0.0	30.9
Betula leaf	0.0	0.6	4.0	1.1
Populus balsamifera stem	2.6	0.5	0.2	15.7
Populus tremuloides stem	1.0	1.0	-	5.6
Populus tremuloides leaf and stem	0.0	0.0	4.4	0.0
Salix stem	9.3	-	-	36.8
Salix barclayi leaf and stem	-	23.0	15.8	-
Salix bebbiana leaf and stem	-	12.2	12.4	-
Salix pulchra leaf and stem	-	2.3	7.7	-
Salix scouleriana leaf and stem	-	27.5	30.3	-
Salix spp. leaf	0.6	-	-	0.5
Viburnum stem	3.1	0.4	0.3	0.5
Viburnum leaf	1.4	0.0	0.0	0.0
Other Shrub stem	3.4	0.0	0.0	8.3
Other Shrub leaf and stem	3.4	8.8	10.0	0.2
Total Shrub	**30.3**	**76.3**	**85.1**	**99.6**

Table 2.1 continued.

Species	Spring	Early Summer	Late Summer	Winter
Equisetum	16.7	7.3	3.5	0.0
Chamerion angustifolium	0.0	0.5	6.0	0.0
Fern	0.0	2.5	0.0	0.0
Fern Rhizome	33.6	1.9	0.0	0.0
Grass	15.5	3.9	2.3	0.3
Other Herbacious	4.0	7.7	3.0	0.0
Total Non-Shrub	**69.8**	**23.8**	**14.8**	**0.3**
Shannon Diversity Index[a]	**1.9**	**2.1**	**2.1**	**1.4**
Adjusted Shannon Diversity Index[a, b]	**1.9**	**1.3**	**1.3**	**1.4**

[a] Proportions of stems and leaves of the same species were combined for calculation

[b] Proportions of all *Salix* spp. were combined for comparison across seasons because *Salix* spp. stems could not be resolved to species.

Table 2.2. Diet selection values for moose near Anchorage, Alaska, USA.

Species	Strauss' Linear Index	Ivlev's Electivity Index
Late Summer		
Betula papyrifera	-0.35	-1.00
Populus balsamifera	-0.16	-0.98
Populus tremuloides	0.02	0.31
Salix barclayi	0.15	0.85
Salix bebbiana	-0.13	-0.40
Salix glauca	-0.01	-1.00
Salix pulchra	0.08	0.99
Salix scouleriana	0.27	0.77
Viburnum edule	-0.12	-1.00
Winter		
B. papyrifera	-0.07	-0.10
P. balsamifera	0.05	0.18
P.tremuloides	0.03	0.28
Salix spp.	-0.04	-0.05
V. edule	-0.07	-0.87

Table 2.3. Dry matter composition of the average diet consumed by moose near Anchorage, Alaska, USA.

Season	NDF[a] (%DM)	ADF[b] (%DM)	DDM[c] (%DM)	DNDF[d] (%NDF)	Phenols (mg/g DM)	Total N (%DM)	ADFN[e] (%N)
Spring	44.3	22.6	73.7	57.5	16.2	2.6	18.0
Early Summer	44.9	19.4	86.3	75.1	20.0	2.8	12.1
Late Summer	39.2	19.0	74.5	59.1	21.1	2.0	12.5
Winter	51.7	37.2	56.0	32.0	59.4	1.2	21.3

[a] Neutral Detergent Fiber

[b] Acid Detergent Fiber

[c] Digestible Dry Matter

[d] Digestible Neutral Detergent Fiber

[e] Proportion of Total Nitrogen in Acid Detergent Fiber

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2.11 Appendices

Appendix 2.1. Habitat classifications from Joint Base Elmendorf-Richardson GIS databases used to establish new classifications of habitat for moose.

New Classification	Original Classification
Barrens	Barrens (<5% veg)
	Cassiope Tundra
	Crowberry Tundra
	Disturbance Complex
	Dryas-Lichen Tundra
	Partially Vegetated (5-30%)
	Aquatic Herb
	Brackish Water
	Marine Water
	Water
Conifer	Closed Dwarf Mountain Hemlock
	Open Black Spruce
	Open Black Spruce-White Spruce
	Open White Spruce
Deciduous	Closed Paper Birch
	Closed Paper Birch
	Closed Paper Birch-Aspen
	Closed Paper Birch-Aspen
	Closed Quaking Aspen
	Closed Quaking Aspen
	Open Balsam Poplar
	Open Black Cottonwood
	Open Paper Birch
	Open Paper Birch-Aspen
	Open Quaking Aspen
Grassland	Bluejoint Meadow
	Mixed Herbs
	Moist Graminoid, post burn or disturbance
	Subarctic Lowland Sedge-Moss Bog Meadow
Mixed	Closed Quaking Aspen-Spruce

Appendix 2.1 continued

New Classification	Original Classification
	Closed Spruce-Paper Birch
	Open Black Cottonwood-White Spruce
	Open Quaking Aspen-Spruce
	Open Spruce-Paper Birch
Shrub	Closed Low Willow
	Closed Tall Alder
	Closed Tall Scrub, post burn or disturbance
	Closed Tall Willow
	Open Low Scrub, post burn or disturbance
	Open Low Shrub Birch-Willow
	Open Low Willow
	Open Tall Alder
	Open Tall Scrub, post burn or disturbance
	Open Tall Willow
Shrubby Wetland	Elymus
	Halophytic Grass Wet Meadow
	Halophytic Herb Wet Meadow
	Halophytic Sedge Marsh
	Halophytic Sedge Wet Meadow, brackish
	Halophytic Sedge Wet Meadow, slightly brackish
	Open Black Spruce
	Open Dwarf Black Spruce
	Open Low Shrub Birch-Ericaceous Shrub Bog
	Open Low Sweetgale-Graminoid Bog
	Open Low Sweetgale-Graminoid Shrub Meadow, slightly brackish

Appendix 2.2. Relationships between stem diameter and the dry biomass of leaves and stems for deciduous browse available to moose near Anchorage, Alaska, USA.

	y = Leaf Biomass (g) x = Stem Diameter (mm)		y = Stem Biomass (g) x = Stem Diameter (mm)		Mean Leaf Biomass (g) Per Leaf Cluster
Species	Equation	R^2	Equation	R^2	Equation
Betula papyrifera	$y = 0.52x - 0.81$	0.87	$y = (0.29x - 0.29)^2$	0.92	0.24
Populus balsamifera	$y = (0.37x - 0.17)^2$	0.87	$y = (0.02x^2 + 0.16x - 0.18)^2$	0.93	0.90
Populus tremuloides	$y = (0.23x + 0.11)^2$	0.91	$y = (0.29x - 0.30)^2$	0.96	0.05
Salix barclayi	$y = (0.30x + 0.02)^2$	0.85	$y = (0.04x^2 + 0.15x - 0.09)^2$	0.93	
Salix bebbiana	$y = (0.01x^2 + 0.15x + 0.11)^2$	0.92	$y = (0.03x^2 + 0.03x - 0.06)^2$	0.95	
Salix glauca	$y = (0.19x)^2$	0.79	$y = (0.04x^2 + 0.16x + 0.18)^2$	0.90	
Salix pulchra	$y = (0.22x)^2$	0.91	$y = (0.36x - 0.40)^2$	0.95	
Salix Scouleriana	$y = (0.33x - 0.16)^2$	0.96	$y = (0.03x^2 + 0.09x - 0.06)^2$	0.98	
Viburnum edule	$y = (0.25x + 0.01)^2$	0.82	$y = (0.04x^2 + 0.04x - 0.06)^2$	0.97	0.10

Appendix 2.3. Selected parameters for calculating nutritional demands of moose near Anchorage, Alaska, USA

Model Parameter	Units	Winter	Spring	Early Summer	Late Summer
Baseline Energy Demands					
Body mass	kg	428	397	397	400
Fat mass	kg	44	12	12	16
Basal metabolic rate	$kJ\cdot kg^{-0.75}\cdot d^{-1}$	28802	38067	38067	38295
Additional cost for activity and thermoregulation	$kJ\cdot kg^{-0.75}\cdot d^{-1}$	28802	38067	38067	38295
Energy from change in body fat	$kJ\cdot d^{-1}$	-11179	0	0	2775
Reproductive Energy Demands					
Additional cost for gestation	$kJ\cdot d^{-1}$	0	1164	0	0
Milk production	g	0	0	4397	0
Additional cost of lactation	$kJ\cdot d^{-1}$	0	0	29663	0
Seasonal Energy Demands					
Net Energy demand	$kJ\cdot d^{-1}$	46425	77298	110194	79364
Diet digestibility	%	56	74	86	75
Gross energy demand	$kJ\cdot d^{-1}$	142120	171377	204474	243335
Seasonal Nitrogen Demands					
Unbound N (Metabolizability)	%	39	71	63	52
Endogenous urinary N	$g\cdot d^{-1}$	13.36	7.02	7.89	9.66
Metabolic fecal N	$g\cdot d^{-1}$	41.78	50.38	60.12	71.54
N demand for maintenance	$g\cdot d^{-1}$	55.15	57.41	68.01	81.20
Additional N for gestation	$g\cdot d^{-1}$	0	5.88	0	0
Additional N for lactation	$g\cdot d^{-1}$	0	0	49.62	0

Appendix 2.3 continued.

Model Parameter	Units	Winter	Spring	Early Summer	Late Summer
Dry Matter Intakes and Nitrogen Demands					
Dry matter intake	$kg \cdot d^{-1}$	7.55	9.10	10.86	12.92
Dry matter intake adjusted for measured browse	$kg \cdot d^{-1}$	7.38	2.76	8.08	10.93
Digestible N demand	$g \cdot d^{-1}$	55.15	63.28	117.63	81.20
Digestible N demand adjusted for measured browse	$g \cdot d^{-1}$	54.23	28.16	102.24	70.18

Appendix 2.4. Forage leaf and stem biomass densities (kg dry matter/ha) by habitat in August 2009 and 2010 near Anchorage, Alaska, USA.

	Conifer		Deciduous		Grassland		Mixed		Shrub		Shrubby Wetland	
Species	Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem	Leaf	Stem
Besp	1.79	0.50	11.64	5.02	1.68	0.65	6.25	2.62	140.36	48.99	27.49	6.88
Posp	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	86.7	18.89	0.00	0.00
Potr	0.62	0.41	2.31	0.93	0.00	0.00	3.37	1.49	0.00	0.00	0.00	0.00
Saba	0.00	0.00	0.00	0.00	0.85	0.59	0.00	0.00	4.59	2.32	7.26	2.99
Sabe	3.1	0.55	0.55	0.16	0.12	0.10	4.26	1.62	137.75	51.82	0.00	0.00
Sagl	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.79	2.95	0.00	0.00
Sapu	0.00	0.00	0.00	0.00	0.08	0.08	0.00	0.00	0.00	0.00	0.64	0.41
Sasc	1.39	0.36	1.16	0.51	0.00	0.00	6.54	2.13	1.69	0.53	0.00	0.00
Vied	1.07	0.38	22.7	4.68	0.00	0.00	8.73	1.69	3.81	0.98	0.62	0.15
Shannon Diversity Index	**1.48**	**1.60**	**1.01**	**1.13**	**0.90**	**1.07**	**1.56**	**1.59**	**1.26**	**1.24**	**0.67**	**0.82**

Besp: *Betula papyrifera*, Posp: *Populus balsamifera/trichocarpa*, Potr: *Populus tremuloides*, Saba: *Salix barclayi*, Sabe: *Salix bebbiana*, Sagl: *Salix glauca*, Sapu: *Salix pulchra*, Sasc: *Salix scouleriana*, Vied: *Viburnum edule*

Appendix 2.5. Nitrogen concentration in dry mass of major forage items for moose near Anchorage, Alaska, USA. % N is the nitrogen content (%) of dry matter. ADFN is the nitrogen content (%) of the acid detergent fiber

Species	Season	%N	n	SD	ADFN	n	SD
Betula papyrifera	Spring	3.49	15	0.32	1.24	3	0.23
	E. Summer	2.51	17	0.35	1.47	3	0.36
	L. Summer	2.42	21	0.29	1.54	2	0.05
	Winter	1.22	12	0.09	0.60	4	0.05
Populus balsamifera	Spring	3.81	7	0.50	1.99	3	1.18
	E. Summer	2.42	4	0.50	1.63	3	0.68
	L. Summer	1.85	7	0.15	1.42	2	0.06
	Winter	1.11	7	0.11	0.58	3	0.12
Populus tremuloides	Spring	5.07	8	0.55	1.24	3	0.19
	E. Summer	2.62	12	0.34	1.16	3	0.54
	L. Summer	2.30	12	0.22	2.31	3	0.55
	Winter	1.16	8	0.14	0.71	3	0.14
Salix barclayi	Spring	3.94	8	0.93	1.50	3	0.48
	E. Summer	2.70	8	0.39	1.27	3	0.32
	L. Summer	2.10	7	0.15	1.32	3	0.34
	Winter	1.24	4	0.10	0.78	3	0.17
Salix bebbiana	Spring	4.17	14	0.32	0.83	3	0.31
	E. Summer	2.84	15	0.43	0.84	3	0.04
	L. Summer	2.21	15	0.23	1.17	3	0.11
	Winter	1.08	6	0.09	0.68	3	0.14
Salix glauca	Spring	3.74	1	.	1.46	1	.
	E. Summer	2.56	1	.	1.13	1	.
	L. Summer	1.70	1	.	2.92	1	.
	Winter	1.00	1	.	0.94	1	.
Salix pulchra	Spring	3.64	2	0.07	1.82	1	.
	E. Summer	2.37	3	0.07	1.83	1	.
	L. Summer	2.05	5	0.11	1.44	2	0.07
	Winter	1.26	2	0.14	0.75	1	.
Salix scouleriana	Spring	4.12	12	0.20	1.13	3	0.21
	E. Summer	2.64	12	0.42	1.22	3	0.12
	L. Summer	2.12	15	0.18	1.37	3	0.41
	Winter	1.05	9	0.14	0.56	3	0.16
Viburnum edule	Spring	3.46	9	0.36	.	.	.
	E. Summer	2.04	11	0.30	.	.	.
	L. Summer	1.66	12	0.54	.	.	.
	Winter	1.00	7	0.12	.	.	.
Chamerion angustifolium	E. Summer	2.83	5	0.59	0.65	4	0.21
	L. Summer	1.82	14	0.47	0.59	6	0.19
Equisetum spp.	Spring	4.26	3	0.40	2.15	3	0.29

Appendix 2.5 continued

Species	Season	%N	n	SD	ADFN	n	SD
	E. Summer	3.17	3	0.64	2.29	3	0.32
Fern	E. Summer	3.25	3	0.47	2.74	3	0.59
Fern Rhizome	Spring	2.05	3	0.89	1.55	3	0.17
	E. Summer	1.55	3	0.49	1.52	3	0.08
Grass	Spring	3.66	5	0.24	1.39	5	0.82
	E. Summer	2.77	5	0.26	0.49	5	0.15
	L. Summer	1.57	3	0.55	0.65	3	0.35

Appendix 2.6. Concentrations of neutral detergent fiber (NDF g/g), acid detergent fiber (g/g) and total phenols (mg gallic acid equivalents/g) in dry mass of major forages for moose near Anchorage, Alaska, USA.

Species	Season	NDF	n	SD	ADF	n	SD	Total Phenols	n	SD
Betula papyrifera	Spring	34.81	14	3.68	10.26	6	0.45	13.67	6	3.90
	E. Summer	49.02	13	3.30	19.66	14	3.15	9.72	6	1.21
	L. Summer	48.94	5	1.40	22.21	11	2.53	10.82	6	2.75
	Winter	54.73	3	2.92	40.10	3	2.56	46.67	3	6.24
Populus balsamifera	Spring	26.69	3	2.38	12.15	6	1.69	36.19	6	6.65
	E. Summer	33.35	4	5.79	14.90	3	3.20	30.88	4	9.64
	L. Summer	37.39	3	2.59	17.75	7	1.71	28.07	6	8.23
	Winter	42.48	3	2.82	29.76	3	2.86	70.17	3	5.45
Populus tremuloides	Spring	30.02	4	2.29	9.83	3	0.63	22.00	4	11.88
	E. Summer	40.32	6	3.73	18.68	5	2.35	31.38	6	9.24
	L. Summer	45.26	5	2.85	24.97	4	3.85	21.04	6	4.65
	Winter	50.49	3	4.89	35.47	3	4.75	47.21	3	6.39
Salix barclayi	Spring	29.37	4	4.35	11.65	4	2.22	12.51	3	1.04
	E. Summer	35.44	5	3.75	15.56	7	2.91	26.73	6	11.39
	L. Summer	35.61	3	0.13	15.42	3	1.46	35.76	4	5.61
	Winter	48.22	3	7.97	34.60	3	7.00	70.73	3	17.31
Salix bebbiana	Spring	36.89	5	3.25	18.95	3	0.36	8.53	6	4.00
	E. Summer	42.44	6	2.66	18.19	7	1.38	10.90	6	1.67
	L. Summer	42.93	7	2.45	19.89	7	2.08	11.12	6	3.36
	Winter	51.75	3	4.38	38.08	3	3.72	69.58	2	3.54
Salix glauca	Spring	41.91	1	.	17.67	1	.	11.90	1	.
	E. Summer	43.52	1	.	20.90	1	.	9.90	1	.
	L. Summer	45.76	1	.	22.51	1	.	8.97	1	.
	Winter	47.90	1	.	35.52	1	.	56.83	1	.
Salix pulchra	Spring	32.76	2	1.28	11.98	2	0.84	51.41	2	9.99
	E. Summer	30.99	3	3.82	13.64	3	1.24	88.50	3	26.19
	L. Summer	36.48	5	2.85	16.47	5	1.42	52.88	4	1.27

Appendix 2.6 continued

Species	Season	NDF	n	SD	ADF	n	SD	Total Phenols	n	SD
	Winter	50.75	2	0.97	35.62	2	2.15	72.82	2	0.60
Salix scouleriana	Spring	35.71	3	4.13	16.81	3	0.71	13.26	3	3.98
	E. Summer	41.33	6	4.46	18.24	6	2.20	22.53	6	11.53
	L. Summer	39.73	4	5.02	20.90	9	1.80	21.25	6	3.29
	Winter	56.51	3	6.61	42.71	3	5.97	55.56	3	22.91
Viburnum edule	Spring	39.59	9	3.83	20.06	9	2.40	10.39	4	3.14
	E. Summer	45.23	11	5.33	19.82	8	1.22	8.37	5	2.15
	L. Summer	35.70	3	2.24	21.03	7	2.34	10.72	5	1.81
	Winter	52.08	3	2.41	37.15	3	1.59	41.24	3	4.64
Chamerion angustifolium	E. Summer	24.90	3	7.04	14.42	3	5.21	20.84	4	11.69
	L. Summer	38.68	6	2.43	20.43	6	8.10	20.61	6	9.72
Equisetum spp.	Spring	34.15	3	2.12	15.11	.	1.09	0.68	3	0.08
	E. Summer	50.65	3	1.73	20.83	3	1.05	0.80	3	0.04
Fern	E. Summer	49.26	3	2.98	22.00	3	1.92	0.75	3	0.17
Fern Rhizome	Spring	40.03	3	7.11	19.17	3	4.35	1.61	3	0.61
	E. Summer	46.39	3	9.28	24.22	3	6.01	1.97	3	1.14
Grass	Spring	55.66	5	1.59	17.95	5	2.22	0.49	5	0.07
	E. Summer	61.69	5	1.51	19.13	5	1.02	0.73	5	0.15
	L. Summer	61.39	3	3.52	23.44	3	1.78	1.11	3	0.35

Appendix 2.7. Proportions of plant fragments (%) determined by microhistology of pooled fecal samples (n = 5 except for winter where n = 10) from moose near Anchorage, Alaska, USA.

Species	Spring (%)	Early Summer (%)	Late Summer (%)	Winter (%)
Woody Browse Species (Shrubs)				
Alnus spp. leaf	0.0	1.2	1.3	0.0
Alnus spp. stem	2.6	0.9	0.0	2.9
Betula spp. leaf	0.0	1.2	5.7	1.8
Betula spp. stem	11.7	0.0	1.5	38.4
Cornus canadensis leaf	0.0	1.4	0.0	0.0
Menziesia ferruginea leaf	1.0	1.9	2.5	0.3
M. ferruginea stem	2.1	0.3	0.6	0.8
Populus tremuloides leaf	0.0	0.0	1.3	0.5
Populus balsamifera stem	3.4	1.0	0.4	11.9
Populus tremuloides stem	1.6	2.4	3.9	5.1
Rosa acicularis stem	0.0	1.0	0.0	0.0
Rubus spp. leaf	0.1	1.2	0.8	0.0
Rubus spp stem	0.5	0.3	0.3	1.2
Salix barclayi leaf	0.0	7.9	6.8	0.0
Salix bebbianna leaf	0.0	9.9	8.5	0.0
Salix pulchra leaf	0.0	2.8	9.7	0.0
Salix scouleriana leaf	0.0	19.2	20.9	0.0
Salix spp. leaf	0.5	0.0	0.0	0.8
Salix spp. stem	14.0	16.7	16.8	32.4
Sambucus racemosa leaf	0.0	0.0	3.4	0.0
Vaccinium spp. leaf	0.4	0.9	0.7	0.0
Vaccinium spp stem	0.0	0.0	0.0	2.6
Viburnum edule leaf	0.9	0.0	0.0	0.0
V. edule stem	5.8	1.0	0.8	0.5
Shrub leaf	1.0	0.7	0.7	0.0
Shrub stem	0.2	0.0	0.0	0.3
Total Shrub	**45.8**	**71.9**	**86.6**	**99.5**
Non-Shrub				
Undetermined Forb	0.0	0.8	0.0	0.0
Chamerion angustifolium	0.1	0.4	4.8	0.0
Equisetum spp.	4.1	3.3	1.4	0.0

Appendix 2.7 continued.

Species	Spring (%)	Early Summer (%)	Late Summer (%)	Winter (%)
Lupinus arcticus	0.0	1.3	1.1	0.0
Composite Forb	0.0	1.1	0.0	0.0
Forb	0.0	2.1	0.6	0.0
Fern Rhizome	39.3	4.1	0.0	0.0
Fern[1]	0.5	3.8	0.0	0.0
Carex	0.6	1.7	1.3	0.0
Grass	8.3	6.4	3.6	0.5
Classic Moss	0.0	3.1	0.6	0.0
Total Non-shrub	**54.2**	**28.1**	**13.4**	**0.5**

Appendix 2.8. In sacco digestibility (g/g) of dry matter (DDM) and NDF (DNDF) major forage items for moose near Anchorage, Alaska, USA.

Species	Season	DDM	n	SD	DNDF	n	SD
Betula papyrifera	Spring	70.81	14	3.16	68.03	5	4.67
	E. Summer	66.65	11	2.75	56.68	8	2.15
	L. Summer	63.79	4	0.87	53.21	3	1.69
	Winter	43.96	3	5.29	19.82	3	12.30
Populus balsamifera	Spring	89.80	6	1.50	82.67	3	3.82
	E. Summer	89.23	4	4.43	74.65	3	2.98
	L. Summer	82.44	7	3.51	72.00	3	5.25
	Winter	65.77	3	3.62	36.79	3	7.59
Populus tremuloides	Spring	92.23	3	1.53	83.89	3	5.28
	E. Summer	82.67	6	1.32	68.55	6	7.49
	L. Summer	76.31	5	2.48	64.02	4	1.88
	Winter	58.65	3	2.42	33.97	3	0.91
Salix barclayi	Spring	92.51	3	0.11	83.53	3	3.70
	E. Summer	89.89	4	1.53	80.13	3	5.10
	L. Summer	86.68	4	3.17	75.91	3	5.06
	Winter	63.73	3	8.67	39.02	3	6.63
Salix bebbiana	Spring	76.73	6	3.36	66.93	5	4.50
	E. Summer	80.62	7	2.25	67.81	6	4.18
	L. Summer	80.83	3	1.50	64.36	4	7.56
	Winter	60.27	3	5.51	38.16	3	5.80
Salix glauca	Spring	72.22	1	.	53.69	1	.
	E. Summer	79.98	1	.	62.64	1	.
	L. Summer	79.25	1	.	64.22	1	.
	Winter	61.64	1	.	34.84	1	.
Salix pulchra	Spring	81.28	2	1.19	61.93	2	7.07
	E. Summer	72.43	3	1.72	38.27	3	2.94
	L. Summer	68.53	5	4.24	37.71	5	9.25
	Winter	63.20	2	6.83	40.66	2	12.53
Salix scouleriana	Spring	86.13	3	2.94	75.27	3	4.38
	E. Summer	82.86	6	6.31	75.09	5	3.82
	L. Summer	80.82	6	4.66	63.78	4	5.23
	Winter	54.64	3	11.42	35.03	3	10.49
Viburnum edule	Spring	83.41	9	6.08	74.75	9	8.40
	E. Summer	86.44	10	4.45	82.89	8	4.18
	L. Summer	91.13	5	2.64	88.42	3	3.91
	Winter	50.55	3	6.74	26.50	3	9.70

Appendix 2.8 continued.

Species	Season	DDM	n	SD	DNDF	n	SD
Chamerion angustifolium	E.Summer	85.81	4	7.00	49.75	3	29.43
	L. Summer	83.89	3	3.70	60.41	6	21.78
Equisetum spp.	Spring	93.51	3	0.76	90.21	3	1.23
	E. Summer	92.00	3	2.38	92.72	3	2.20
Fern	E. Summer	72.51	3	4.83	59.20	3	8.59
Fern Rhizome	Spring	69.17	3	5.52	44.99	3	2.73
	E. Summer	62.47	3	10.07	42.33	3	6.33
Grass	Spring	85.85	5	1.83	80.52	5	2.93
	E. Summer	71.19	5	3.45	61.72	5	5.15
	L. Summer	67.70	3	3.15	58.22	3	3.15

Appendix 2.9. Blood values for moose near Anchorage, AK, and the Moose Research Center (MRC), AK. March values are from 2009, 2010, and 2011. November values are from 2009 and 2010. Standard deviations are in parenthesis. MRC values are from February.

Parameter	Units	March (n = 31)		November (n = 24)		Moose Research Center, winter (n = 6)	
BUN[a]	mg/dL	9.29	(3.89)	9.91	(3.39)	-	
Creatinine	mg/dL	1.91	(0.37)	1.90	(0.36)	2.23	(0.32)
Phosphorus	mg/dL	4.57	(0.96)	4.21	(1.26)	6.05	(0.78)
Calcium	mg/dL	9.61	(0.66)	9.78	(1.05)	9.12	(0.45)
Total Protein	g/dL	6.65	(0.39)	6.84	(0.56)	6.63	(0.43
Albumin	g/dL	4.17	(0.24)	4.20	(0.32)	4.20	(0.33)
Globulin	g/dL	2.47	(0.31)	2.63	(0.44)	2.43	(0.12)
Glucose	mg/dL	92.71	(11.46)	112.04	(17.70)	74.33	(17.28)
Cholesterol[b]	mg/dL	72.97	(17.41)	58.25	(9.91)	53.83	(4.96)
ALT[c]	IU/L	34.32	(11.46)	38.17	(11.15)	41.50	(6.35)
ALP[d]	IU/L	64.19	(22.21)	42.71	(9.66)	86.33	(14.4)
GGT[e]	IU/L	25.26	(8.58)	31.5	(6.67)	22.83	(4.26)
Total Bilirubin	mg/dL	0.11	(0.03)	0.12	(0.06)	0.1	(0.0)

[a] Blood urea nitrogen

[b] Samples below the detection limit of 50 mg/dL were valued at 50.

[c] Alanine amino transferase

[d] Alkaline phosphatase

[e] Gamma glutamyl transferase

CHAPTER 3: RELATIONSHIPS BETWEEN MOVEMENT, DIET, AND HABITAT QUALITY OF URBAN MOOSE[2]

3.1 Abstract: We studied movements and foraging behavior of adult female moose in urban Anchorage and Joint Base Elmendorf-Richardson, Alaska. From summer to winter, moose reduced the proportion of time spent active from 52% (12 % SD) to 40% (6 % SD), reduced bedding events from 7.1 (0.9 SD) to 6.0 (1.1 SD) per day, and reduced mean turning angles between locations from 87º (18º SD) to 70º (15º SD). Mean distance traveled between locations did not change by season. Moose diet composition changed from summer to winter with major differences in diets explained by the increase in the proportion of *Betula papyrifera* and other minor shrubs. Moose were more active and more likely to forage in higher quality habitats when foraging on more digestible diets that contained less *B. papyrifera* and more *Salix* spp. In winter, when energetic costs are high and forage quality is relatively low, moose in our study area reduced movement and sought higher quality diets and habitats to increase energetic returns.

3.2 Introduction

Studies that have attempted to determine the effect of urbanization on moose behavior have provided mixed conclusions. Human approach on foot, backcountry skiing, motor vehicle, and low altitude aircraft flights all can elicit significant increases in activity and movements in moose (Andersen et al. 1996, Neumann et al. 2009, Støen et al. 2010). However, some studies have shown that moose can become habituated to human

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[2] Welch, J.H., S.D. Farley and P.S. Barboza. Relationships between movement, diet and habitat quality of urban moose. Prepared for the journal Alces

infrastructure and may use areas near development for protection from predators especially during calving (Belant et al. 2006, Berger 2007, Tinoco Torres et al. 2011). Intense disturbance from overhead aircraft, simulated aircraft noise, and devices specifically designed to frighten urban ungulates have also had little effect on animal activity in some areas (Krausman et al. 2004, Lawler et al. 2005, Vercauteren et al. 2005, Weisenberger et al. 1996).

Behavioral responses of moose to forage distribution and quality are likewise inconsistent. High browse density has been correlated not only with increased activity and increased diet selectivity (Vivas and Saether 1987), but also with decreased activity (Dussault et al. 2005). Low browse density has been shown to decrease distance travelled and decrease diet selection (Saether and Andersen 1990), but low browse density may also increase search time and distance travelled (Risenhoover 1987). Anthropogenic disturbances that alter the distribution and quality of forages for moose would be expected to influence activity and diet. However, the foraging behavior of urban moose has received little attention even though moose frequent developed areas in North America and Europe.

The fragmented landscape of Anchorage, Alaska and the adjacent military lands of Joint Base Elmendorf-Richardson (JBER) support a hunted population of moose. Habitats differ in nutritional quality within this urbanized landscape (Chapter 2, this thesis). Moose are exposed to a range of anthropogenic disturbances common to urban landscapes (i.e., traffic, pedestrians, and industrial activity), as well as disturbances unique to active military bases (i.e., armored vehicles, low-flying jet aircraft, and weapons fire). We captured 4 moose in urban portions of JBER and Anchorage and fitted them with Global Positioning System (GPS) collars programmed to record hourly locations. Tri-axial accelerometers in the GPS collars recorded the activity level (number of active seconds per minute) every minute. The purpose of our study was to determine daily bedding rates and patterns in the proportion of time spent active during a day for moose living in this fragmented, urban-military environment. We compare daily bedding rates and patterns in the proportion of time spent active during a day of this urban moose population to previous descriptions of non-urban populations. This study also determined relationships between moose movement parameters (proportion of time spent active, bedding rates, mean distance between GPS locations, mean magnitude of turning between GPS locations), diet quality, and the nutritional quality of habitat. We hypothesized that moose diet quality would improve as moose increased movement parameters. We also hypothesized that diet quality would increase as moose moved through shrublands.

3.3 Study Area

The study was conducted on JBER and an adjacent suburban district of Anchorage, AK, USA (Fig. 3.1). The entire city of Anchorage and JBER has a population of over 300,000 people (US Department of Defense 2012, US Census Bureau 2010). Greenbelts, municipal parks, and other lightly developed areas are common throughout Anchorage (McDonald 1991). JBER is primarily forested (66 %) but includes habitats ranging from coastal mudflats to alpine tundra. A detailed description of JBER habitats available to moose has been provided in chapter 2 of this thesis. The region has a transitional climate between the maritime Gulf of Alaska and the continental interior. Average daily air temperatures range from +15°C in July to -9°C in January. Average annual total precipitation is approximately 40 cm (rain equivalent), with 186 cm of snowfall (Alaska Climate Research Center 2012).

3.4 Methods

3.4.1 Animal Captures

Animals were studied under approved protocols for animal care and assurance from Alaska Department of Fish and Game (#90-05) and from the University of Alaska Fairbanks (#148885, 182744). Adult female moose were captured in March 2009 ($n = 4$) within 0.5 km of roads by methods provided in chapter 2 of this thesis.

3.4.2 Fecal Collections and Diet Analysis

Fecal Collections.—Fresh fecal samples were collected from 4 animals at the time of their capture, as well as periodically throughout the study. At the time of collection, the date and location of the fecal sample was recorded. Later in GIS, we identified the movement paths recorded on GPS collars of moose that deposited each fecal sample using the date and location of defecation. If the moose was not observed defecating, we estimated the time since the fecal sample was voided given how long we had been tracking it, and the temperature, moisture content, and color of the fecal sample (D. Spalinger, Univ. of AK-Anchorage, unpubl. data). Fresh fecal samples were placed on dry ice in the field and stored at -20 ºC within 8 h of collection and later freeze dried to constant mass for analysis. Fecal collections occurred during winter of 2009 and 2010 (*n*

= 6 fecal samples), summer of 2010 (*n* = 21 fecal samples) and winter of 2010 and 2011 (*n* = 14 fecal samples).

Microhistology and Diet Determination.—Dried fecal samples were analyzed for plant composition by microhistology at the Wildlife Habitat and Nutrition Laboratory (Washington State University, Pullman, WA). We used the mean digestible dry matter (DDM) values of moose forages in south-central Alaska (chapter 2, this thesis) to correct microhistology proportions (Boertje 1984). We divided each plant's microhistology result by its respective indigestibility (1-DDM), and then standardized the results across entire fecal samples on a scale of 0-100% (chapter 2, this thesis). We used the mean DDM for all shrubs (chapter 2, this thesis) to correct the proportions of unidentified shrubs and minor browse species in the diet that included *Alnus* spp., *Cornus canadensis*, *Menziesia ferruginea*, *Rosa acicularis*, *Rubus* spp., *Sambucus racemosa*, and *Vaccinium spp*. Likewise, we used the mean DDM for all forbs (chapter 2, this thesis) to correct proportions of unidentified forbs as well as late summer *Equisetum* spp. and *Lupinus arcticus*. Proportions of *Salix myrtilliofolia* leaves were corrected with the mean digestibility of all *Salix* species. Proportions of sedge were corrected with the digestibility of grass. Proportions of moss, lichen, and conifer were corrected with published digestibilities of these forages in ruminants (Person et al. 1980, Ullrey et al. 1967). Finally, because *Salix* spp. stems could not be resolved to species in winter, we corrected the winter proportions of *Salix* spp. stems in the feces by the DDM of the most abundant *Salix* species (*S. bebbiana*) in the study area.

Seasonal digestibility (%DM) and available nitrogen (%DM) of each diet were estimated from the individual proportions of plants in the diets and the mean digestibility and available nitrogen content of each plant (chapter 2, this thesis).

3.4.3 Habitat Classification and Delineation

The landscape on JBER was classified into 7 habitat types as described by in chapter 2 of this thesis. These 7 habitats included barrens, conifer forest, deciduous forest, grasslands, mixed conifer/deciduous forest, shrublands, and shrubby wetlands. We classified Anchorage habitats into the same 7 habitats classes as JBER using baseline data from the 2001 National Land Cover Database (NLCD; U.S. Geological Survey). This coverage classified 12 habitats in 30 m x 30 m cells for our study area in Anchorage. These classifications were condensed to: barrens (high intensity developed, medium intensity developed, low intensity developed, and open water); grasslands (open space developed, emergent herbaceous wetlands, and pasture/hay); shrublands (shrub/scrub); deciduous forests; conifer (evergreen); mixed forests; and shrubby wetlands (woody wetlands). The reclassified NLCD map (raster) was converted to the same format as the JBER habitat map (shapefile). Since the NLCD raster resolution (30 m grid) was coarser than the JBER habitat map (10 m polygons), we compared the reclassified Anchorage habitat map with recent aerial photos in GIS and assessed the accuracy of habitat classifications and boundaries by direct observation. Researchers assessed the accuracy of habitat classifications and boundaries by visiting the portion of Anchorage included in our study and marking habitat boundaries and habitat classifications on hard-copy aerial photos. Subjective classifications were made by researchers familiar with JBER habitats to best approximate the classifications on JBER. It was not possible to delineate small fragments of barrens, grasslands, and shrublands within neighborhoods and other lightly developed areas in GIS. Therefore, we classified these lightly developed neighborhoods as a separate habitat type. In GIS, we corrected the boundaries and classifications of habitat polygons in the Anchorage habitat shapefile with the aid of 0.25 m – 9.0 m resolution aerial photos

3.4.4 Movements

To correlate movements associated with the diets from collected feces, we first defined the time period moose were likely consuming food (foraging period). Due to retention time of food particles in the digestive tract, there is a time lag between foraging and defecation. We used mean retention times (MRT; h) of particles in moose fed browse during summer and winter to define the foraging period: the end of the period was MRT – 1 standard deviation (SD) for small (2 mm) particles whereas the start of the period was MRT + 1 SD for large (20 mm) particles for moose fed browse (Lechner et al. 2010). Our estimated foraging period was 34 – 55 h prior to defecation in summer and 70 – 93 h prior to defecation in winter.

Hourly locations during foraging periods were selected and exported as new datasets in GIS. GPS collars recorded activity data every minute. Activity data was measured with a three-axis accelerometer. Three axis accelerometers recorded the number of seconds during a minute that detected acceleration or tilt in any of the three planes of motion (Telonics 2009). Inactive points were defined as locations with a mean activity value <1.0 active seconds per minute for the five minute interval around each point (D.

Battle, AK Dept. Fish & Game, unpubl. data). Inactive points were assumed to be from a bedded moose. Data for each foraging period was visually screened in GIS to locate bedding events. A bedding event was defined as a single inactive point or a group of successive inactive points located closer than the sum of their GPS horizontal errors. Only one location per bedding event was used for calculations for the distance moved between locations (step length) and the angle turned when moving from one location to another (turning angle). We used the "Calculate Path Metrics" command in Geospatial Modeling Environment (GME; Spatial Ecology LLC) to calculate step length and turning angle. Step length was calculated as the linear distance between locations at time t and $t + 1$. Turning angle was the angle at time t formed as the moose moved between location $t - 1$, t, and $t + 1$ (-180° to 180°). We used the mean absolute value of the turning angle to represent mean turning magnitude. The mean step length and mean turning magnitude was calculated for each foraging period.

3.4.5 Habitat Value

In a GIS, we estimated the nutritional value of the habitats encountered by a moose during a foraging period. In a GIS, we connected all locations in a foraging period with a straight line and buffered all lines by the mean step length of the foraging period. We defined the buffered area for each foraging period as the foraging extent. The area (ha) of each habitat within the foraging extent was summed. We multiplied the summed area of each habitat by the nutritional value of each habitat. The nutritional value of each habitat was expressed as the number of adult female reproductive moose that could be supported per hectare of habitat per day, or daily animal unit (AU; chapter 2, this thesis).

We used AU values derived from the limiting nutrients for this population in summer (energy intake) and winter (nitrogen; chapter 2, this thesis). AU values were not available for the newly defined neighborhood habitat. We estimated the proportion of habitats within neighborhoods from 100 random points generated in GIS and overlaid on aerial photos. Random points were visually screened and classified as barrens, grasslands, or shrublands. We estimated that neighborhoods were 49% barrens, 28% grasslands, and 23% shrublands. Estimated compositions were used to estimate the AU value of neighborhoods. Mean AU values for foraging extents were compared by statistical analysis.

3.4.6 Statistical Analysis

We analyzed data at two temporal scales: season and sub-season. The season scale included: summer (6 Jun —26 Aug) and winter (8 Nov —14 Mar). The sub-season scale included: early summer (6 Jun — 12 Jul), late summer (23 Jul —26 Aug), early winter (8 Nov — 12 Jan), and late winter (8 Mar — 14 Mar). To test for crepuscular behavior, we analyzed for significant differences between the proportion of time spent active near civil twilight and the proportion of time spent active during mid-day. Civil twilight is the time period before sunrise and after sunset when terrestrial objects can still be seen clearly without the aid of artificial light (US Naval Observatory, http://www.usno.navy.mil/USNO). We tested for differences between time periods with analysis of variance (ANOVA) followed by Tukey HSD (honestly significant difference) tests for multiple comparisons between time periods. For comparisons of time periods, we used the mean activity levels of the two hours near civil twilight (late summer: 0500 –

0600 and 2200 – 2300; early winter: 0900 – 1000 and 1600 – 1700; late winter: 0700 – 0800 and 1900 – 2000) and the two hours surrounding mid-day (late summer: 1000 – 1100; early winter: 1200 –1300; late winter: 1000 – 1100 and 1500 – 1600). In early summer when there was no civil twilight, we used the early-day period from 0200 – 0300, the mid-day period of 1100 – 1200, and the late-day period of 2100 – 2200.

To test for differences in diets by season, we first grouped diet components into 6 main categories: *Salix* spp., *Betula papyrifera*, *Populus balsamifera*, *Populus tremuloides*, other shrubs, and non-shrubs. We used principal components analysis (PCA) to describe diet composition as two orthogonal variables. Diet, movement, and AU data were transformed if they originally did not meet assumptions of normality and homogeneity of variance. Activity for all seasons and mean AU values during summer seasons were 4th root transformed (Zar 1999), while step length was Log_{10} transformed (Quinn and Keough 2002). All diet proportions were transformed to the arcsine square-root except for total non-shrubs. We used a purely nested design with Type I Sums of Squares to test for ordered effects of season with individual nested within season. Individual effects in the models were not significant unless otherwise noted. Post-hoc multiple comparisons were made with Tukey HSD tests once it was determined that the analysis had sufficient power (> 0.9). Total non-shrubs could not be normalized so seasonal differences were analyzed with the non-parametric Wilcoxon test. We found uneven residuals when analyzing seasonal differences in available nitrogen of the diet so we used the non-parametric Kruskal-Wallis test.

We used least squares linear regression to examine relationships between diet (i.e., digestibility, available N), movement parameters, activity parameters, and mean AU values. We used Cook's D_i to test for the influence of each observation. We used the criteria of *Di* > 1.0 to indicate influential points. Statistical analyses were conducted in JMP Statistical Packages (version 9.0.02, SAS Institute Inc. Cary NC). Means are presented with ± one standard deviation ($\bar{x}$ ± SD).

3.5 Results

3.5.1 Activity and Movements

A total of 880 locations were recorded from November 2009 to March 2011 during 39 foraging periods. Activity for each hour of the day ranged from 0 % to 91 % in summer and 0 % to 86 % in winter. In all sub-seasons, peaks in mean activity were present throughout the day (Fig. 3.2). In early and late summer, peaks in activity coincided with the mean time of civil twilight in late summer (Fig. 3.2B). In both summer sub-seasons, mean activity was low during mid-day. Only the late-day peak in activity in early summer was significantly higher than the mid-day lull ($F = 6.09$; 2, 51 df; $P < 0.01$), whereas in late summer both peaks in activity were significantly higher than the mid-day lull ($F = 5.58$; 2, 40 df; $P < 0.01$). In winter, activity was also high around civil twilight (Fig. 3.2C, 3.2D) with lulls during mid-day. In early winter both peaks were significantly higher than the mid-day lull ($F = 7.32$; 2, 73 df; $P < 0.01$), whereas in late winter only the late day peak was significantly higher than the mid-day lulls ($F = 5.25$; 3, 49 df; $P < 0.01$).

Moose spent a significantly higher proportion of their time active in summer (52 % ± 12 %) than winter (40 % ± 6 %; $F = 14.01$; 1, 31 df; $P = 0.0007$), bedded more often in summer (7.1 ± 0.9) than winter (6.0 ± 1.1; $F = 12.12$; 1, 31 df; $P = 0.0015$), and had a greater mean turning magnitude in summer (87º ± 18º) compared to winter (70º ± 15º; $F = 12.70$; 1, 31 df; $P = 0.0012$. Although all other activities declined, the distance moved between hourly locations was not significantly different by season ($\bar{x} = 115 \pm 87$ m; $F = 0.03$; 1, 31 df; $P = 0.86$).

3.5.2 Diets, Diet Quality, and Habitat Value

Principal components analysis (PCA) of all diets encompassed 67 % of the variation in diet composition in 2 derived variables (PC 1: 44 %, PC 2: 23 %; Fig. 3.3, Table 3.1). *Betula papyrifera* had the largest influence on PC 1 followed by other shrubs, *Salix* spp., and *Populus tremuloides* (Table 3.1). PC 2 was mainly influenced by *P. balsamifera*, non-shrubs, and *Salix spp* (Table 3.1). Evaluation of the scree plot distinguished winter and summer diets (Fig. 3.3), but did not distinguish diets between sub-seasons. ANOVA of PC 1 by season was significant ($F = 17.21$; 3, 26 df; $P < 0.001$). The Tukey HSD test confirmed that early summer was similar to late summer and early winter was similar to late winter, but summer was different from winter diets. ANOVA of PC 2 did not significantly improve the prediction of seasonal diets. Therefore we pooled data into summer and winter and derived new PC scores for each season for further analysis. PC 1 encompassed 46 % of the variation in winter diets and was mainly influenced by *Betula papyrifera*, *Salix spp*., *Populus tremuloides*, and other shrubs (Table 3.1). PC 2 encompassed 25 % of the remaining variation and was largely influenced by

P. balsamifera. Differences in summer diet composition were again largely influenced by *Salix spp*. and *B. papyrifera* (Table 3.1).

Salix spp. was the most prevalent forage in the diet and proportions were similar in the summer and winter (48% ± 14%, $n = 42$; Table 3.2). Dietary proportions of *B. papyrifera* decreased from 29 % ± 11 % ($n = 20$) in winter to only 2 % ± 2 % in summer ($n = 22$; $F = 144.57$; 1, 34 df; $P < 0.001$; Table 3.2). In winter, there was a significant, inverse relationship between the proportion of *Salix spp*. and *B. papyrifera* in the diet ($R^2 = 0.36$, $P < 0.01$). Non-shrub forages also had moderate changes in their prevalence, that increased from 1 % ± 2 % ($n = 20$) of the diet in winter to 15 % ± 11 % ($n = 22$) of the diet in summer ($X^2 = 28.47$; 1 df; $P < 0.01$; Table 3.2). Proportions of *P. balsamifera* in the diet were consistent and moderate across seasons (11 % ± 7 %, $n = 42$; Table 3.2), whereas proportions of *P. tremuloides* were low but increased significantly from 5 % ± 3 % ($n = 20$) in winter to 10 % ± 6 % ($n = 22$) in summer ($F = 14.67$; 1, 34 df; $P < 0.001$; Table 3.2). No significant effect of individual moose was found when analyzing diet plant composition.

As forage quality changed by season (chapter 2, this thesis), so did diet digestibility ($F = 599.61$; 3, 26 df; $P < 0.001$). Diet digestibility in early summer and late summer were distinct, but there was no difference between early winter and late winter diet digestibility. Diet digestibility was 84 % ± 2 % ($n = 13$), 80 % ± 1 % ($n = 9$), and 56 % ± 2 % ($n = 20$) in early summer, late summer, and winter, respectively. Available N also differed by season ($X^2 = 35.59$; 3 df; $P < 0.001$). Differences in nitrogen availability were tested with a non-parametric test and therefore, we were not able to test for effects of individual animals. The available nitrogen content of early and late summer diets were distinct from all other sub-seasons, whereas the available nitrogen content of early and late winter diets were similar to each other. Available nitrogen in the diet was 1.75% ± 0.1% ($n = 13$), 0.97% ± 0.03% ($n = 9$), and 0.46% ± 0.02% ($n = 20$) in early summer, late summer, and winter, respectively.

Mean AU values differed by sub-season ($F = 5.41$; 3, 23 df; $P < 0.01$). Mean AU values were 1.05 ± 0.93 AU ($n = 11$) in early summer, 2.42 ± 1.25 AU ($n = 8$) in late summer, 0.68 ± 0.41 AU ($n = 13$) in early winter, and 0.67 ± 0.28 AU ($n = 7$) in late winter.

3.5.3 Relationships Between Movement, Diet, and Habitat Value

There were no significant relationships between movement, diet, or habitat value in summer. In winter, higher levels of activity were positively correlated with higher values for both PC 1 ($R^2 = 0.34$, $P < 0.01$; Fig. 3.4A) and digestibility ($R^2 = 0.21$, $P = 0.044$; Fig. 3.4B). Also during winter, mean AU values for foraging paths were positively correlated with PC 1 ($R^2 = 0.26$, $P = 0.02$; Fig. 3.4C) and digestibility ($R^2 = 0.21$, $P = 0.04$; Fig. 3.4D). No observations were particularly influential because D_i values were less than 1.0.

3.6 Discussion

Moose in our study exhibited the same crepuscular activity described for populations across their range (Fig. 3.2A, 3.2B; Dungan et al. 2010, Renecker and Hudson 1989). Our study moose also spent a similar proportion of their time active, and bedded just as often, as other populations of non-urban moose (Van Ballenberghe and Miquelle 1990, Dungan et al. 2010, Renecker and Hudson 1989). We would expect to see higher activity rates and more frequent bedding events if human stimuli were causing frequent flight responses or increased movements to avoid human contact. However, these moose do not appear to be affected by urban and military activities.

Habituation is common in many ungulates, and is often food related. Frightening devices placed over food sources were ineffective in deterring urban elk (*Cervus elaphus)* and mule deer (*Odocoileus hemionus)* from feeding (Vercauteren et al. 2005). Propane powered exploding devices and electronic light flashers and sirens had no effect on white-tailed deer habituated to consuming corn crops (Gilsdorf et al. 2004). Key deer have become more urbanized over the past 30 years as indicated by shorter flight distances and shifts to larger groups of individuals and smaller home ranges (Harveson et al. 2007). Reliable food sources also increase group size of deer (Peterson et al. 2005). Moose in Anchorage and JBER likely benefit from the high prevalence of shrub and edge habitat that provide patchy distributions of forage at high density.

Increased activity in summer coincides with the presence of high quality diet items and increased nutritional requirements and intakes (Regelin et al. 1985, Schwartz et al. 1984). Moose must use this short, nutrient rich period to replenish body stores and support the added costs of lactation (Reese and Robbins 1994, Schwartz et al. 1987). Renecker and Hudson (1989) found that as forage fiber decreased and digestible dry matter increased in summer, rumination time decreased and allowed more time to forage. Highly digestible diets in summer allow moose to quickly break down food and more completely empty the rumen (Jiang and Hudson 1996, Renecker and Hudson 1989, White et al. 1984). Higher densities of food allow moose to more efficiently ingest forage (De Jager et al. 2009) and fill the larger available gut space in summer (Van Ballenberghe and Miquelle 1990). Faster, more complete rumination, and higher intake rates allow moose to maximize nutrient intakes.

Summer forbs are highly digestible forages that contain high amounts of available nitrogen and varying amounts of micro and macro elements (chapter 2, this thesis, Oldemeyer et al. 1977). In summer, forbs constituted 12 % to 18 % of moose diets in this study (Table 3.2). These forages may be important diet items for moose in spring and summer. However, forbs may be rare on the landscape or have patchy distributions. Increased turning in summer could be the result of more movement to search for rare forages or forbs that are patchily distributed. Reindeer were found to adopt a random search strategy when forages were distributed beyond their detection range (Mårell et al. 2002). Turning was reduced in winter when the energetic costs of moving through snow may be increased (Parker et al. 1984) and when fat stores are being depleted (chapter 2, this thesis). Through simulation, Zollner and Lima (1999) found that when resources have patchy distributions and risk or cost of movement is increased, uni-directional movement is more successful than random movements in encountering resources. Moose could also be drawing from long term spatial memory, or a cognitive map, of the distribution of food resources to direct their movements along the most profitable or least costly paths (i.e. through shrublands and along roads, sidewalks, through conifer stands; Gautestad and Mysterud 2010, Moen et al. 1997).

When foraging on diets containing higher proportions of *Salix* spp., our urban moose were more likely to move through high quality habitats and increase activity levels (Fig. 3.4). Similar foraging patterns were found for moose foraging on preferred forages in Europe (Saether and Andersen 1990, Vivas and Saether 1987). *Salix* spp. is 11 – 20 % more digestible than *Betula papyrifera* (chapter 2, this thesis), but *B. papyrifera* still comprised 28 – 30% of the diet in winter (Table 3.2). Increasing proportions of *Salix* spp. (Winter PC 1 loading: 0.72) and decreasing proportions *of B. papyrifera* (Winter PC 1 loading: -0.84) and other shrubs (Winter PC 1 loading: -0.69) in the diet result in higher activity levels in winter (Fig. 3.3, 3.4A). PC 1 was positively correlated to diet digestibility ($R^2 = 0.59$, $P < 0.001$) and diet digestibility was positively correlated with activity level (Fig. 3.4B). The inverse relationship between the proportions of *Salix* spp. and *Betula* in the diet, and the relationships between PC 1 and diet digestibility and activity, all imply there is a trade-off between using *Salix* and *Betula*.

A more digestible diet containing higher proportions of *Salix* spp. will yield more digestible energy per gram of dry matter intake (Schwartz, Hubbert, and Franzmann 1988a). This reduces the reliance on body stores during winter. Maintaining good body condition throughout winter reduces the chance of fetal loss (Testa and G. P. Adams 1998). Moose foraging on the poorer quality diets containing *B. papyrifera* could increase intakes to compensate for the less digestible diet (Schwartz et al. 1988). However, if forage densities are reduced below a level where moose are no longer able to achieve maximum intakes, they may no longer be able to compensate for the reduced quality diet and would need to metabolize additional body stores for survival.

3.7 Figures

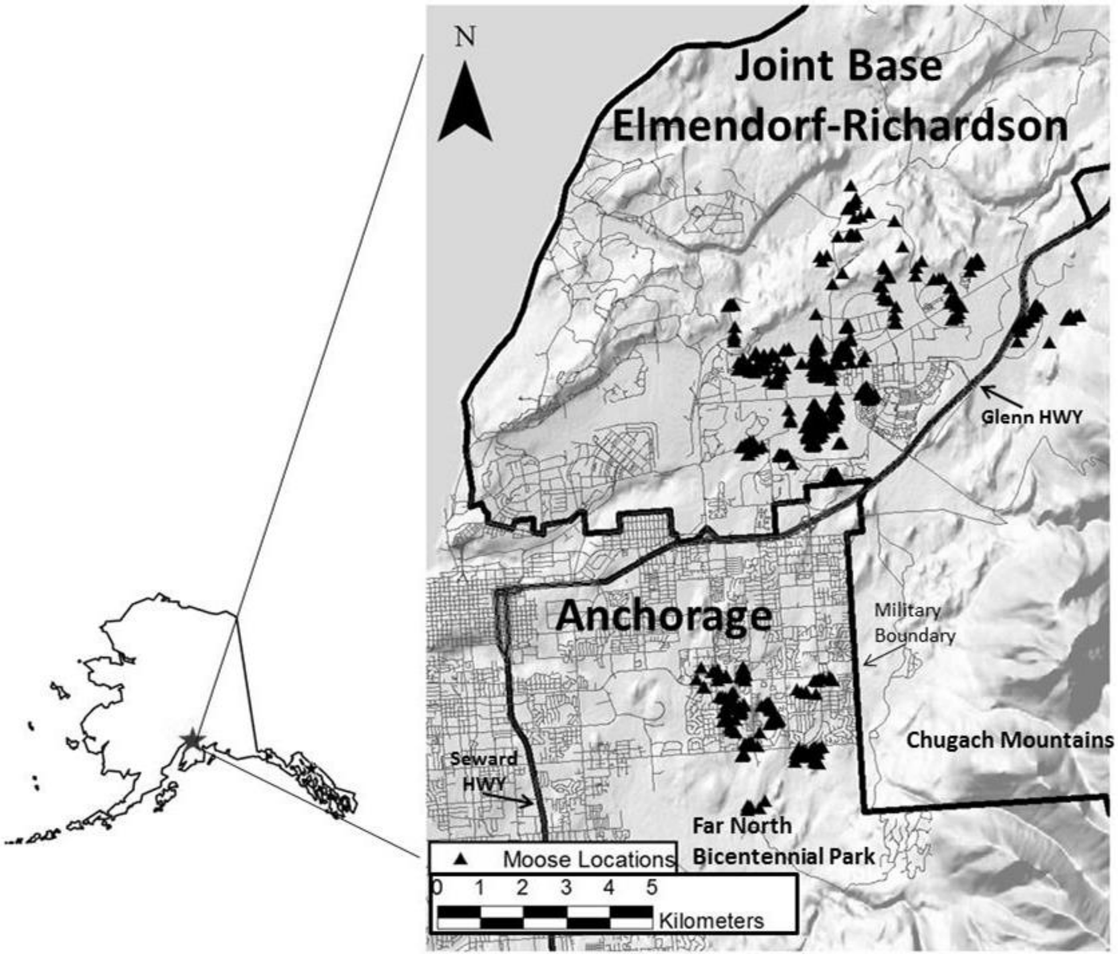

Figure 3.1. Study area for female moose foraging in Anchorage and Joint Base Elmendorf-Richardson, Alaska, USA. Black triangles indicate moose locations used in our analysis

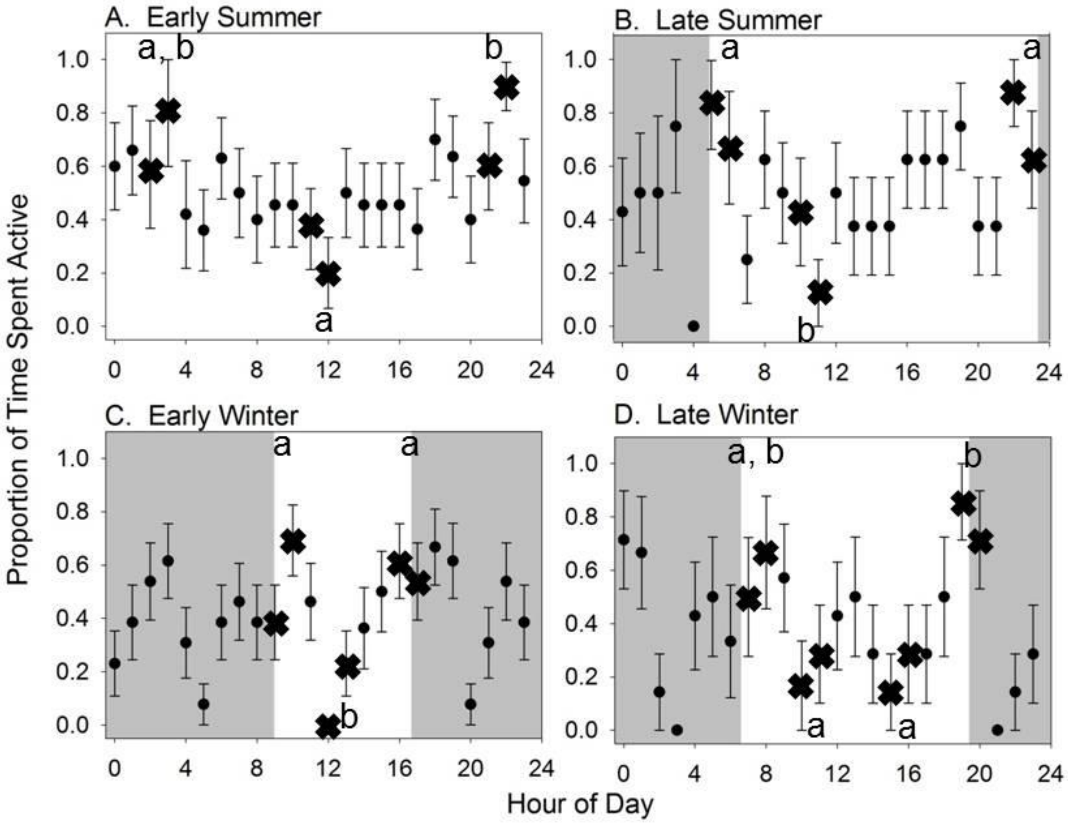

Figure 3.2. Mean (± 1 SE) proportion of time spent active by hour of day for moose in Anchorage and Joint Base Elmendorf-Richardson, AK. Shading edge represents the mean start and end for civil twilight during the respective season. Early summer lacks a civil twilight period due to long days. Bold crosses indicate two-hour time periods that were compared with ANOVA for differences in activity level. A post hoc Tukey HSD test was used for multiple comparisons. Matching lower case letters denote time periods that were not significantly different. Dates for each period were: A. 23 Jul to 26 Aug. B. 6 Jun to 12 Jul. C. 8 Nov to 12 Jan. D. 8 Mar to 14 Mar.

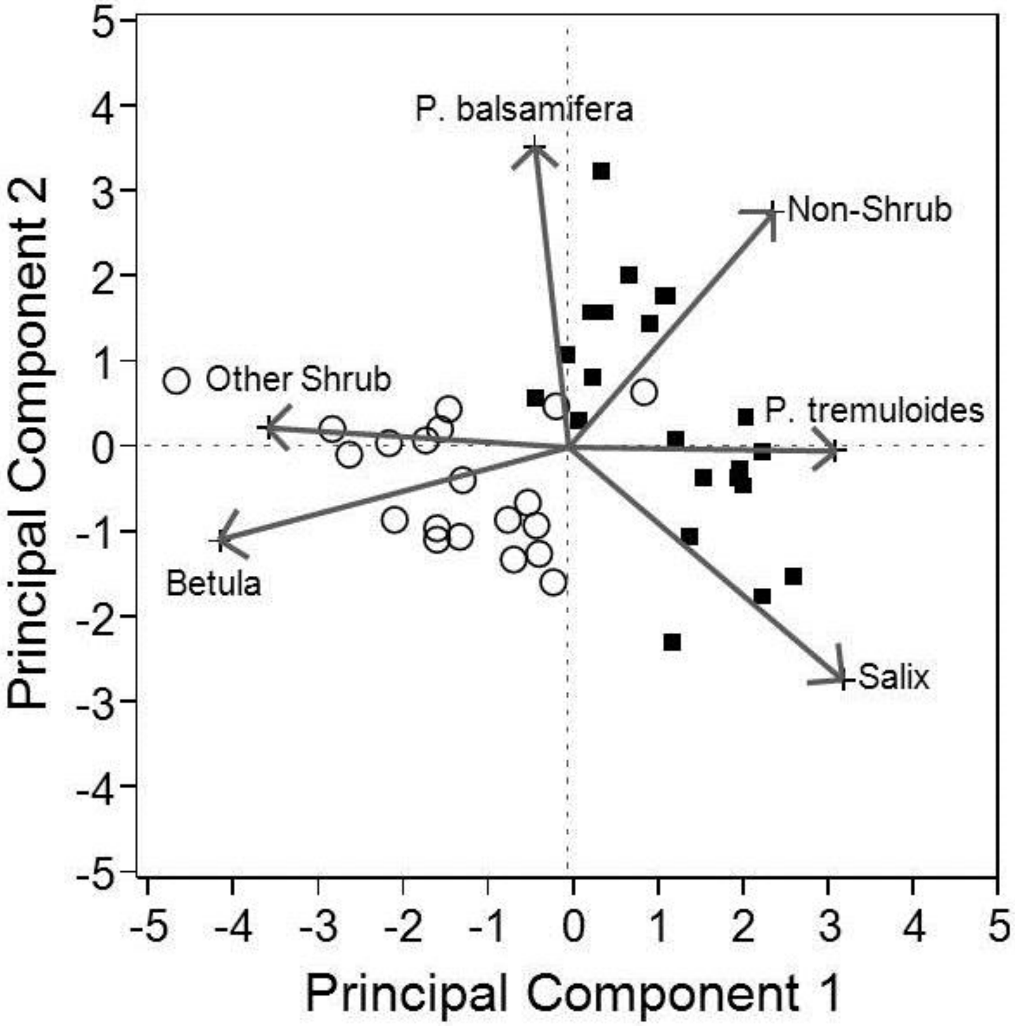

Figure 3.3. Biplot of principal component analysis of diet composition for moose in Anchorage, Alaska during summer (black squares) and winter (open circles). Principal component 1 (PC 1) explained 43.9% of the variance in diets while principal component 2 (PC 2) explained 22.6% of the variance in diets. PC 1 distinguished between the higher proportion of *Betula papyrifera* and other shrubs in winter and the consumption of *Salix* spp., *Populus tremuloides*, and non-shrubs in summer.

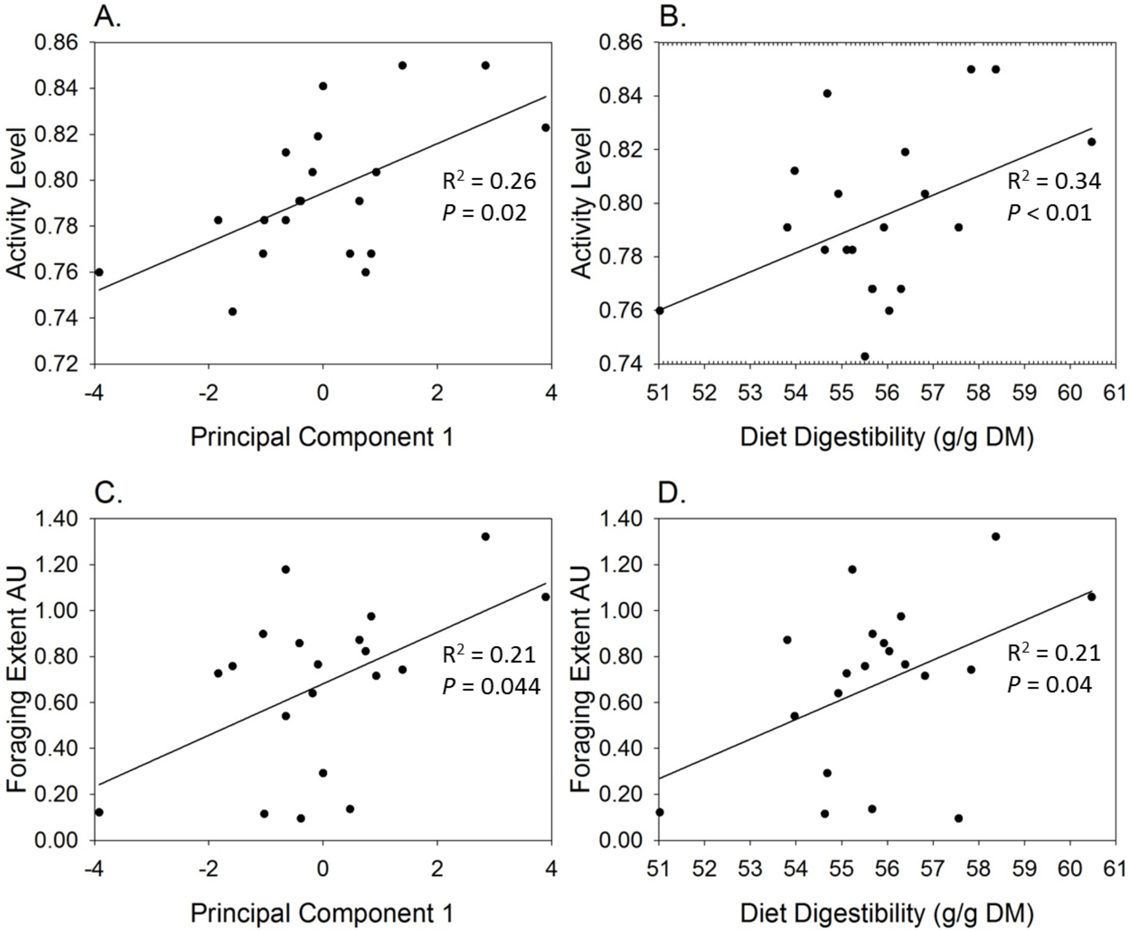

Figure 3.4. Winter relationships between diet, activity level, and mean AU value of foraging extent for adult female moose in Anchorage, AK. Activity level was 4th root transformed for normality. Principal component 1 (PC 1) was derived from winter diet composition. Eigenvector values for PC 1 were *Betula papyrifera*: -0.51, other shrub: -0.41, non-shrubs: 0.45, *Salix* spp.: 0.43, *Populus tremuloides*: 0.41, and *Populus balsamifera* (0.12).

3.8 Tables

Table 3.1. Principal component analysis of diet composition for moose in Anchorage, Alaska, USA.

			Loadings					
Season	Component	Eigenvalue	*Betula papyrifera*	*Populus balsamifera*	*Populus tremuloides*	*Salix* spp.	Other Shrub	Non-Shrub
Combined	PC 1	44%	-0.89	-0.09	0.68	0.70	-0.77	0.52
	PC 2	23%	-0.23	0.77	-0.01	-0.59	0.05	0.60
Winter	PC 1	46%	-0.84	0.20	0.69	0.72	-0.69	0.74
	PC 2	25%	0.08	0.88	0.29	-0.64	0.22	0.40
Summer	PC 1	41%	0.75	0.50	-0.57	-0.86	0.47	0.63
	PC 2	19%	-0.22	-0.58	0.52	-0.32	0.39	0.47

Table 3.2. Percent (%) composition of moose diets for four moose near Anchorage, Alaska, USA. Summer shrub values are for combined stem and leaf. Winter shrub values are for stems unless noted. Sample sizes by season were: early winter: 13; late winter: 7; early summer: 13; late summer: 9.

Species	Early winter	SD	Late winter	SD	Early summer	SD	Late summer	SD
Alnus spp.	7.1	4.8	5.3	2.7	0.3	0.6	0.3	0.4
Betula papyrifera	27.6	13.8	30.4	5.4	2.2	1.8	2.9	3.0
Populus balsamifera	11.3	5.3	9.1	3.5	13.0	8.9	11.2	8.6
Populus tremuloides	4.7	3.4	5.4	2.8	11.2	5.5	8.6	5.5
Salix barclayi					8.9	6.0	10.9	2.6
Salix bebbiana	0.1[1]	0.2	0.1[1]	0.3	10.7	6.1	13.7	4.8
Salix pulchra	0.1[1]	0.3			5.8	3.6	7.3	2.4
Salix scouleriana	0.1[1]	0.2			25.7	7.6	26.8	10.2
Salix spp. Stem	40.6	13.9	46.1	8.9				
Total *Salix* spp.	40.9	14.0	46.2	8.9	48.52	14.7	58.9	11.4
Total Other Shrub	7.1	3.5	3.6	1.4	7.1	6.3	6.7	4.4
Total Shrub	**98.7**	**2.3**	**100**	**0**	**82.0**	**12.1**	**88.2**	**7.7**
Chamerion angustifolium	0.0		0.0		4.4	3.9	5.7	5.7
Equisetum spp.	0.0		0.0		4.1	1.4	0.5	0.6
Grass	0.7	1.4	0.0		5.1	5.1	2.9	1.6

Table 3.2 continued

Species	Early winter	SD	Late winter	SD	Early summer	SD	Late summer	SD
Total Other Forb	0.6	1.2	0.0		4.4	3.9	2.6	1.6
Total Non-Shrub	**1.5**	**2.2**	**0.0**		**18.6**	**11.9**	**12.6**	**7.8**

[1] Proportions represent senesced winter leaves

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CHAPTER 4: CONCLUSION

4.1 Overview

Moose are common on Joint Base Elmendorf-Richardson (JBER), a military base adjacent to Anchorage, which has a long history of land development. The population of moose in Game Management Unit 14C (GMU 14C), which encompasses JBER and Anchorage, has increased since the 1940's as urban and industrial development increased in both area and intensity (Sinnott 2008). The military lands on JBER and the adjacent Ship Creek drainage contain only 27 % of moose in GMU 14C, but provide 57 % of the total harvest from this unit. Wildlife managers on JBER desired to know more about the overall nutritional condition of this heavily harvested moose population and how land development could impact moose nutrition. My objectives for this study were to determine: 1) the relative nutritional value of habitats; 2) the relative nutritional condition of this moose population compared to others in Alaska; and 3) the potential effects of habitat and diet quality on moose movements in this fragmented, urban landscape. During this study, I successfully determined the nutritional condition of this population, evaluated the relative nutritional value of habitats on JBER as reflected by the hypothetical number of animal units (AU; moose-days per hectare) the habitats could support in three seasons, and evaluated the influence of diet and habitat quality on moose movements in a fragmented, urban landscape.

4.2 Moose Nutritional Condition and Habitat Value

To calculate the relative nutritional value of each habitat, I developed a nutritional model. The model divided nutrient availability per hectare by nutrient demands of a moose per day. To estimate model parameters and to establish an index of population health, I: (1) assessed animal nutritional condition via blood chemistry, reproductive data, rump fat depth, and shoulder muscle depth; (2) estimated nutrient availability as a function of diet, forage quality, and forage biomass, and; (3) estimated nutritional requirements for survival, body store production, and reproduction.

4.2.1 Body Condition

Nutritional indices from blood, reproduction, and fat levels indicated moose on JBER were similar to other populations of moose in Alaska. Twinning rates (0 – 22%) were consistently low and comparable to populations in Alaska with higher browse removal rates (Seaton et al. 2011). However, sample sizes for estimating twinning rates were low (5 –19 animals/year). Twinning rates were estimated from on-the-ground confirmations and were limited to the number of moose accessible by vehicle and on foot during the calving season. Better estimates of twinning would require a dedicated study. Rump fat depths, as measured by portable ultrasound (Stephenson et al. 1998), were consistent with high pregnancy rates (Keech et al. 2000, Testa and Adams 1998), and low twinning rates (Stephenson 2003). Differences in shoulder muscle depth from November to March were insignificant, though our sample size was small. Ultrasonic measurement of large muscle groups needs more research before they can be reliably implemented as a measure of body condition in the field or for nutritional models.

4.2.2 Nutrient Availability

Estimates of forage quantity, diet composition, and diet quality were necessary to calculate both nutritional requirements and nutrient availability in the model. I used chemical analysis of forages during multiple seasons to estimate forage quality. I used microhistological analysis of feces to determine diet composition throughout the summer and winter. I used the individual plant quality and the dietary proportions of each component to calculate diet DDM and available N content. During the study, I also estimated total available biomass of forages through the year. I had very large variances for biomass estimates, which was partially because there is large natural variation in the amount of forage biomass contained in each habitat (Morrison et al. 2002). It was also an artifact of only surveying 5 plots per habitat for biomass. Increasing the sample size would decrease the variance and give better estimates of biomass, which would be necessary if a true carrying capacity is desired.

4.2.3 Nutritional Demands

Total nutritional demands for an adult reproductive female moose was the sum of basal metabolic rate, the incremental cost of activity and thermoregulation, and the daily cost for reproduction, and fat production. Total demand was converted to dry matter intake (DMI) and nitrogen (N) intake. I calculated intakes of DM and N from the proportions of plants in the feces as estimated by microhistology.

4.2.4 Calculating Habitat Value

Biomass and N intakes for each species were divided by the availability of each species in each habitat to calculate the number of moose one hectare of each habitat could support for one day, which was the number of animal units (AU; moose-days/ha). I found that AU was limited by energy (DM) in the summer and nitrogen in winter. I also found that winter was the most limiting season. In all seasons, shrublands supported the greatest number of AU. In winter, each hectare of shrublands was estimated to support 3.57 AU, which was equivalent to 11 ha of shrubby wetlands, 17 ha of mixed forest, 19 ha of deciduous forest, 75 ha of coniferous forest and 81 ha of grasslands.

Results from this study will be used to model the effects of land development projects on the moose population. Once sites have been selected for development, my results can be used by to calculate the potential loss of AU. Managers will also be able to account for AU gained from shrublands or grasslands created as edge habitat. If habitat remediation is necessary to make up for lost AU, this information will help managers create an adequate amount of early successional shrublands.

4.3 The Effect of Urbanization and Food on Movements

During this study, I also evaluated the effect of urbanization, diet, and habitat value on moose movements. I found that in summer, moose spent a significantly higher proportion of their time active, had significantly more bedding events, and turned more between hourly GPS locations as compared to winter. These activity patterns were similar to those of non-urban moose (Van Ballenberghe and Miquelle 1990, Dungan et al. 2010, Renecker and Hudson 1989), indicating that moose in urban areas of JBER and Anchorage have become habituated to human activity.

In winter, moose were more likely to move through high quality habitats and have increased activity level when foraging on more digestible diets that contained greater proportions of *Salix* spp. A more digestible diet yields more digestible energy per gram of dry matter intake (Schwartz, Hubbert, and Franzmann 1988a). This reduces the reliance on body stores during winter. Therefore, high value habitats with a high proportion of *Salix* spp, such as shrublands and vegetated wetlands, are important for minimizing winter losses in this population.

These results can also be used to inform land management decisions. If creation of shrubland is necessary to augment moose habitat, wildlife managers should not create shrublands near heavy traffic areas. Shrublands may increase the local density of moose (Suring and Sterne 1998, Telfer 1988), increase conflicts with humans, and increase the frequency of moose-vehicle collisions as animals increase activity in these high quality habitats.

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Moose Habitat Selection within the Military Joint Base Elmendorf – Richardson, Anchorage Alaska

Final Report

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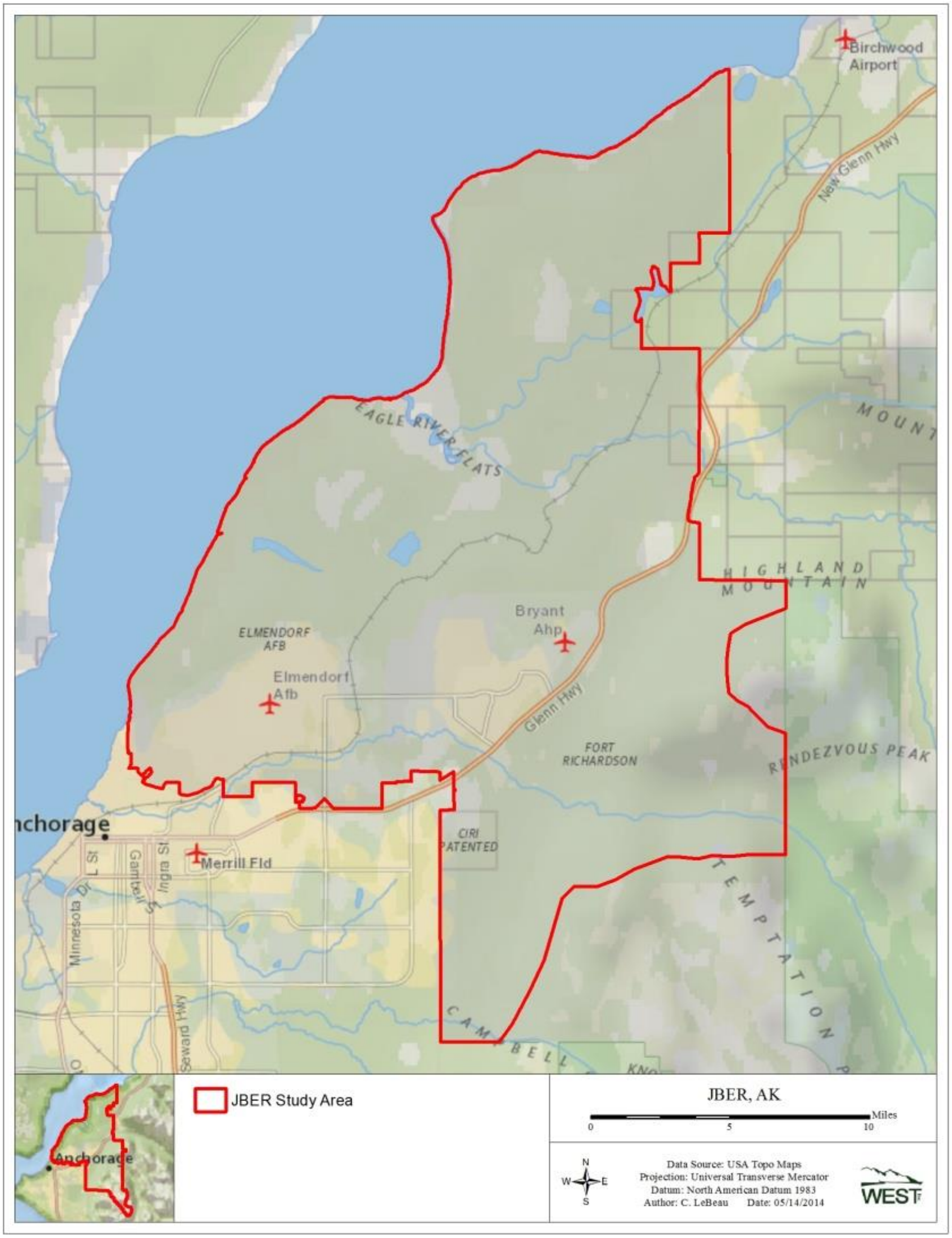
INTRODUCTION

Alaska Department of Fish and Game (ADFG) is interested in female moose (*Alces alces*) habitat selection within the military Joint Base Elemendorf – Richardson (JBER) near Anchorage, Alaska. The population is exposed to both urban and industrial development as well as natural predation and inhabits a highly fragmented landscape. ADFG is interested in identifying moose habitat selection patterns within the JBER to provide future development planning information. The objective of this study was to develop seasonal, behavior-specific resource selection functions (RSF) based on data collected from GPS-collared moose occupying the JBER.

STUDY AREA

The study area was located within the JBER military base near the city of Anchorage Alaska. The JBER military base consisted of 117 mi^2 (303 km^2) and contained a variety of habitat types including mountain ranges (Temptation Peak) and coastal areas. The study area within JBER was the extent of observed moose locations (95 mi^2; [303 km^2]), excluding the mountain ranges located in the southern portion of the JBER (hereafter study area; Figure 1). Elevations within the study area ranged from 0 to 3,012 ft (0-918 m) and contained 8 different landcover habitat types. Deciduous and barren landcover were the dominant habitat types within the study area. The entire base is not ringed by fencing, however sections of fencing are used in places for exclusion zones around ammunition dumps and other sensitive areas. The Glenn highway that bisects JBER has fencing along a portion of the roadway and wildlife gates are placed in the fence at periodic intervals.



Data Source: USA Topo Maps
Projection: Universal Transverse Mercator
Datum: North American Datum 1983
Author: C. LeBeau Date: 05/14/2014

Figure 1. Study area used to develop moose resource selection functions within the JBER military base.

METHODS

Field Methods

Nineteen adult female moose were captured in March 2009 (n=7) and November 2009 (n=12). Moose were darted from the ground with 3 cc darts containing a mixture of 3.0 – 3.9 mg carfentanil (carfentanil citrate, Wildlife Pharmaceuticals, Fort Collins, CO) and 100 mg xylazine (xylazine hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO). Dart wounds were cleaned with 0.1% providone iodine solution and packed with Fura-Zone ointment (0.2% nitrofurazone, Squire Laboratories, Inc., Revere, MA) to reduce risk of infection. A prophylactic dose of 600 - 5,000 mg oxytetracycline (Oxytet, Norbrook, Lenexa, NJ) was administered intramuscularly at the rump. Anesthesia was reversed within 30 minutes of darting by intravenous injection of 400 mg Naltrexone (naltrexone-hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO) and 800 mg Tolazoline (tolazoline-hydrochloride, Wildlife Pharmaceuticals, Fort Collins, CO). All animals were fitted with Telonics Global Positioning System (GPS) Generation IV store-on-board collars equipped with VHF transmitters. Collars were programmed to record one GPS relocation every 30 or 60 minutes. Some animals were successfully recaptured in March and November of 2009, 2010, and 2011 in order to recover location data stored on collars. Because of the partial recapture success the data set used for RSF analyses only contains data from some of the animals.

GIS Covariates

A suite of anthropogenic and environmental (non-anthropogenic) covariates were developed and considered in the habitat selection modeling. Anthropogenic covariates consisted of building density, distance to buildings, and distance to roads (Table 1). Buildings were digitized in the GIS and building density was calculated using the proportion of digitized buildings within 90 m of a location. Roads were classified into 3 groups, tertiary, secondary, and primary based on varying levels of traffic use. Environmental covariates included topographic features (elevation and slope) and landcover (Table 1). Landcover values were derived from the 30 x 30 m pixel level JBER landcover habitat map (2010) and included barren, water, coniferous, deciduous, grassland, mixed deciduous coniferous, shrub, and vegetated wetland. Shrub density was calculated using the proportion of the shrub landcover layer within 90 m of a location. In addition, distance to stream was created from a USGS stream GIS layer.

Table 1. Explanatory anthropogenic and environmental habitat characteristics considered in habitat selection model development for female moose within the JBER study area.

Variable	Description
bden90	Building density within 90 meters of a location
d_build	Distance to buildings (km)
d_cover	Distance to cover: Cover was defined as coniferous, deciduous, and mix deciduous/coniferous landcover types (km)
d_dirtrd	Distance to dirt road (tertiary; km)
d_food	Distance to food: Food was defined as shrub, vegetated wetland, and mixed deciduous/coniferous landcover types (km)
d_majrd	Distance to major road (primary; km)
d_pave	Distance to paved road (secondary; km)
d_stream	Distance to stream (km)
d_water	Distance to water bodies (excluding streams; km)
elevation	Elevation (m)
barren	Barrens landcover type
coniferous	Coniferous landcover type
deciduous	Deciduous landcover type
grassland	Grassland landcover type
mixed deciduous/coniferous (mixed)	Mixed deciduous/coniferous landcover type
shrub	Shrub landcover type
wetland	Vegetated wetland landcover type
water	Water landcover type
shrub90	Density of shrub within 90 meters of a location
slope	Slope (degrees)

Statistical Analysis

Seasonal, behavior-specific female moose habitat selection was assessed by first assigning behavioral states to moose locations, then developing RSFs using discrete choice models (McDonald et al. 2006) separately for each season-behavior combination. Seasons of interest were winter (November 15—May 15), when moose undergo a net energy loss and late summer (July 15—September 15) when moose obtain a large portion of their yearly nutritional intake. Behavioral states of interest were an "encamped" state assumed to be associated with bedding and local foraging, as well as a "traveling" state assumed to be associated with large scale, directed movements between resource patches (Morales et al. 2004).

Assigning Behavioral States

Hidden Markov Models (HMMs; Morales et al. 2004; Langrock et al. 2012) were used to assign a behavioral state to each moose location based on the leg length (distance between consecutive GPS locations) and the turning angle (angle between consecutive GPS locations). Between consecutive GPS locations, movement paths were defined to be a straight line.

Movement characteristics of the encamped state were assumed to be short leg lengths and large turning angles while the movement characteristics of the traveling state were assumed to be long leg lengths and small turning angles (Morales et al. 2004). GPS measurement error was not modeled—we assumed measurement error was negligible relative to the scale of movement during traveling and GPS measurement error is generally consistent with the distributions we expected for the encamped state (small in magnitude and no directional persistence).

Two-state HMMs were fit to seasonal and individual data sets via maximum likelihood (Patterson et al. 2009, Langrock et al. 2012) in R (R Core Team 2012). This maximum likelihood method assumed the transition matrix for the probability of being in each behavioral state was stationary at the first location. Models for winter movements were fitted separately to individuals. Thus, winter locations were pooled across years for each individual. Summer locations were less frequent (approx. 1500 locations per individual); consequently, a single summer period HMM was estimated by pooling summer locations across individuals and years. Due to the Markov property, this pooling of summer locations across years and individuals starts each new year/individual with state probabilities from the last observation of the previous year/individual rather than the stationary transition matrix. Since transitions between years/individuals were infrequent relative to the number of observations (<0.0004% of transitions for all data sets), we assumed this effect on parameter estimates would be negligible.

We considered 4 distributions for leg length—Weibull, gamma, lognormal, and shifted lognormal, and 2 distributions for turning angles—wrapped Cauchy and wrapped normal (leading to 8 models). After fitting all eight models, the relative fit of each was assessed by comparing AIC*c* (Burnham and Anderson 2002). Goodness-of-fit of the top models was assessed using three types of pseudo-residual plots (Patterson et al. 2009, Langrock et al. 2012). Pseudo-residuals were plotted through time, and autocorrelation among pseudo-residuals was plotted. Pseudo-residuals were calculated as in Patterson et al. (2009), using the posterior state probabilities. Behavioral states were assigned using the model that performed best for the majority of moose. Global decoding via the Viterbi algorithm (Zucchini and

MacDonald 2009) was used to produce the most likely sequence of behavioral states for each moose given the observed data.

Development of Choice Sets

Discrete-choice models are usually applied to situations in which a set of resources units are available for selection (the choice set) and a single choice of 1 unit is made from each choice set (McDonald et al. 2006). We developed a choice set for each GPS location that included 5 unused locations. Unused locations in the choice sets were constructed using the distribution of turning angles and leg lengths specific to the moose, season, and behavioral state. The unused locations in a choice set associated with a location at time *t* were constructed by randomly selecting 5 combinations of leg lengths and turning angles, then applying those combinations to the location at time *t-1* (Figure 2). Locations following a missing fix were excluded from the analysis. While this may exacerbate bias due to missing GPS locations (Frair et al. 2004, Nielson et al. 2009, Augustine et al. 2011), the fix rate in this study was high enough that bias should be negligible (Frair et al. 2004).

Encamped locations were characterized by small leg lengths and large turning angles and were generally confined to a small spatial area. Choice sets for encamped locations were small and similar to used locations. This limited our ability to detect non-random habitat selection patterns. Because of this limitation, we averaged multiple encamped locations within a time series (i.e., consecutive locations designated as encamped) to create one encamped location that was representative of the multiple locations within a time series.

Due to impermeable and nearly impermeable boundaries on the study area, the placement of unused locations in the choice set was restricted in certain areas. All unused locations were forced to fall within the study area. Exclusionary fences were present on several parts of the study area. In cases where moose never entered the fenced areas, we did not allow unused points to fall inside the fenced area. In cases where a moose entered a fenced area briefly, perhaps when someone left the gate open, we again did not allow unused points to fall in these areas. Finally, the Glenn Highway was a fenced, low-permeable boundary on the study area that was rarely crossed by moose. Therefore, we did not consider areas on the opposite side of the Glenn Highway from current moose locations as available for use. In cases where a moose did cross the Glenn Highway, locations on the other side of the highway were considered available for locations after the first location on the other side of the road.

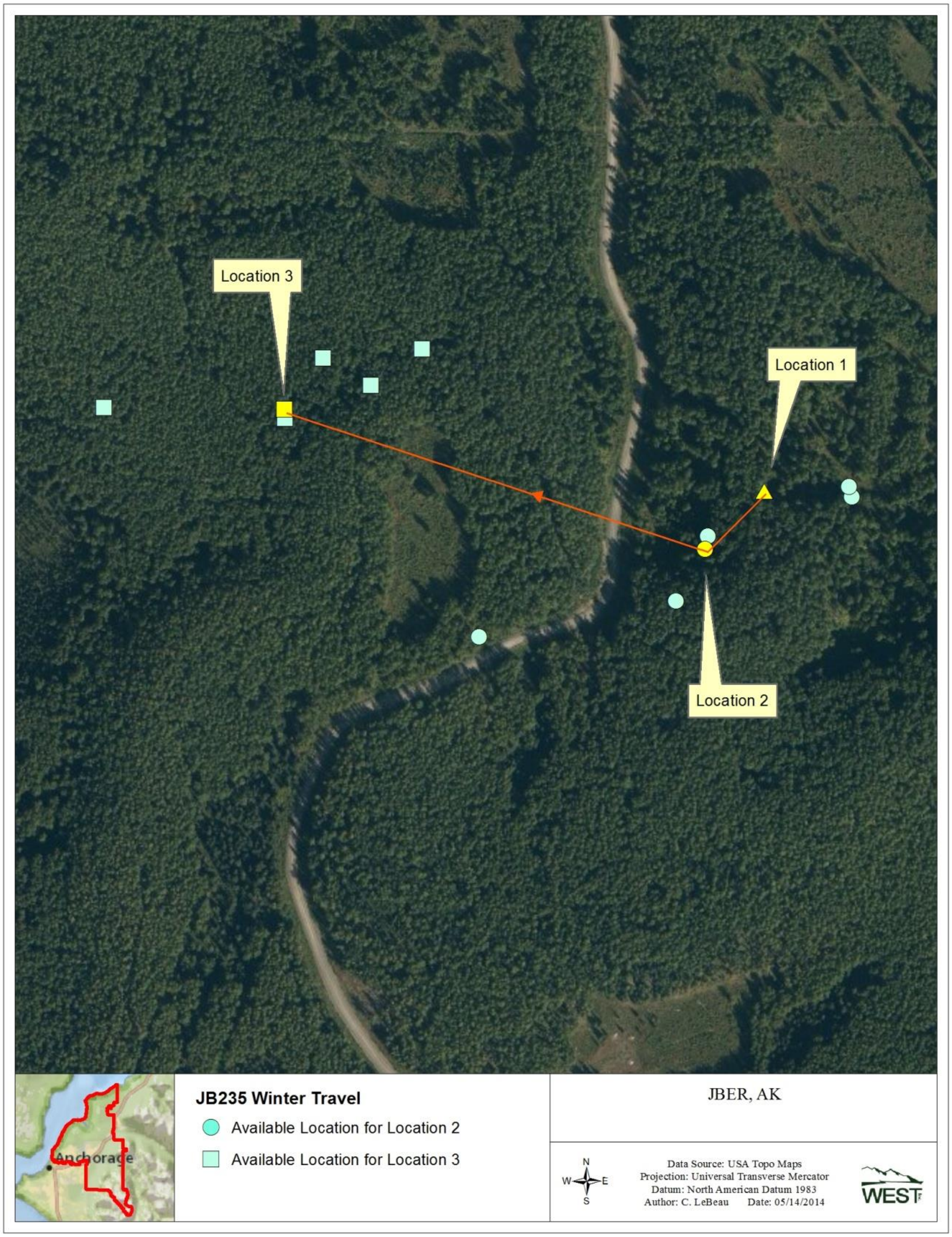


Figure 2. Choice set example for moose JB235 for traveling behavior during the winter period.

Model Development

We considered all covariates listed in Table 1 to be explanatory of female moose habitat selection. Correlations among covariates could disrupt the modeling process and result in erroneous inferences (Neter et al. 1996). Prior to model building, we conducted a pairwise correlation analysis to identify potential colinearities between covariates. Based on the results of the correlation analysis, we did not allow mutually correlated variables (pair-wise $|r| < 0.6$) in any one model. We incorporated the uncorrelated covariates into a discrete-choice model to estimate an exponential RSF for each individual during each time period (summer and winter) and movement state (traveling and encamped; McDonald et al. 2006). We developed a habitat selection model for each individual using forward, stepwise selection (Neter et al. 1996) and the Bayesian information criterion (BIC; Burnham and Anderson 2002). Models with smaller BIC values had more support in the data and were considered parsimonious (Burnham and Anderson 2002). For example, the covariate selected first resulted in the lowest BIC score among other univariate models. We added remaining covariates to the first selected covariate and re-evaluated the model to see if the BIC score could be lowered. If the model BIC was further reduced, the model building process continued looking forward (adding covariates) until the BIC value could not be further reduced or until the model reached a maximum of 5 covariates. We limited each RSF to 5 covariates to maintain simplicity and consistency among the individuals. Model building and most other computations were performed in R (R Development Core Team 2012).

To make predictions of use we placed a 30 m X 30 m grid over the study area and extracted covariate values for each cell. Using these values, we predicted the relative probability of selection from individual RSF's, and created predictive maps to aid in management decisions. Predictive maps were developed for the four combinations of season and state – traveling behavior during the summer, encamped behavior during the summer, traveling behavior during the winter, and encamped behavior during the winter.

Estimating individual RSFs allowed us to investigate habitat selection patterns and variability among individuals. For example, the habitat selection analysis for one moose might indicate that a particular covariate (e.g., shrub) was an important predictor; however, this covariate may have had little relationship to the selection patterns for other moose, which suggests some level of variability among the individuals monitored.

We used the individual RSFs to estimate the relative probability of selection by an average moose within the study area. We used an averaging process to account for the variability of selection among individuals. This approach minimizes the effect of uninformative parameters among individual models, particularly if covariates are included in one model and not in another (Burnham and Anderson 2002). This is particularly important when using multiple RSFs to make an overall prediction of the relative probability of use by the average moose within the study area.

We averaged individual predictions to create each overall predictive map. The averaged predictions were calculated using a bootstrapping technique, (Manly et al. 2007) where the individual moose were randomly sampled with replacement and the average prediction was re-estimated for each grid cell in an attempt to capture the variability among individuals. We used 200 bootstrap iterations to calculate the overall average prediction. These predictions were classified into 5 equal-area bins (low, medium-low, medium, medium-high, and high use) using percentiles.

For simplicity we developed two overall predictive maps containing averaged predictions for both seasons. The four average moose predictive maps (i.e., traveling behavior during the summer, encamped behavior during the summer, traveling behavior during the winter, and encamped behavior during the winter) were reduced to two seasonal maps (summer and winter) by averaging the predictions during the travel and encamped behaviors. We also developed a predictive map for each individual during the summer and winter period by averaging the predictions from the two movement states using predictions from individuals that had locations in both the summer and winter periods.

RESULTS

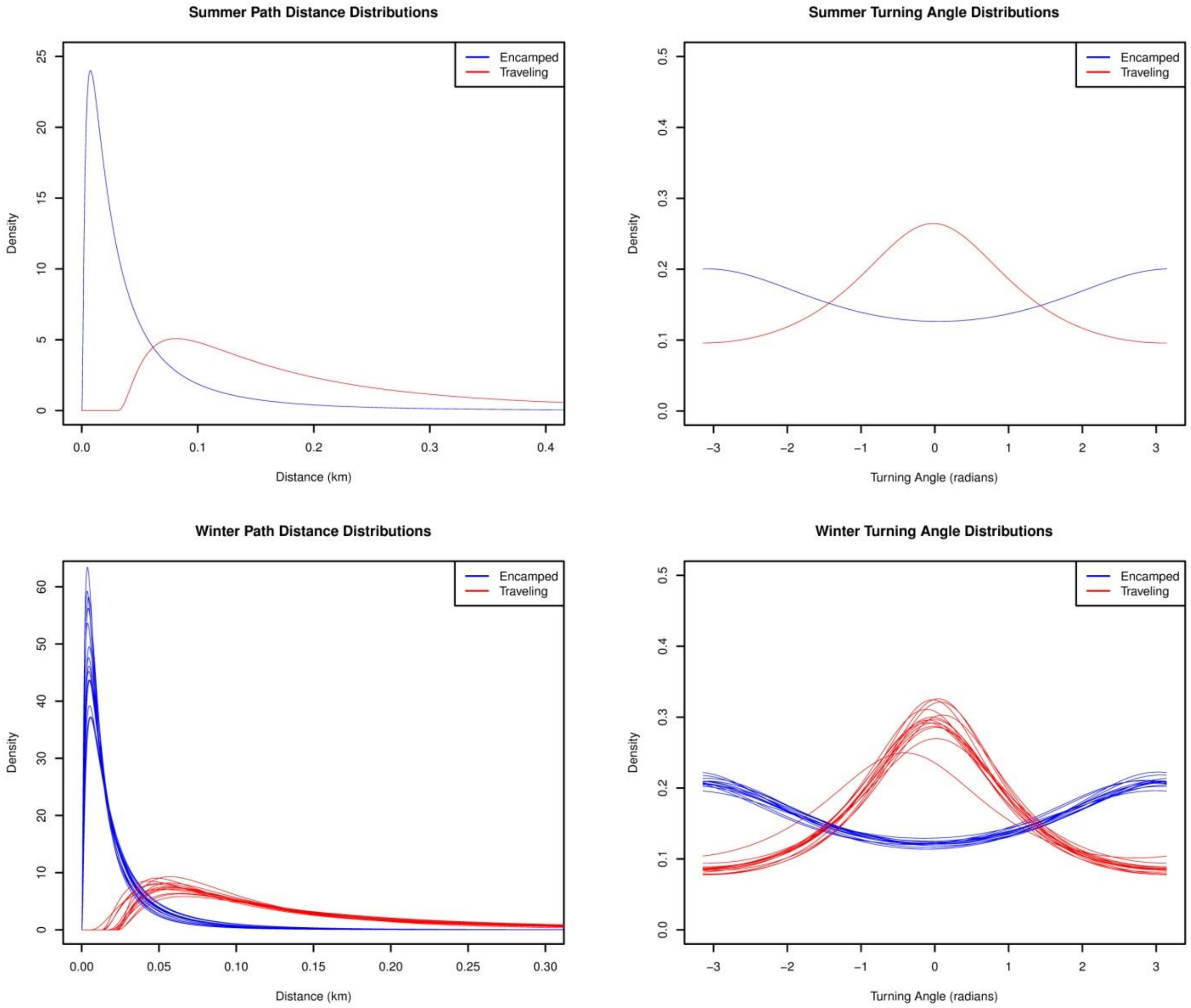
Of the 19 moose monitored, 14 were included in the winter analysis and 10 were included in the summer analysis. While all moose were captured on the study area, , some moose did spend significant amounts of time outside of the study area. Ten moose never left the study area and all locations within the seasons of interest for these moose were included in the analysis. Two moose left the study area for less than 1 day. In these cases, locations off of the study area were excluded from analysis. Two moose were collared on the study area in winter, remained on the study area approximately half of the season, but later spent a considerable amount of time off of the study area. For these two cases, locations before leaving the study area were included in the winter analysis. Three moose (JB030, JB032, and JB327) did not consistently stay on the study area and were excluded from analysis. Two moose (JB361 and JB382) were never recaptured. Their collars were recovered in 2014, but their data are not included in this report. We have winter data but no summer data for four moose: JB235 was killed by an Anchorage resident in defense of life and property before the start of the summer period; JB334 was recaptured in March of 2010, but has not been recaptured since then, so is still collared; The collar worn by JB386 was defective and collected only 1.5 months of data before it ceased data collection. JB385's collar was recovered too late for analysis. For moose wearing GPS collars that recorded locations every 30 minutes, only hourly locations were analyzed so that the temporal scale was the same for all moose.

Behavioral State

AIC*c* favored the wrapped Cauchy distribution over the wrapped normal in all but 2 of 60 comparisons for determining turning angle distributions. The shifted lognormal distribution was favored for all but 3 winter models where a lognormal model had a lower AIC*c* for determining leg length distributions. In these cases, the ΔAIC*c* was between 0.27 and 3.73. Since the AIC*c* differences were relatively small and the shifted lognormal is more biologically plausible (very short distances were not considered plausible traveling behavior), we used the shifted lognormal-Cauchy model for all state assignments. This model generally lead to better pseudo-residual plots than alternative models; however, some lack of fit remained, due to poor predictions of the largest leg lengths.

The fitted movement model was generally consistent with the encamped and traveling behavioral states that were of interest (Figure 3). The Viterbi algorithm predicted moose were traveling and encamped on average during winter 32 and 68% of the time, respectively. In the summer, moose were predicted to be traveling and encamped 21 and 79% of the time, respectively. These predictions were consistent with the estimated stationary behavioral state distributions. There was more variation in the percent of time moose were predicted to spend in each state in the summer, compared to winter.

The average median encamped and traveling distances across individuals in the winter were 13.3m and 111.1m, respectively. Median encamped and traveling distances in the summer were 32.3m and 195.2m on average, respectively. The empirical turning angle distributions did not correspond to the fitted distribution, indicating that the leg length distribution was largely determining state assignment.



Summer Path Distance Distributions

Summer Turning Angle Distributions

Winter Path Distance Distributions

Winter Turning Angle Distributions

Figure 3. Fitted leg length and turning angle distributions used to define movement states for the winter and summer period. A single summer period HMM was estimated by pooling summer locations across individuals and years.

Resource Selection

Distance to major roads and distance to building were the only 2 linearly correlated covariates (|r| > 0.60) and consequently were not included in the same model at any time during model building.

Habitat selection patterns were variable among individual moose (Table 2 and 3). No models were consistent among individuals within the two time periods and movement states. We did not detect any habitat selection patterns for moose JB373 during the encamped behavior during the summer period which was likely due to its small home range and the highly fragmented landscape that JB373 occupied during this period (Table 2).

Summer models

Slope and distance to water were the most common covariates included in the summer models (Table 4). Seven RSFs from 4 moose included slope as a covariate and the relative probability of moose habitat selection significantly decreased in habitats with a higher degree of slope for all 7 RSFs (Table 4, Appendix A). Similar to slope, distance to water was included in 7 RSFs from 5 moose and the effect/magnitude of distance to water on the relative probability of selection was variable among the 7 RSFs as only 2 RSFs had significant slope parameter estimates (Table 4, Appendix A). The next most common covariates were density of shrub, building density, and distance to buildings. These covariates were the most consistent where the relative probability of selection significantly increased as building density decreased, density of shrub increased, and as distance from buildings increased (Table 4, Appendix A).

Winter models

Landcover classes barren and grass and the density of shrub were the most common covariates included in the winter models (Table 4). Barren occurred at the highest frequency among individual RSFs and moose overwhelmingly selected habitats that were not characteristic of the barren habitat type (Table 4, Appendix A). Interestingly, the magnitude of this avoidance was almost twice as large during the encamped period than during the traveling period (Appendix A). Similar to barren, moose avoided habitats that consisted of grass landcover class and the magnitude of this avoidance was almost twice as large during the encamped period than during the traveling period (Appendix A). Moose consistently selected for habitats that had a higher density of shrubs and it appears the magnitude was higher during the encamped period compared to the traveling period (Appendix A).

Average models and maps

Numerous predictive maps were created to aid management decisions within the study area. Individual predictive maps show the variability of selection patterns among individuals (Appendix B). Predicted levels of use within the study area for each movement state were similar within each season consistently identifying areas of low predicted levels of use in close proximity to buildings and anthropogenic features (Appendix B). Combining the 2 movement states within each season and creating 2 predictive maps showed similar predicted levels of use within the study area; however, higher use was predicted in the northern and southern portions of the study area during the summer period compared to the winter period (Appendix B). One predictive map that represents both movement states and both time periods showed low predicted levels of use within habitats in close proximity to anthropogenic features (Figure 4). There were pockets of high predicted use located throughout the study area and these likely represent the most suitable moose habitat (Figure 4). The high use habitats were characterized by high shrub density, large distances from buildings and major roads, and little or no barren or grass landcover type (Table 5).

Table 2. Top models identified by the lowest BIC score and number of locations during the summer period for each individual moose.

Moose ID	Model	# of Locations
Encamped Behavior: Summer		
JB037	d_build+barren+shrub90	76
JB042	slope+mix+shrub90+d_water	89
JB234	d_build+barren+grass+deciduous+d_water	201
JB291	bden90+grass+d_dirtrd+elevation	109
JB336	bden90+d_stream	117
JB367	d_cover	77
JB373	Null	126
JB983	d_build+elevation+d_dirtrd	148
JB987	slope+shrub90+d_cover+deciduous	236
JB991	d_build+d_water+slope	223
Travel Behavior: Summer		
JB037	bden90	279
JB042	shrub90+slope+mix	317
JB234	d_build+d_water+shrub90+elevation+mix	784
JB291	d_water+bden90+grass	459
JB336	grass+bden90	508
JB367	d_cover+water	247
JB373	barren+d_water	523
JB983	slope+d_dirtrd	581
JB987	shrub90+deciduous+slope+barren+mix	911
JB991	d_water+bden90+deciduous+slope+d_build	824

Table 3. Top models identified by the lowest BIC score and number of locations during the winter period for each individual moose.

Moose ID	Model	# of Locations
	Encamped Behavior: Winter	
JB037	mix+deciduous+bden90+shrub90	185
JB042	barren+d_cover+shrub90+mix+deciduous	1125
JB234	shrub90+d_cover+water+d_water+bden90	1336
JB235	coniferous+d_dirtrd+bden90+water+d_pave	195
JB291	grass+barren+water+shrub90+d_water	895
JB334	barren+grass	490
JB336	barren+water+d_stream+grass+coniferous	492
JB367	barren+grass+d_build+coniferous+elevation	1032
JB373	barren+elevation+grass+d_food+d_stream	961
JB385	grass+slope+coniferous+barren+water	795
JB386	shrub90	203
JB983	shrub90+barren+grass+slope	763
JB987	barren+grass+slope+coniferous+mix	1159
JB991	barren+grass+slope+d_dirtrd+bden90	1034
	Travel Behavior: Winter	
JB037	barren+mix+bden90+d_dirtrd+d_pave	719
JB042	barren+d_cover+shrub90+d_food+grass	3349
JB234	shrub90+bden90+d_water+water+d_cover	4633
JB235	d_dirtrd+d_food+barren+d_pave	625
JB291	grass+barren+d_cover+water+d_water	3066
JB334	grass+barren+shrub90+mix	1617
JB336	barren+coniferous+d_pave+elevation+deciduous	1641
JB367	barren+grass+d_water+coniferous+d_stream	3322
JB373	barren+shrub90	3115
JB385	grass+elevation+water+barren+slope	2864

JB386	shrub90	592
JB983	shrub90+barren+grass+wetland	2418
JB987	barren+shrub90+wetland+d_cover+d_stream	4012
JB991	bden90+slope+d_dirtrd+barren+shrub90	3390

Table 4. Frequency of covariates within individual moose resource selection models during the summer and winter period and during each movement state.

Covariate	Summer			Winter			Overall Total
	Travel	Encamped	Total	Travel	Encamped	Total	
barren	2	2	4	12	10	22	26
shrub90	3	3	6	8	6	14	20
grass	2	2	4	6	9	15	19
bden90	4	2	6	3	4	7	13
slope	4	3	7	2	4	6	13
d_water	4	3	7	3	2	5	12
d_cover	1	2	3	4	2	6	9
mix	3	1	4	2	3	5	9
water	1	0	1	3	5	8	9
d_dirtrd	1	2	3	3	2	5	8
coniferous	0	0	0	2	5	7	7
d_build	2	4	6	0	1	1	7
deciduous	2	2	4	1	2	3	7
elevation	1	2	3	2	2	4	7
d_stream	0	1	1	2	2	4	5
d_pave	0	0	0	3	1	4	4
d_food	0	0	0	2	1	3	3
wetland	0	0	0	2	0	2	2

Table 5. Average value of each covariate included in at least one individual resource selection model for each use category observed within the overall predictive map (see Figure 4).

Covariate	Low	Medium-Low	Medium	Medium-High	High
bden90	0.02	0.00	0.00	0.00	0.00
d_build	*0.70*	*0.91*	*0.82*	*0.95*	*2.23*
d_cover	0.19	0.02	0.01	0.01	0.02
d_food	0.00	0.00	0.00	0.00	0.00
d_majrd	*1.87*	*2.69*	*3.22*	*3.58*	*5.30*
d_pave	0.51	0.62	0.45	0.44	0.49
d_water	7.64	7.31	6.33	6.58	7.08
elevation	132.38	180.52	113.57	100.78	115.11
shrub90	*0.04*	*0.08*	*0.07*	*0.09*	*0.23*
slope	4.37	7.76	3.15	2.01	2.11
d_dirtrd	0.38	0.43	0.35	0.33	0.33
d_stream	0.82	0.75	0.93	0.89	1.14
barren	*100%*	*0%*	*0%*	*0%*	*0%*
coniferous	4%	31%	43%	11%	12%
cover	4%	25%	25%	25%	21%
deciduous	3%	30%	33%	20%	14%
food	4%	19%	18%	28%	31%
grass	*91%*	*8%*	*0%*	*0%*	*1%*
mix	4%	20%	16%	32%	28%
water	35%	61%	3%	1%	1%
wetland	0%	12%	42%	25%	22%

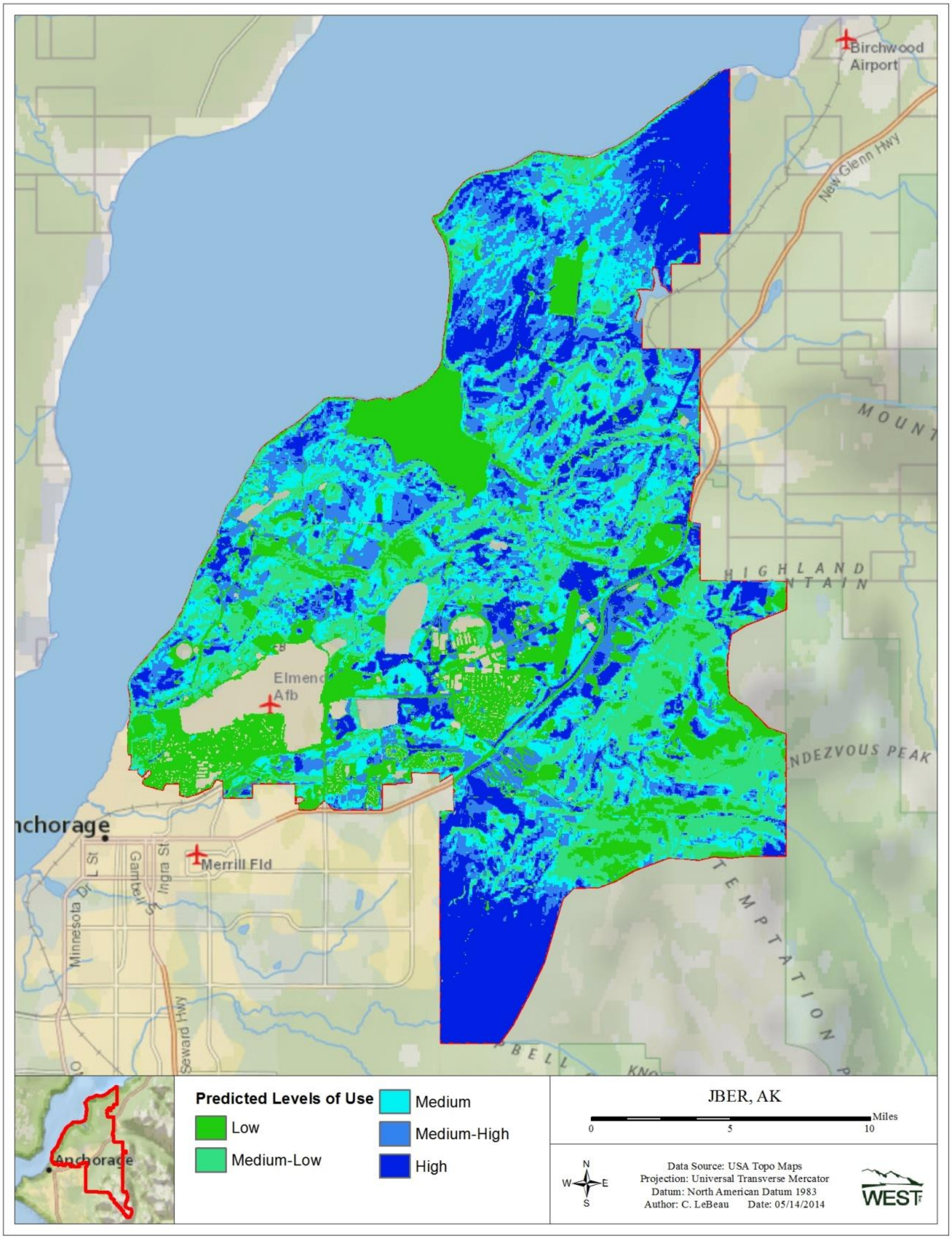


Figure 4. The relative predicted levels of use for moose occupying the JBER during the summer and winter period.

DISCUSSION

Moose habitat selection patterns within the study area varied among individuals. The level of fragmentation that exists within the study area may have limited our ability to identify covariates that were most influential to the average moose. However, we did develop predictive maps that provide managers with information that details the varying degrees of use within the study area. These areas can be incorporated in future development plans to limit negative impacts on moose habitat. Although the barren landcover type was the most common landcover class within the study area, moose appear to strongly avoid barren areas. In addition, moose appear to avoid areas of grass landcover classes within the study area. On the other hand, moose appeared to select for habitats with a high density of shrub cover.

The movement model accurately assessed moose states (traveling or encamped) during the winter and summer periods, but had difficulty assigning state to movements with large leg lengths. While some states with large leg lengths could have been miscategorized, the overall effect of these miscategorized movements on the overall habitat selection patterns is likely very small.

We assessed habitat selection at a very fine scale (meters and hourly intervals), while the habitat covariates that we considered were derived at a larger landscape scale. This difference in scale may have limited our ability to detect consistent habitat selection patterns among individuals. Because the study area is a highly fragmented landscape, moose are likely selecting specific habitats at a very small scale (i.e., a very small shrub patch that is surrounded by buildings or forest) and the habitat covariates we considered may not have captured these potential features. Overlaying the nutritional predictive model with the estimates from the habitat selection model might provide further insight into the selection patterns of moose within the study area.

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Appendix A. Parameter estimates and 90% confidence intervals (alpha = 0.90) for covariates included in individual moose top habitat selection models within the study area

Appendix A. Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB991	JB987	JB983	JB373	JB367
Travel Behavior: Summer					
barren	--	-0.466 (-0.564, -0.369)	--	-0.432 (-0.525, -0.339)	--
bden90	-7.592 (-9.647, -5.536)	--	--	--	--
d_build	0.155 (0.056, 0.254)	--	--	--	--
d_cover	--	--	--	--	-0.271 (-0.805, 0.262)
d_dirtrd	--	--	-0.007 (-0.147, 0.132)	--	--
d_water	-0.002 (-0.01, 0.006)	--	--	0.001 (-0.006, 0.008)	--
deciduous	-0.151 (-0.213, -0.09)	-0.164 (-0.233, -0.094)	--	--	--
elevation	--	--	--	--	--
grass	--	--	--	--	--
mix	--	-0.009 (-0.07, 0.051)	--	--	--
shrub90	--	0.167 (0.085, 0.249)	--	--	--
slope	-0.051 (-0.067, -0.035)	-0.04 (-0.055, -0.025)	-0.046 (-0.061, -0.031)	--	--
water	--	--	--	--	-0.053 (-0.239, 0.133)
Encamped Behavior: Summer					
barren	--	--	--	--	--
bden90	--	--	--	--	--

Appendix A. Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB991	JB987	JB983	JB373	JB367
d_build	0.723 (0.546, 0.9)	--	0.505 (0.347, 0.664)	--	--
d_cover	--	-5.051 (-6.463, -3.638)	--	--	-2.307 (-3.373, -1.24)
d_dirtrd	--	--	-0.154 (-0.464, 0.156)	--	--
d_stream	--	--	--	--	--
d_water	-0.002 (-0.017, 0.014)	--	--	--	--
deciduous	--	-0.084 (-0.206, 0.038)	--	--	--
elevation	--	--	0.001 (-0.002, 0.004)	--	--
grass	--	--	--	--	--
mix	--	--	--	--	--
shrub90	--	0.631 (0.469, 0.794)	--	--	--
slope	-0.164 (-0.2, -0.129)	-0.119 (-0.152, -0.087)	--	--	--

Appendix A. Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB991	JB987	JB983	JB373	JB367
Travel Behavior: Winter					
barren	-0.506 (-0.55, -0.462)	-0.452 (-0.495, -0.408)	-0.538 (-0.58, -0.496)	-0.512 (-0.554, -0.471)	-0.57 (-0.612, -0.528)
bden90	-0.451 (-0.983, 0.081)	--	--	--	--
coniferous	--	--	--	--	-0.122 (-0.157, -0.088)
d_cover	--	-1.174 (-1.455, -0.893)	--	--	--
d_dirtrd	-0.009 (-0.068, 0.049)	--	--	--	--
d_food	--	--	--	--	--
d_pave	--	--	--	--	--
d_stream	--	0.008 (-0.006, 0.021)	--	--	0.016 (0.003, 0.029)
d_water	--	--	--	--	0.002 (-0.001, 0.004)
deciduous	--	--	--	--	--
elevation	--	--	--	--	--
grass	--	--	-0.323 (-0.361, -0.286)	--	-0.353 (-0.39, -0.316)
mix	--	--	--	--	--
shrub90	0.124 (0.094, 0.153)	0.207 (0.173, 0.241)	0.102 (0.072, 0.131)	0.133 (0.104, 0.162)	--
slope	-0.009 (-0.013, -0.005)	--	--	--	--
water	--	--	--	--	--
wetland	--	0.187 (0.13, 0.245)	0.099 (0.043, 0.155)	--	--

Appendix A. Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB991	JB987	JB983	JB373	JB367
			Encamped Behavior: Winter		
barren	-1.13 (-1.222, -1.038)	-1.244 (-1.333, -1.155)	-1.195 (-1.283, -1.107)	-1.21 (-1.298, -1.122)	-1.257 (-1.346, -1.168)
bden90	-3.158 (-4.355, -1.961)	--	--	--	--
coniferous	--	-0.246 (-0.307, -0.184)	--	--	-0.232 (-0.291, -0.172)
d_build	--	--	--	--	-0.105 (-0.145, -0.065)
d_cover	--	--	--	--	--
d_dirtrd	-0.129 (-0.236, -0.022)	--	--	--	--
d_food	--	--	--	-124.881 (-168.731, -81.032)	--
d_pave	--	--	--	--	--
d_stream	--	--	--	0.033 (0.01, 0.056)	--
d_water	--	--	--	--	--
deciduous	--	--	--	--	--
elevation	--	--	--	-0.001 (-0.001, 0)	-0.001 (-0.001, 0)
grass	-0.769 (-0.844, -0.694)	-0.79 (-0.867, -0.714)	-0.738 (-0.814, -0.663)	-0.763 (-0.838, -0.688)	-0.796 (-0.871, -0.721)
mix	--	0.019 (-0.017, 0.055)	--	--	--
shrub90	--	--	0.194 (0.142, 0.245)	--	--
slope	-0.032 (-0.039, -0.025)	-0.037 (-0.044, -0.03)	-0.029 (-0.037, -0.022)	--	--

Appendix A. Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB991	JB987	JB983	JB373	JB367
water	--	--	--	--	--

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB234	JB042	JB037	JB386	JB385
Travel Behavior: Summer					
barren	--	--	--	--	--
bden90	--	--	-7.794 (-9.84, -5.748)	--	--
d_build	0.143 (0.045, 0.241)	--	--	--	--
d_cover	--	--	--	--	--
d_dirtrd	--	--	--	--	--
d_water	0.002 (-0.007, 0.01)	--	--	--	--
deciduous	--	--	--	--	--
elevation	-0.001 (-0.002, 0.001)	--	--	--	--
grass	--	--	--	--	--
mix	0.08 (0.024, 0.135)	0.107 (0.052, 0.161)	--	--	--
shrub90	0.321 (0.244, 0.398)	0.287 (0.211, 0.364)	--	--	--
slope	--	-0.041 (-0.056, -0.026)	--	--	--
water	--	--	--	--	--
Encamped Behavior: Summer					
barren	-1.111 (-1.335, -0.886)	--	-0.951 (-1.174, -0.727)	--	--
bden90	--	--	--	--	--

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB234	JB042	JB037	JB386	JB385
d_build	0.42 (0.235, 0.605)	--	0.392 (0.228, 0.556)	--	--
d_cover	--	--	--	--	--
d_dirtrd	--	--	--	--	--
d_stream	--	--	--	--	--
d_water	0.021 (0.006, 0.036)	-0.028 (-0.042, -0.014)	--	--	--
deciduous	-0.289 (-0.407, -0.171)	--	--	--	--
elevation	--	--	--	--	--
grass	-0.448 (-0.635, -0.261)	--	--	--	--
mix	--	0.392 (0.289, 0.495)	--	--	--
shrub90	--	0.589 (0.439, 0.738)	0.43 (0.289, 0.571)	--	--
slope	--	-0.14 (-0.175, -0.105)	--	--	--

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB234	JB042	JB037	JB386	JB385
			Travel Behavior: Winter		
barren	--	-0.528 (-0.573, -0.484)	-0.505 (-0.55, -0.46)	--	-0.569 (-0.61, -0.527)
bden90	-1.84 (-2.368, -1.312)	--	-0.507 (-1.042, 0.028)	--	--
coniferous	--	--	--	--	--
d_cover	-1.683 (-1.954, -1.412)	-0.17 (-0.433, 0.093)	--	--	--
d_dirtrd	--	--	-0.067 (-0.125, -0.009)	--	--
d_food	--	-43.333 (-58.324, -28.341)	--	--	--
d_pave	--	--	-0.052 (-0.092, -0.011)	--	--
d_stream	--	--	--	--	--
d_water	-0.002 (-0.005, 0.001)	--	--	--	--
deciduous	--	--	--	--	--
elevation	--	--	--	--	0 (-0.001, 0)
grass	--	-0.321 (-0.36, -0.282)	--	--	-0.353 (-0.39, -0.316)
mix	--	--	0.041 (0.022, 0.061)	--	--
shrub90	0.248 (0.214, 0.281)	0.106 (0.072, 0.139)	--	0.166 (0.137, 0.195)	--
slope	--	--	--	--	-0.012 (-0.016, -0.007)
water	-0.379 (-0.478, -0.28)	--	--	--	-0.483 (-0.582, -0.383)
wetland	--	--	--	--	--

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB234	JB042	JB037	JB386	JB385
			Encamped Behavior: Winter		
barren	--	-0.789 (-0.883, -0.695)	--	--	-1.265 (-1.353, -1.177)
bden90	-5.916 (-7.125, -4.707)	--	-5.844 (-7.035, -4.653)	--	--
coniferous	--	--	--	--	-0.266 (-0.326, -0.206)
d_build	--	--	--	--	--
d_cover	-4.459 (-5.004, -3.914)	-1.688 (-2.235, -1.141)	--	--	--
d_dirtrd	--	--	--	--	--
d_food	--	--	--	--	--
d_pave	--	--	--	--	--
d_stream	--	--	--	--	--
d_water	-0.003 (-0.008, 0.002)	--	--	--	--
deciduous	--	0.324 (0.272, 0.375)	0.495 (0.447, 0.543)	--	--
elevation	--	--	--	--	--
grass	--	--	--	--	-0.811 (-0.886, -0.736)
mix	--	0.337 (0.291, 0.384)	0.51 (0.467, 0.553)	--	--
shrub90	0.577 (0.518, 0.636)	0.664 (0.6, 0.729)	0.73 (0.671, 0.79)	0.379 (0.329, 0.429)	--
slope	--	--	--	--	-0.038 (-0.045, -0.03)
water	-0.937 (-1.18, -0.695)	--	--	--	-1.197 (-1.439, -0.954)

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB336	JB291	JB334	JB235
		Travel Behavior: Summer		
barren	--	--	--	--
bden90	-7.781 (-9.829, -5.733)	-7.793 (-9.848, -5.739)	--	--
d_build	--	--	--	--
d_cover	--	--	--	--
d_dirtrd	--	--	--	--
d_water	--	0.001 (-0.006, 0.007)	--	--
deciduous	--	--	--	--
elevation	--	--	--	--
grass	0.147 (0.067, 0.227)	0.147 (0.067, 0.227)	--	--
mix	--	--	--	--
shrub90	--	--	--	--
slope	--	--	--	--
water	--	--	--	--
		Encamped Behavior: Summer		
barren	--	--	--	--
bden90	-24.308 (-32.019, -16.597)	-24.527 (-32.281, -16.774)	--	--

Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB336	JB291	JB334	JB235
d_build	--	--	--	--
d_cover	--	--	--	--
d_dirtrd	--	0.061 (-0.25, 0.371)	--	--
d_stream	-0.033 (-0.1, 0.033)	--	--	--
d_water	--	--	--	--
deciduous	--	--	--	--
elevation	--	0.001 (-0.002, 0.004)	--	--
grass	--	-0.344 (-0.528, -0.16)	--	--
mix	--	--	--	--
shrub90	--	--	--	--
slope	--	--	--	--

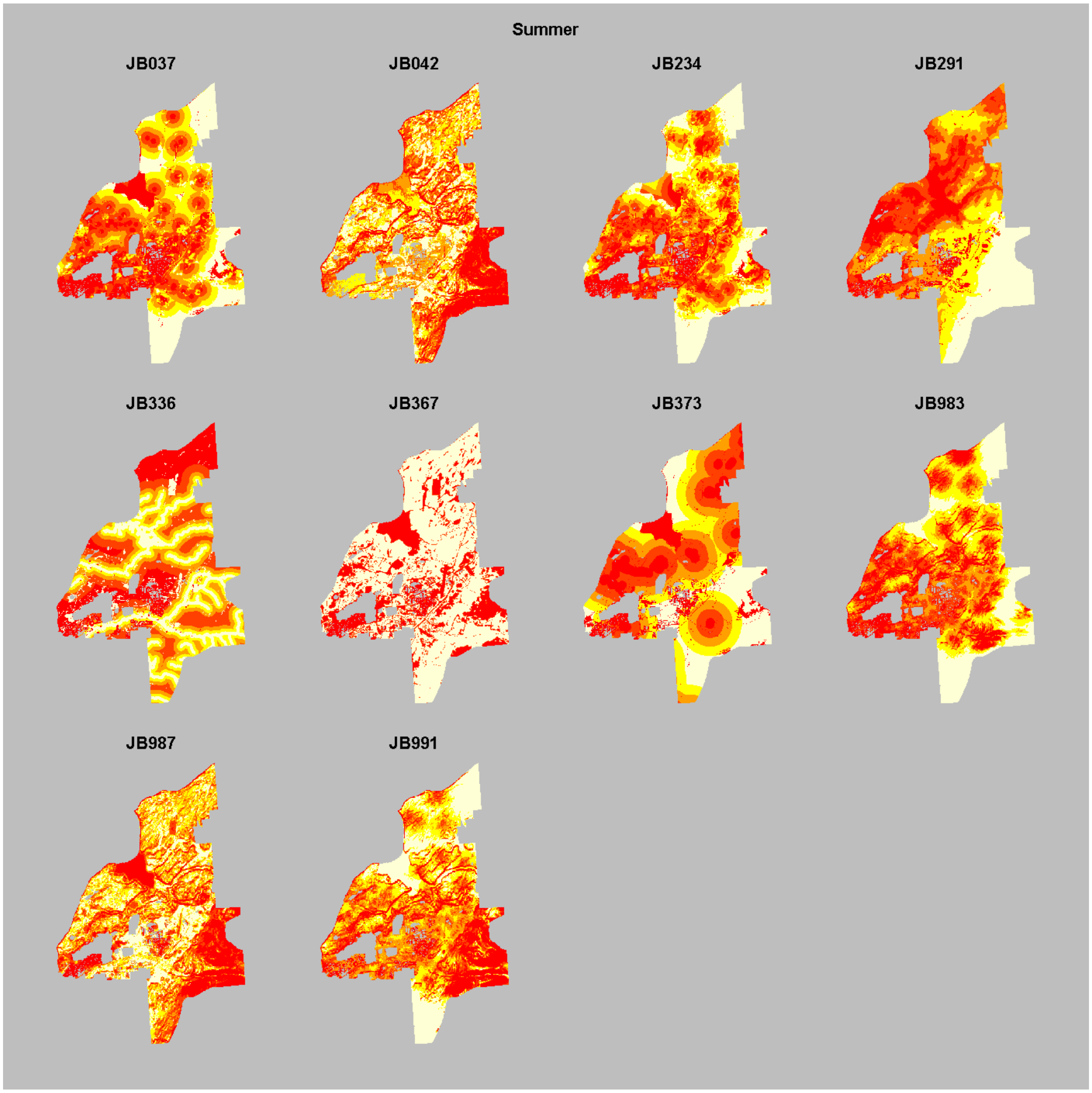
Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB336	JB291	JB334	JB235
		Travel Behavior: Winter		
barren	-0.535 (-0.578, -0.493)	-0.568 (-0.611, -0.525)	-0.531 (-0.574, -0.489)	-0.53 (-0.572, -0.488)
bden90	--	--	--	--
coniferous	-0.084 (-0.119, -0.05)	--	--	--
d_cover	--	0.168 (-0.051, 0.388)	--	--
d_dirtrd	--	--	--	-0.063 (-0.121, -0.005)
d_food	--	--	--	-44.298 (-59.302, -29.294)
d_pave	-0.036 (-0.078, 0.006)	--	--	-0.049 (-0.089, -0.008)
d_stream	--	--	--	--
d_water	--	0.002 (-0.001, 0.005)	--	--
deciduous	0.031 (0.009, 0.054)	--	--	--
elevation	0 (-0.001, 0)	--	--	--
grass	--	-0.353 (-0.39, -0.315)	-0.316 (-0.355, -0.277)	--
mix	--	--	0.023 (0.002, 0.044)	--
shrub90	--	--	0.109 (0.078, 0.141)	--
slope	--	--	--	--
water	--	-0.469 (-0.568, -0.37)	--	--
wetland	--	--	--	--

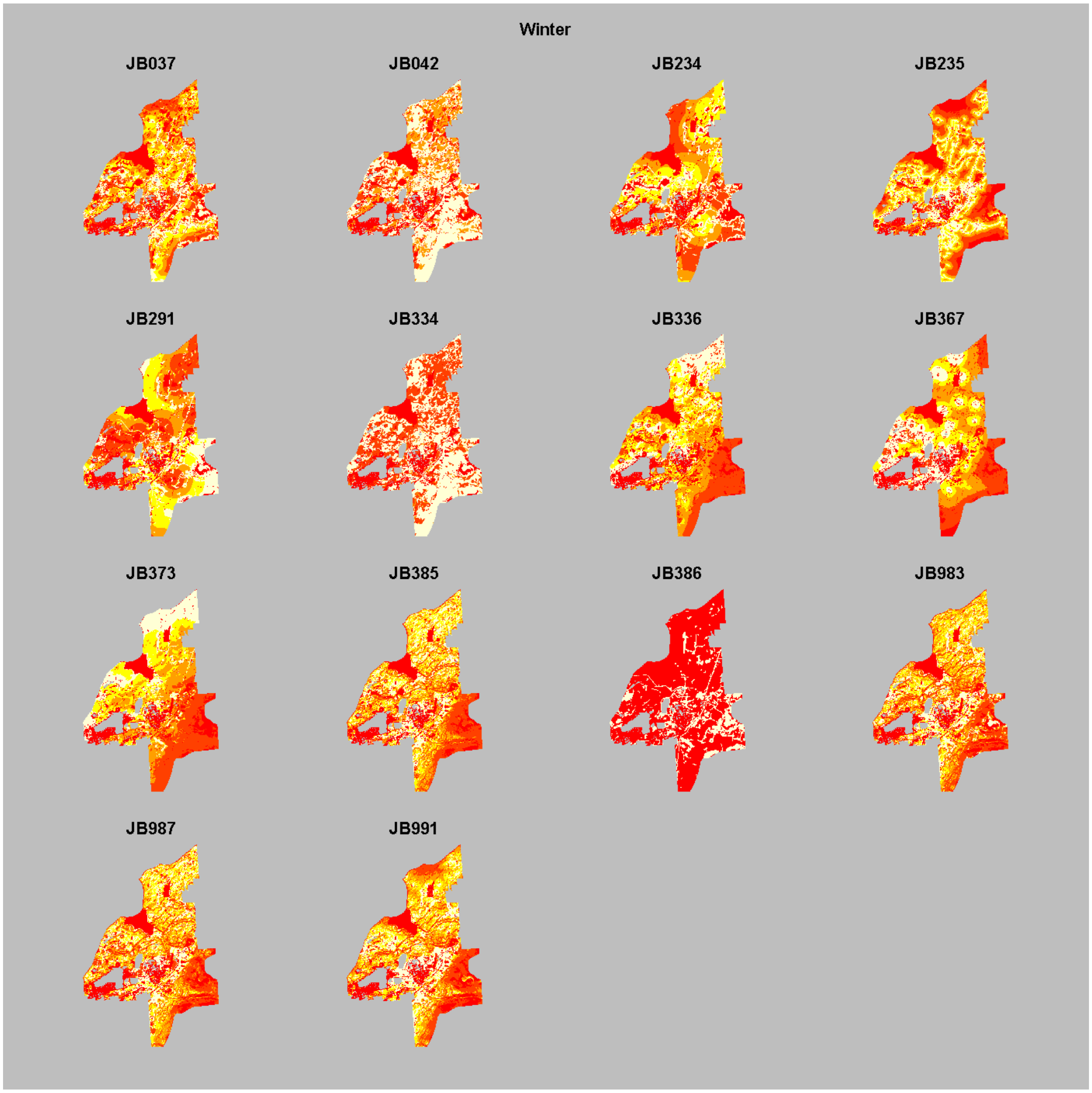
Appendix A (Cont). Model estimates and 90% confidence intervals (alpha = 0.90) for each covariate within each individual moose habitat selection model during the winter and summer periods and each movement state within the study area.

Covariate	JB336	JB291	JB334	JB235
		Encamped Behavior: Winter		
barren	-1.237 (-1.325, -1.149)	-1.182 (-1.27, -1.094)	-1.198 (-1.285, -1.11)	--
bden90	--	--	--	-8.439 (-9.666, -7.212)
coniferous	-0.235 (-0.295, -0.175)	--	--	-0.104 (-0.163, -0.044)
d_build	--	--	--	--
d_cover	--	--	--	--
d_dirtrd	--	--	--	-0.12 (-0.224, -0.015)
d_food	--	--	--	--
d_pave	--	--	--	0.037 (-0.033, 0.107)
d_stream	0.019 (-0.004, 0.042)	--	--	--
d_water	--	0.001 (-0.004, 0.006)	--	--
deciduous	--	--	--	--
elevation	--	--	--	--
grass	-0.79 (-0.864, -0.715)	-0.733 (-0.808, -0.658)	-0.756 (-0.831, -0.681)	--
mix	--	--	--	--
shrub90	--	0.205 (0.153, 0.256)	--	--
slope	--	--	--	--
water	-1.162 (-1.405, -0.92)	-1.12 (-1.363, -0.878)	--	-1.038 (-1.28, -0.796)

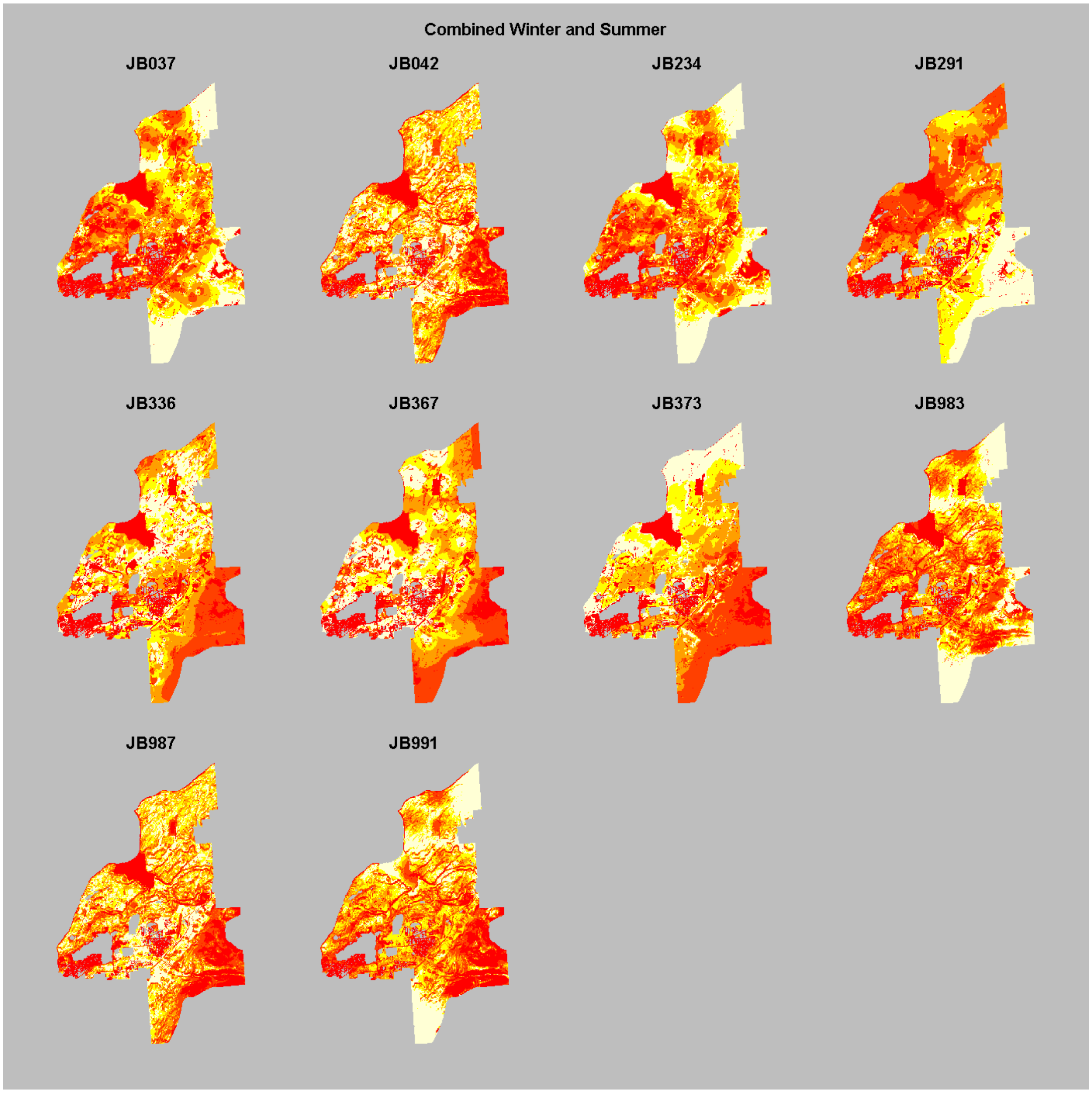
Appendix B. Moose predictive maps developed from resource selection models within the study area



Appendix B-1. Averaged summer encamped and travel behavior predictions for individual moose within the study area. Use is displayed from low=red to high=white.

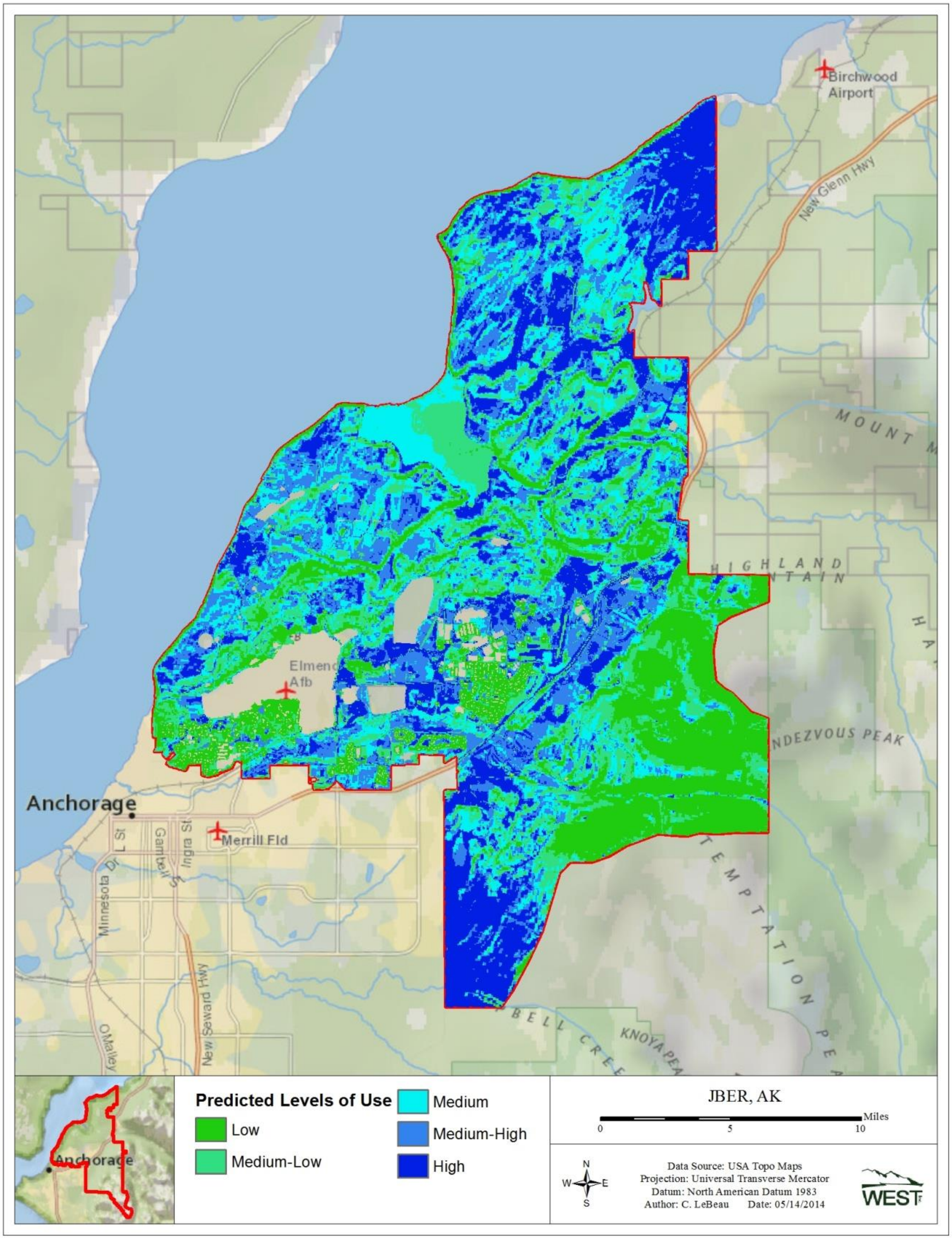


Appendix B-2. Averaged winter encamped and travel behavior predictions for individual moose within the study area.



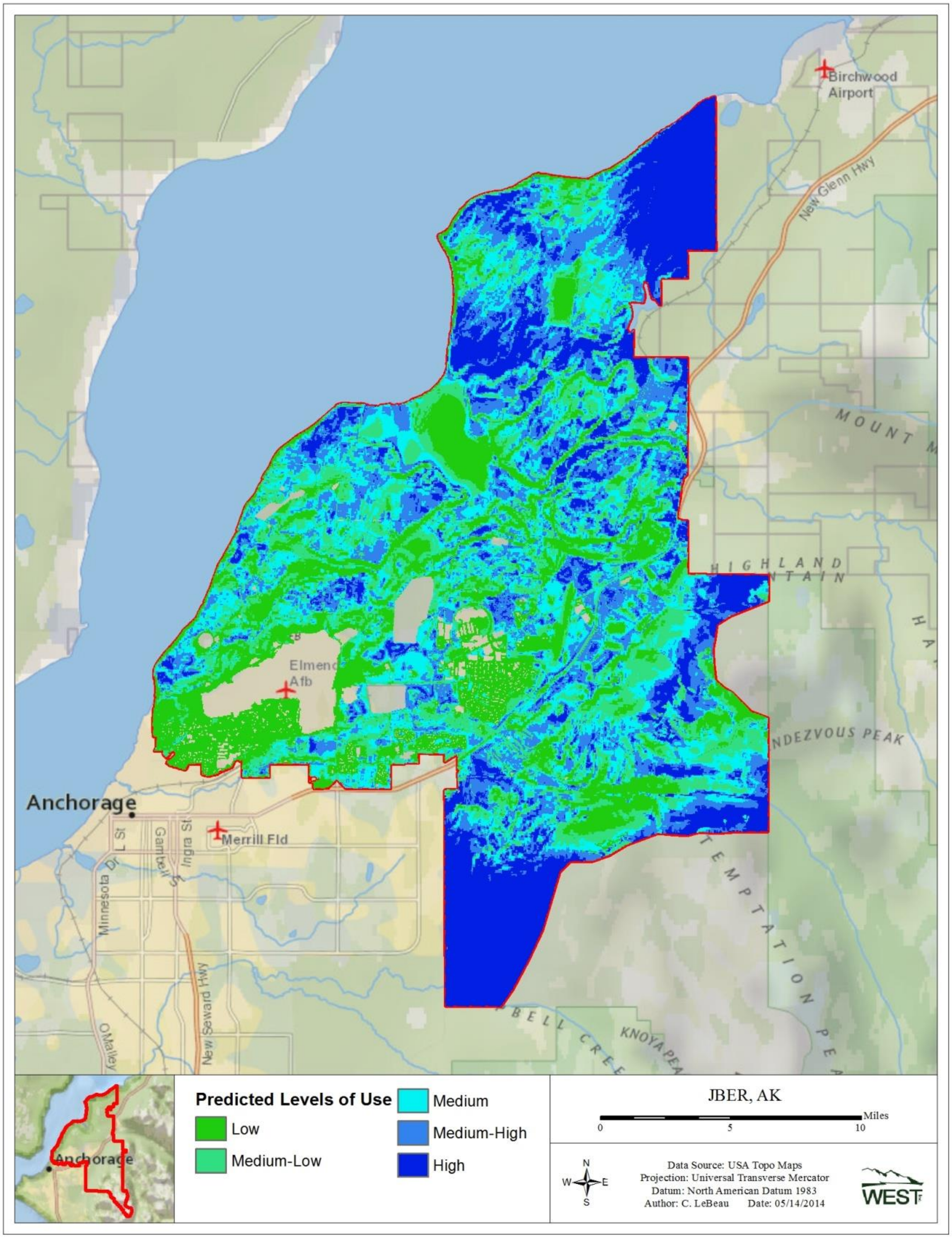
Appendix B-3. Averaged winter and summer behavior predicitions for individual moose within the study area. Use is displayed from low=red to high=white.

Traveling Behavior: Summer



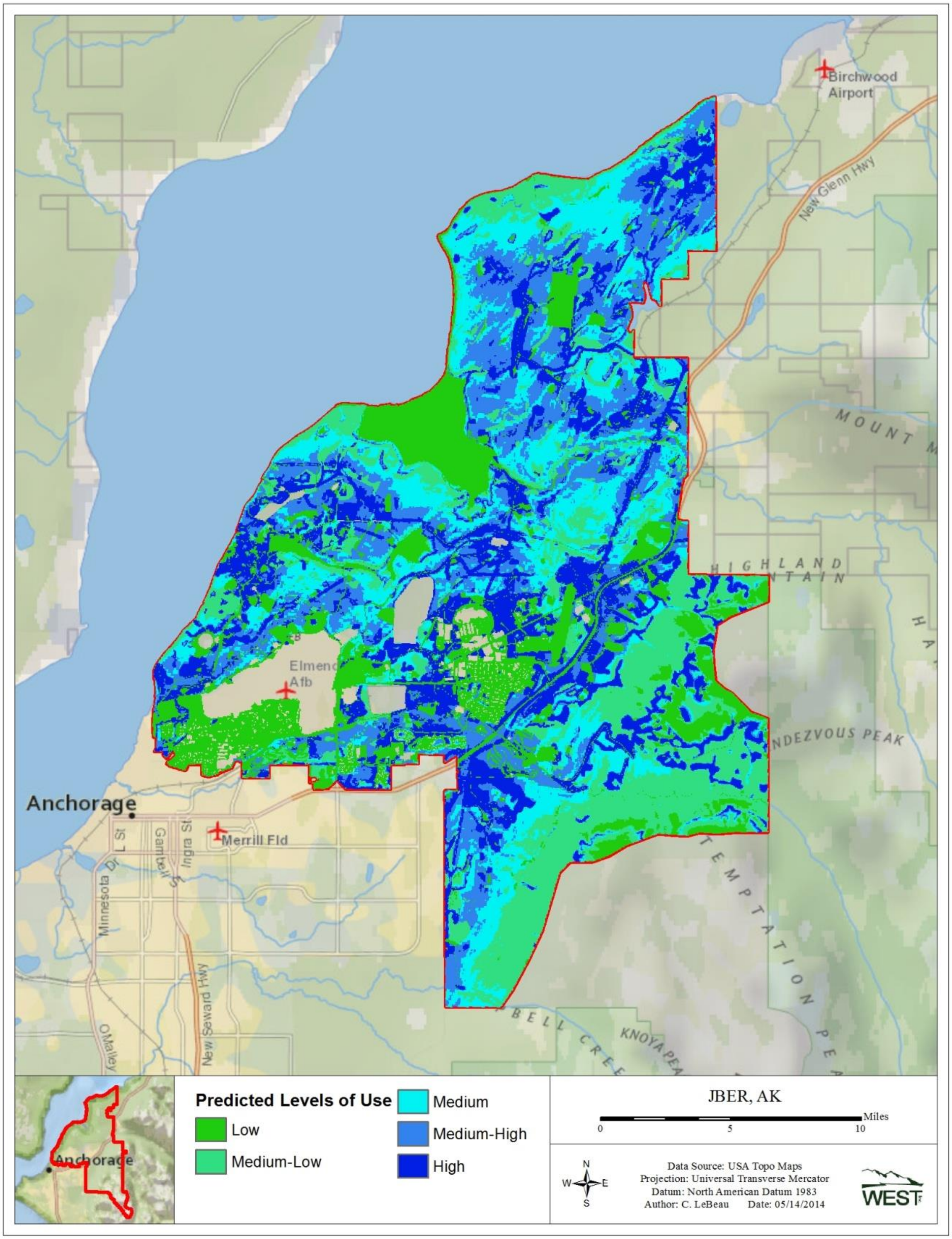
Appendix B-4. The relative predicted levels of use for traveling behavior by moose occupying the JBER during the summer period.

Encamped Behavior: Summer



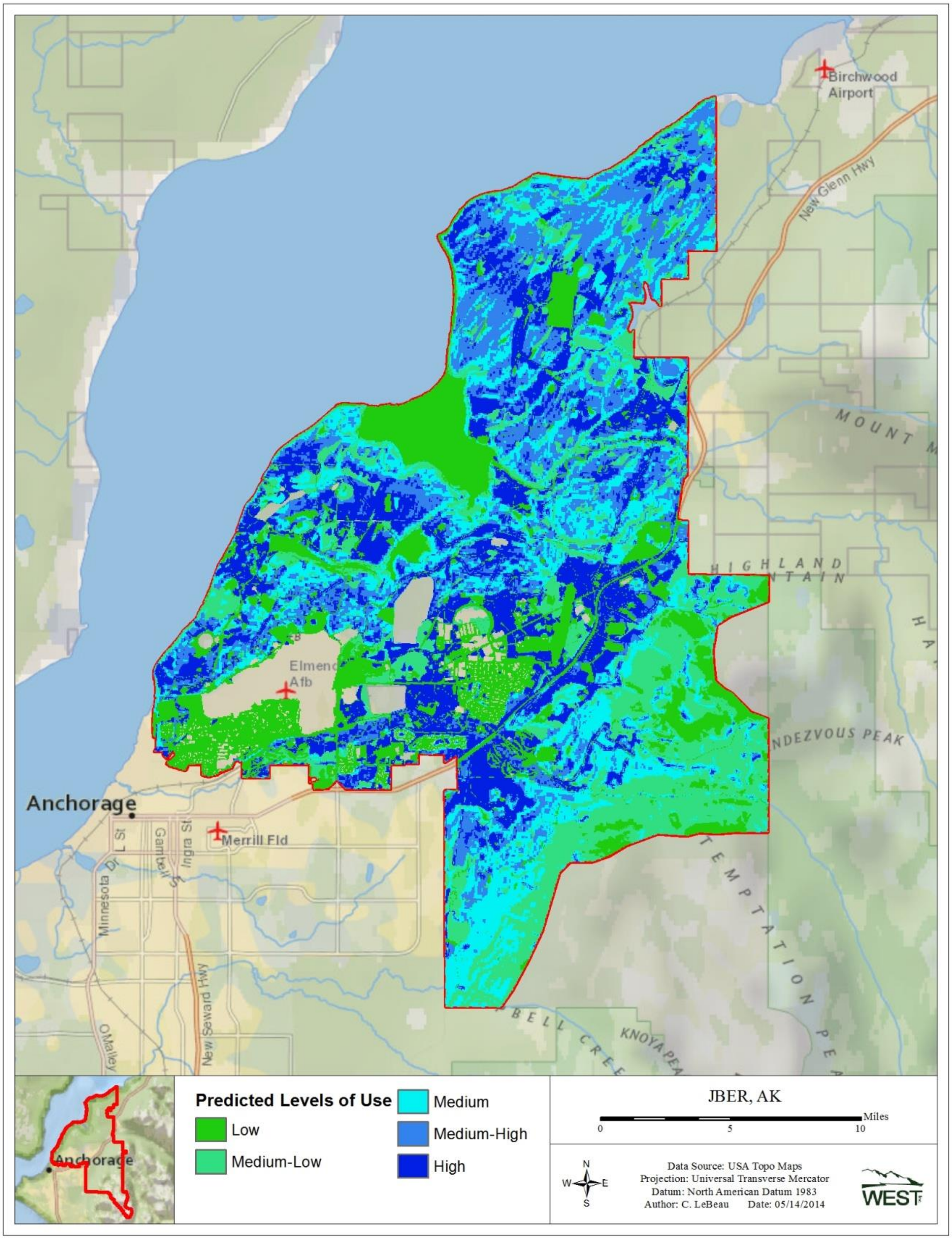
Appendix B-5. The relative predicted levels of use for encamped behavior by moose occupying the JBER during the summer period.

Traveling Behavior: Winter



Appendix B-6. The relative predicted levels of use for traveling behavior by moose occupying the JBER during the winter period.

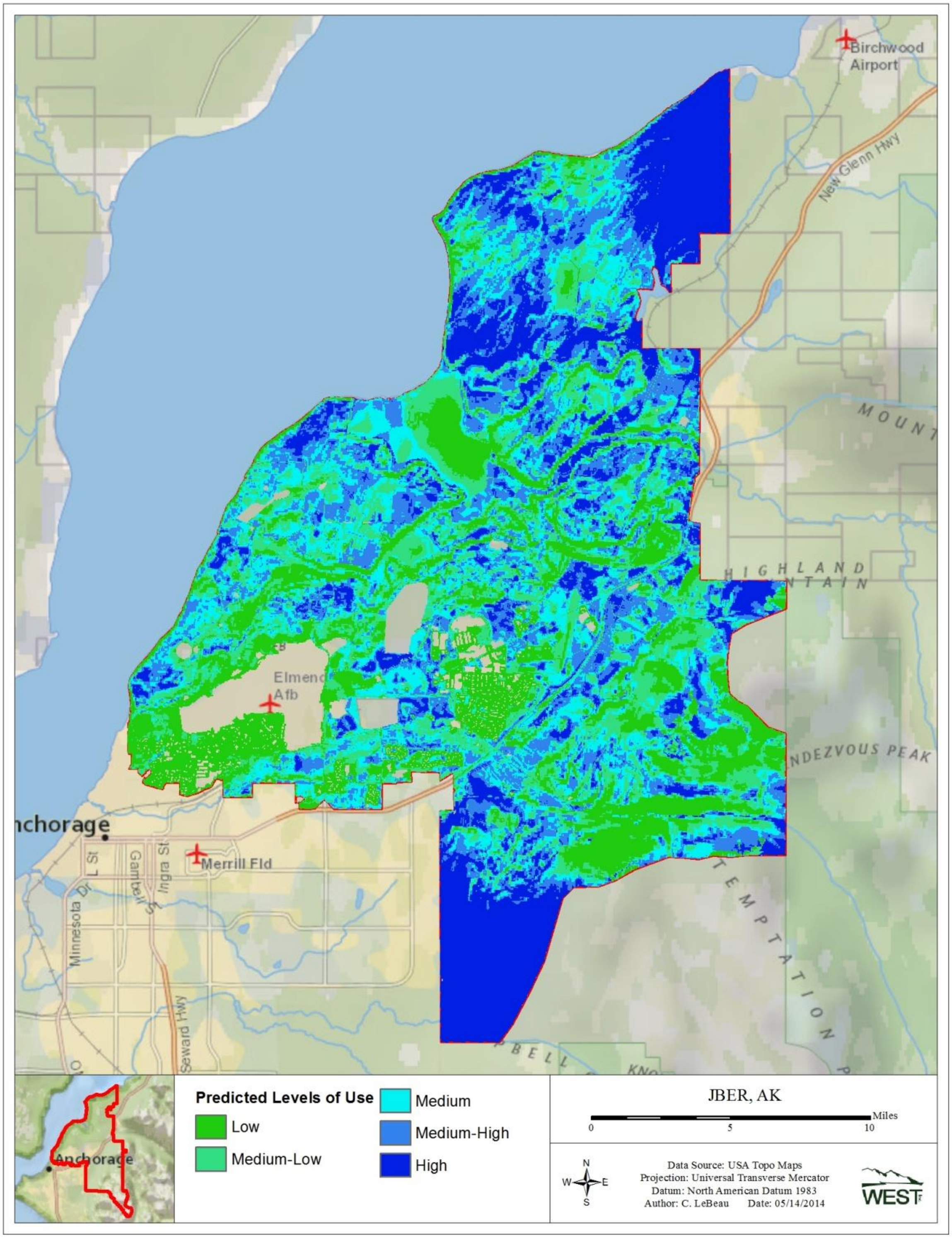
Encamped Behavior: Winter



Data Source: USA Topo Maps
Projection: Universal Transverse Mercator
Datum: North American Datum 1983
Author: C. LeBeau Date: 05/14/2014

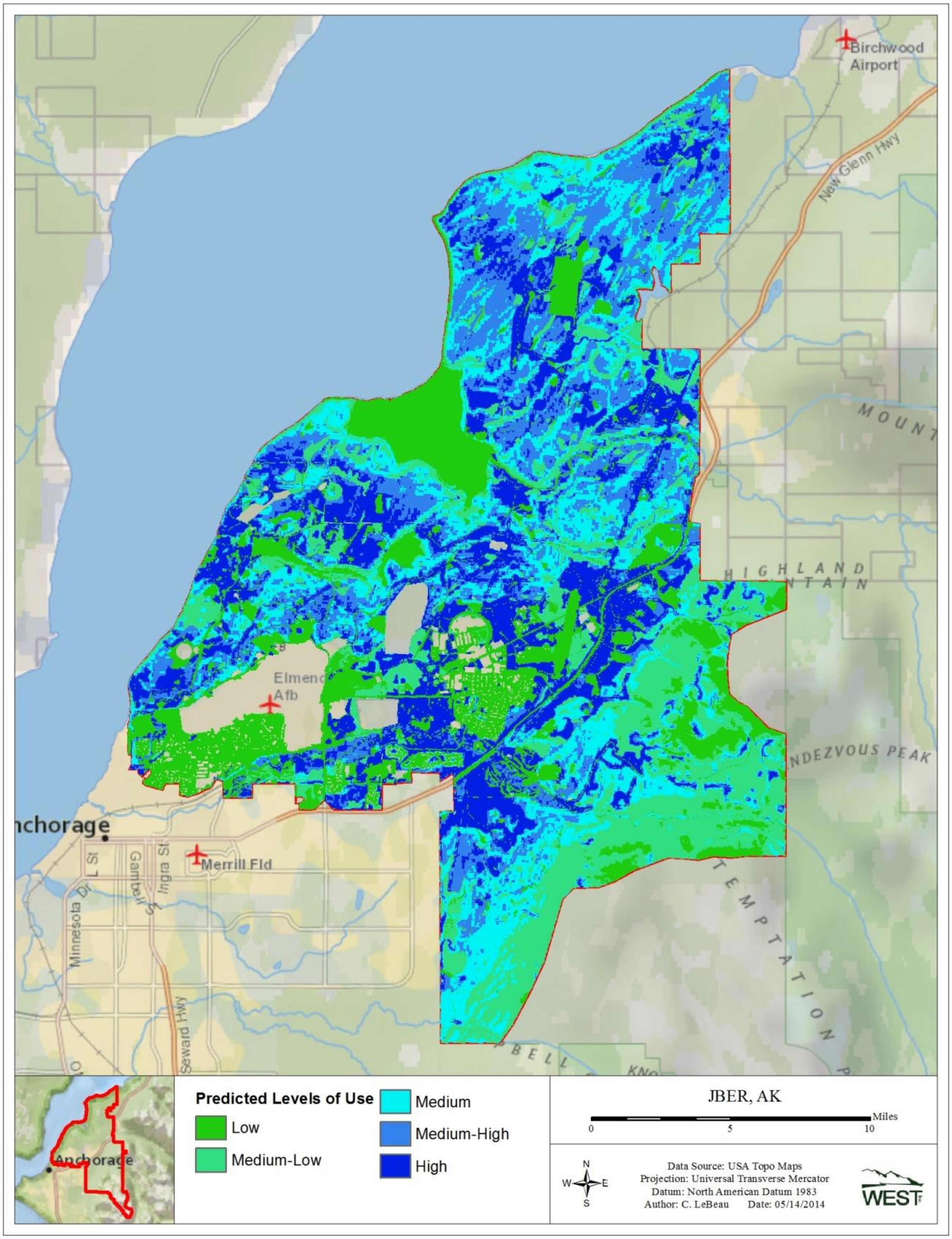
Appendix B-7. The relative predicted levels of use for encamped behavior by moose occupying the JBER during the winter period.

Encamped and Traveling Behavior: Summer



Appendix B-8. The relative predicted levels of use for all behaviors by moose occupying the JBER during the summer period.

Encamped and Traveling Behavior: Winter



Appendix B-9. The relative predicted levels of use for both behaviors by moose occupying the JBER during the winter period.

Appendix C

Population Genetic Structure of Moose (*Alces alces*) of south-central Alaska

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ABSTRACT

The location of a population can influence the genetic structure and diversity by impacting the degree of isolation and connectivity to other populations. Populations at range margins are often thought to have less genetic variation and increased genetic structure. A reduction in genetic diversity can have negative impacts on the health of population. We explored the genetic diversity and connectivity between three peripheral populations of moose (*Alces alces*) with differing potential for connectivity to other areas. Moose populations on the Kenai Peninsula and Anchorage were found to be significantly differentiation with a significantly lower level of genetic diversity within the Kenai population. There was little evidence of contemporary gene flow between Anchorage and Keani suggesting that these two areas are fairly isolated from each other. Although gene flow is restricted outside the peninsula, high levels of gene flow were detected within the Kenai, which can most likely be explained by male dispersal. In addition, the directionality of gene flow within the Kenai Peninsula may follow the highly fluctuating nature of population dynamics of moose that is correlated with habitat change.

Key words: Alaska, population structure, genetic diversity, gene flow

The pattern of geographical variation in genetic diversity and divergence is dictated by the interaction of genetic drift, gene flow, and natural selection (Eckert et al. 2008), and these evolutionary processes can be influenced by the location of a population within a species' geographic range (Briggs 1996, Wisely et al. 2004, Howed and Logheed 2008). At the local and regional scales, the relative position of a population can have strong impacts on the patterns of dispersal and degree of isolation influenced by both historical and contemporary events (Vucetich and Waite 2003, Eckert et al. 2008); ultimately determining the level of genetic structure and diversity. Numerous studies have shown that genetic diversity is lowest at the range margins while highest at the center of a species distribution (Yamashita and Polis 1995, Schwartz et al. 2003, Eckert et al. 2008, Howes and Loughheed 2008). These margins are more likely to be isolated, occur in patchy habitat, and recently colonized. Margin areas are less likely to receive immigrants whereas the centers typically are in prime habitat and experience greater levels of gene flow (Hoffman and Blows 1994, Brown et al. 1995, Wisely et al. 2004, Miller et al. 2010, Schrey et al. 2011).

Evolutionary theory suggests that the reduction of genetic diversity within peripheral populations can impede adaptation to differing or changing environmental conditions (Bradshaw 1991, Hoffmann and Parsons 1991, Hoffmann and Blows 1994, Blows and Hoffmann, 2005). Such adaptation would require additive genetic variation in heritable traits with fitness consequences and several studies have shown that even small changes in genetic variation can have large effects of population fitness (Frankham 1995, Reed and Frankham 2003) and within ungulates, juvenile survival (Coulson et al. 1999, Mainguy et al. 2009, Silva et al. 2009), antler growth (Von Hardenberg et al. 2007), and parasite resistance (Coltman et al. 1999). Thus examining the conditions under which peripheral populations exist in terms of their life history and current levels of genetic diversity can better help researchers understand the processes that maintain geographical ranges, predict the consequences of climate change (Parmesan and Yohe 2003, Root et al. 2003, Hampe and Petit 2005) and how to conserve populations at range margins (Howes and Lougheed 2008).

The Kenai Peninsula is situated in south-central Alaska and is separated from the mainland since the end of the last ice age by a narrow (16 km wide) isthmus. Due to its diverse landscape, biodiversity on the peninsula is unusually high at this latitude (Morton et al. 2009) with moose, *Alces alces*, being one of the most recognizable and socio-economic important species. Moose populations on the Kenai Peninsula are characterized by fluctuations in population size peaking with the occurrence of forest fires that promote optimal forage habitat (Oldemeyer et al 1977). While moose populations on the Kenai have generally showed a slight increase from 1985 to 2013 (~5,000 to 6,000; Alaska Department of Fish and Game unpub. data), the increase has not been uniform across the moose management areas. While moose in Game Management Unit (GMU) 15C (southwest Keani) has shown an increase, the moose population in GMU 15A (northwest Kenai) has drastically declined (~ 40%) in the last 20 years as quality food sources have diminished since the last major fire in 1969. Thus relative isolation from neighboring regions with a strong history of fluctuations in population size could lead to reduced genetic variability on the Kenai Peninsula which could ultimately be detrimental to the long-term health of the population.

Using mitochondrial DNA and microsatellite loci, we compared the genetic variation and evolutionary history of three populations on the periphery of moose distribution in Alaska with differing levels of potential connectivity to the core area of interior Alaska. We predict that the disjunct Kenai population which is isolated by ocean and mountain ranges thus limiting opportunities for genetic exchange, would exhibit lower genetic diversity than the Anchorage population. In addition, we investigate the connectivity between areas on the Kenai Peninsula that have been affected by a long history land alteration and demographic changes.

METHODS

Sample Collection

Moose (n = 163) were sampled from three populations in south-central Alaska (Fig. 1, Appendix 1). Ear-plugs and blood were taken from 33 collared female moose in 2008-2010 and 2012 from the city of

Anchorage and adjacent Eagle River (called Anchorage hereafter). In addition, muscle tissue was taken from 32 hunter-killed moose (16 female, 15 male, and 1 unknown) during the winter of 2011-2012. In spring 2012, blood was taken from collared female moose from GMU 15A (*n* = 49) and GMU 15C (*n* = 49) on the Kenai Peninsula. Anchorage samples are archived at the Molecular Ecology Laboratory, U.S. Geological Survey, Anchorage, Alaska and Kenai Peninsula samples at Alaska Department of Fish and Game, Homer, Alaska.

Molecular techniques

Genomic DNA was extracted from blood and tissue samples using a "salting out" procedure described by Medrano et al. (1990), with modifications described in Sonsthagen et al. (2004). Genomic DNA concentrations were quantified using fluorometry and diluted to 50 ng mL^{-1} working solutions. Individuals were initially screened at seventeen microsatellite loci. Thirteen autosomal loci were found to be polymorphic of which nine with dinucleotide repeat motifs were selected for further analysis that were polymorphic in all populations: BL42, BM888, BM203, BM2830 (Bishop et al. 1994), NVHRT21, NVHRT22 (Roed & Midthjell 1998), RT1, RT5, and RT30 (Wilson et al. 1997). Polymerase chain reaction (PCR) amplification and electrophoresis followed protocols described in Roffler et al. (2012). Ten percent of the samples were amplified and genotyped in duplicate for the nine microsatellite loci for quality control.

We also amplified a portion of the mtDNA control region using the primer pair ALACRH (5'-AGGGATCCTTGCCAGCG-3') and L15774b (5'-GAATTGGAGGACAACCAGT-3'). PCR amplifications were carried out in a 25-μL volume with 50 ng/μL genomic DNA, 0.5 μM each primer, 1.0 μM dNTPs, 10x PCR buffer, 2.5 μM MgCl2, and 0.2 units Taq polymerase. PCR reactions began with 94 ºC for 7 min followed by 45 cycles of 94 ºC for 30 sec, 50 ºC for 30 sec, and 72 ºC for 1 min with a 30 min final extension at 72 ºC. Both strands were sequenced with BigDye Terminator Cycle sequencing kits on an ABI 3100 DNA sequencer (Applied Biosystems, Foster City, CA). Sequences from opposite strands were reconciled in Sequencher 4.1.2 (Gene Codes Corporation, Ann Arbor, MI). In agreement with the low variability of mtDNA in other studies that included south-central Alaska (Hundertmark et al. 2002), we found no variation from the resulting 570 bp among 56 individuals within the Anchorage population. Sequences overlapped by 442 bp with previously published sequences and corresponded with Alaska haplotype 2 (Genbank accession number AF412236, Hundertmark et al. 2002). Since only one haplotype was detected within Anchorage and no significant variation was previously found within mainland Alaska (including south-central Alaska), mtDNA was not collected for Keani and no further analysis was conducted.

Analysis of genetic diversity and population genetic subdivision

We calculated allelic richness, inbreeding coefficient (F_{IS}), observed and expected heterozygosities and tested for Hardy-Weinberg equilibrium (HWE), and linkage disequilibrium (LD) for each microsatellite locus and population in FSTAT ver. 2.9.3 (Goudet 1995). The degree of population genetic subdivision among moose populations was assessed by calculating overall and pairwise F_{ST} and R_{ST}, adjusting for multiple comparisons using Bonferroni correction ($\alpha = 0.05$) in Arlequinv3.5.1.3 (Excoffier and Lischer 2010). Because the upper possible F_{ST} value for a set of microsatellite loci is usually <1.0 (Hedrick 2005), we used RECODEDATA, version 1.0 (Meirmans 2006), to calculate the uppermost limit of F_{ST} for our data set.

We also used a Bayesian-clustering program, STUCTURE 2.2.3 (Pritchard et al. 2000), to determine the level of population structure in the autosomal microsatellite data set. We performed two sets of analyses to look at structure within south central Alaska: (1) between Anchorage and Kenai Peninsula and (2) within Kenai Peninsula (GMU 15A and 15C). Structure assigns individuals to populations maximizing Hardy-Weinberg equilibrium and minimizing linkage disequilibrium. The analysis were conducted for 1–10 populations (K) using an admixture model with 100,000 burn-in iterations and 1,000,000 Markov chain Monte Carlo (MCMC) iterations without providing *a priori* information on the geographic origin of the individuals; the analyses was repeated ten times for each K to ensure consistency across runs. We used the ΔK method of Evanno et al. (2005) and evaluation of the estimate of the posterior probability of the data given K, Ln P(D), to determine the most likely number of groups at the uppermost level of population structure. For the Kenai Peninsula only analysis, we used the LOCPRIOR, which is able to detect population structure in datasets with a weak signal of structure not detectable under standard models (Hubisz et al. 2009).

Gene flow

We estimated gene flow between moose populations using two methodologies: MIGRATEv3.2.16 (Beerli and Felsenstein 1999, 2001) and BayesAss 3.0 (Wilson and Rannala 2003). These programs differ in the underlying model used to estimate gene flow. MIGRATE uses a steady-state two-island coalescent model of population differentiation, which incorporates parameters scaled to the mutation rate (μ): the effective population size parameter Θ ($4N_e\mu$) and the migration rate M (m/μ) between populations. BayesAss uses an assignment methodology, which does not incorporate genealogy or assume that populations are in Hardy-Weinberg equilibrium (Wilson and Rannala 2003). Thus, estimates of migration rate can be interpreted differently and at different temporal scales. BayesAss reflects gene flow over the last several generations while MIGRATE gene flow estimates are averaged over the past *n* generations, where *n* equals the number of generations the populations have been at mutation-drift equilibrium (Beerli and Felsenstein 1999, 2001).

MIGRATE was run with a full migration model, θ ($4N_e\mu$, composite measure of effective population size and mutation rate), and all pairwise migration parameters were estimated individually from the data. Gene flow was estimated using a maximum likelihood search parameters; ten short chains (5000 trees used out of 1,500,000 sampled), ten long chains (15,000 trees used out 5,250,000 sampled), and five static heated chains (1, 1.33, 2.0, 4.0, and 1,000,000; swapping interval = 1). Full models were run ten times to ensure the convergence of parameter estimates.

BayesAss was initially run with the default delta values for allelic frequency (P), migration rate (m), and inbreeding (F). Subsequent runs incorporated different delta values to ensure that acceptance rate for proposed changes was between 20–40% for each parameter to maximize log likelihood values and ensure the most accurate estimates (Wilson and Rannala 2003). Final delta values used were ΔP = 0.5 (27% acceptance rate), Δm = 0.2 (27%), and ΔF = 0.85 (31%). We performed ten independent runs (10 million iterations, 1 million burn-in, and sampling frequency of 1000) and two additional longer runs (50 million iterations, 5 million burn-in) with different random seeds to ensure convergence and consistency across runs. Convergence was also assessed by examining the trace file in program Tracer v1.5 to ensure proper mixing of parameters (Rambaut and Drummond 2007).

Population demography

BOTTLENECK compares the number of alleles and gene diversity at polymorphic loci under the infinite allele model (IAM; Maruyama and Fuerst 1985), stepwise mutation model (SMM; Ohta and Kimura 1973), and two-phase model of mutation (TPM; Di Rienzo et al. 1994; parameters: 79% SSM, variance 9; Piry et al. 1999, Garza and Williamson 2001). One thousand simulations were performed for each population and parameters were changed among five runs to evaluate the robustness of results. Significance was assessed using a Wilcoxon sign-rank test, which determines if the average of standardized differences between observed and expected heterozygosities is significantly different from zero (Cornuet and Luikart 1996). Significant heterozygote deficiency relative to the number of alleles indicates recent population growth, whereas heterozygote excess relative to the number of alleles indicates a recent population bottleneck (Cornuet and Luikart 1996). It is important to note that BOTTLENECK compares heterozygote deficiency and excess relative to genetic diversity, not to Hardy-Weinberg equilibrium expectation (Cornuet and Luikart 1996).

RESULTS

Genetic Diversity and population subdivision

Multilocus genotypes were collected from 163 individuals and each individual had a unique genotype. The number of alleles per locus observed ranged from 3.4 to 4.7 per population with an overall estimate of 5.1 (Table 1 & 2). The observed heterozygosity ranged from 43% to 55% with an overall heterozygosity of 49%. The Kenai population exhibited a 19% lower allelic richness (20% in GMU 15A and 25% in GMU 15C) compared to the Anchorage population with three times more private alleles found in the Anchorage (Table 1). In addition, the observed and expected heterozygosity was significant lower (all *P*-values < 0.0001) in Kenai Peninsula (by 18% observed, 16% expected), in GMU 15C (15%, 14%), and in GMU 15A (22%, 20%). On average, individuals on the Kenai showed a greater level of homozygosity based on the number of loci each individual were homozygous for [Kenai: 4.94 loci (SD 1.46) vs. Anchorage: 3.98 loci (SD 1.51); $t = 4.02$, $P < 0.0001$]. The inbreeding coefficient (F_{IS}) did not differ significantly from zero in any population (Table 1). All loci and populations were in HWE and linkage equilibrium.

Significant genetic structure was observed at the nine microsatellite loci between Anchorage and the two GMUs on the Kenai Peninsula (Table 3). No significant differentiation was found within the Kenai Peninsula. The upper limit of the F_{ST} for our microsatellite data set was 0.499. Therefore, the overall F_{ST} of 0.071 accounted for 14.2% of the maximum possible level of genetic structure and accounted for 19% for pairwise comparisons between Anchorage and Kenai Peninsula GMUs.

STRUCTURE uncovered genetic partitioning within south central moose populations; supporting a two-population model ($\Delta K = 188.3$, average Ln P(D) = -2758.7). Most individuals from Anchorage were assigned to one genetic cluster (87.7%), whereas individuals from Kenai GMU 15A and 15C were assigned to a second cluster with high probability, 93.6 and 92.6%, respectively (Fig. 2). Seven Anchorage individuals were assigned to the Anchorage cluster with <60% certainty while only one Kenai individual was assigned to the Kenai cluster with <60%. Genetic partitioning was not observed within Kenai Peninsula, as including capture location was not informative ($r > 9$).

Gene flow

Restricted gene flow over the past several generations was observed under the BayesAss model between Anchorage and Kenai Peninsula, with 96.8% (93.3–100%) of the Anchorage population comprising of a non-migrant origin (Table 4). Within the Kenai Peninsula, there was a signal of a northern direction of short-term gene flow from GMU 15C into 15A (proportion of individuals with migrant origin: 27.8% in 15A vs. 6.9% in 15C); although 95% confidence intervals do overlap (Table 4).

Asymmetrical recent gene flow was observed as estimated by MIGRATE among sampled moose populations. The directionality of gene flow was from Kenai Peninsula into Anchorage (Table 4). The number of migrants per generation (N_em) ranged from 2.6 and 2.8 into Anchorage and 1.0 and 1.1 into the Kenai GMU 15A and 15C, respectively. Within Kenai there was a signal of asymmetrical gene flow from GMU 15A into 15C (3.3 migrants/generation; Table 4).

Population demography

Effective population size ranged from 0.99 to 1.16, with Anchorage population having the largest effective size with non-overlapping 95% CI (1.16, 1.0–1.23). Within Kenai, effective population sizes for GMU 15A (0.99, 0.94–1.06) and 15C (1.01, 0.95–1.07) were similar.

There was no evidence of significant heterozygosity excess or deficit under the SMM or TPM. However, there was evidence of a recent population decline (heterozygote excess) based on the infinite allele model (IAM) for Kenai GMU 15C (Table 5).

DISCUSSION

Climatic and glaciation history has played a major role in shaping the evolutionary history of many taxa in south-central Alaska. It was not until approximately 7,000 years before present that the Kenai Peninsula became distinct and relatively isolated from the mainland by a 16 km wide mountainous isthmus (Pielou 1991, Muhs et al. 2001). This isolation has fostered genetically or morphologically distinct populations for a variety of taxa (e.g., *Gulo gulo* Tomasik and Cook 2005, *Ursus americanus* Robinson et al. 2007, *Melospiza melodia* Patten and Pruett 2009). The moose populations residing on the Kenai are no exception. Using a multi-locus approach, we observed that moose on the Kenai were genetically distinct from those in the mainland Anchorage population and exhibited significantly lower levels of genetic diversity at microsatellite loci.

Loss of genetic diversity between peninsula and mainland

Populations residing in areas with barriers that limit dispersal (e.g. peninsulas, islands, etc.) across the landscape are expected to have lower genetic variation (Gaines et al. 1997). Our results were consistent with Gaines et al. (1997) prediction; moose occupying Kenai Peninsula had significantly reduced genetic diversity compared to the nearest mainland population, Anchorage, by approximately 18%. A reduction of genetic variability has also been reported for other Alaskan moose populations (Hundertmark 2009, Schmidt et al. 2009) as well as other mammals on the Kenai Peninsula (e.g., *Lynx canadensis* Schwartz et al. 2003). The loss of genetic variation in periphery populations may be due numerous factors such as limited number of connections to other populations or smaller population sizes (Schwartz et al. 2003).

The Cook Inlet and mountains along with a major highway and railways may represent a formidable barrier to dispersal between regions. Although Kenai Peninsula and Anchorage are in close geographic proximity (straight line distance: ~104.12 km), the costs of dispersal over the rugged terrain and highways or swimming across the inlet are likely high. In agreement with limited effective dispersal, we found restricted contemporary gene flow between Kenai Peninsula and mainland Anchorage populations with confidence intervals suggesting there has been no genetic exchange over the past several generations. Telemetry studies of the sampled females in this study showed that individuals remained in the same general area throughout the year (Farley 2012, TJM unpublished data) further suggesting the likelihood of long-distance dispersal between these two regions is low. However, connectivity could be mediated through a contact zone north of the isthmus at Portage Valley as observed in black bears *Ursus* *americanus* Robinson et al. 2007). The isthmus is not a strong barrier to moose as movement across the isthmus has been observed (T. Lohuis and TMD unpublished data). Furthermore, STRUCTURE analysis estimated a low probability assignment to a genetic cluster for ~ 12% of the individuals in Anchorage suggestive of the occurrence of gene flow during or after population divergence. Study of moose in areas between Anchorage and Kenai Peninsula could determine if a contact zone exists for moose at the isthmus as seen in other mammals or if these two regions are completely isolated as indicated by contemporary gene flow results.

Relationships within the peninsula

Unlike the potential strong barriers to dispersal between the peninsula and mainland populations, there are relatively few natural barriers to movement in the western part of the peninsula and gene flow estimates suggest that there is ongoing genetic exchange. The directionality of gene flow across western Kenai Peninsula has not remained constant over time. Differences in directionality across time scales may be attributed to the fluctuating nature of moose population dynamics that is correlated with habitat change, in particular in GMU 15A where population sizes have fluctuated with major fire events (Oldemeyer et al. 1977, Schwartz and Franzmann 1989). The habitat in GMU 15A has changed drastically over the last century with ideal moose habitat being formed during the major fires of 1947 and 1969 with low quality characterizing the area prior to the fires and present day (Oldemeyer et al. 1977, Schwartz and Franzmann 1989). If this periodic population increase was quite frequent throughout the history of moose in this area and dispersal is influenced by population density and habitat quality, we might expect the directionality of gene flow to change over time with more moose dispersing from areas of high productivity into areas of lower density or less preferred habitat as competition for resources increases. Indeed, contemporary gene flow estimated in BayesAss indicates gene flow from a higher density area (GMU 15C) with better quality habitat into an area characterized by poor habitat conditions and lower density area (15A).

Moose populations on the Kenai Peninsula have also fluctuated in size partially due to human activities (land development and forest fires), with changes in habitat potentially affecting fertility and survival of young (Klein 1970, Franzmann and Arneson 1973, Schwartz and Franzmann 1989, Testa and Adams 1989). While moose populations initially respond positively to wildfires through the emergence of optimal habitat, population sizes eventually decline as the habitat changes to late succession (non-optimal forage) vegetation. Since the last major fire in GMU 15A in 1969, the population has declined by approximately 40% over the last 20 years. Current and previous assessment of calf survival from this area is characterized by substantially low calf survival (Franzmann et al. 1980, TJM unpublished data). Such a drastic population decline in population size coupled with low productivity can have negative impacts on the genetic diversity of a population, which could partially explain the significant reduction in genetic diversity on the Kenai Peninsula.

A reduction in genetic diversity can lead to inbreeding depression (increased homozygosity), which can lower viability and fecundity (Falconer 1981, Ralls et al. 1983, Franklin 1995, Crnokrak and Roff 1999). Kenai populations have a higher inbreeding coefficient (although not significantly different from zero) and significantly higher levels of homozygosity than the Anchorage population. Whether this decrease in genetic variability is correlated to the declining reproductive rates based on twinning rates (Franzmann and Schwartz 1985, ADF&G unpublished data 2013) or is purely influenced by environmental factors still needs to be investigated. The effects of inbreeding depression can diminish (Lynch 1977). However, the loss of genetic variation can be detrimental over evolutionary time, as reduced genetic variability upon which natural selection can act may lower the ability of populations to respond to novel environmental stressors associated such as novel predators, parasites, or climatic conditions (Lacy 1987, Quattro and Vrijenhoek 1989, Leberg 1993). Thus monitoring the genetic diversity at neutral loci as well as the incorporation of fitness-related genes can further our understanding of how genetic diversity changes through time and the processes by which populations offset the negative impacts of lower genetic diversity especially in important socio-economical species like moose.

CONCLUSIONS

Our conclusions on the negative effects of reduced diversity are reliant on the pattern seen at neutral microsatellite markers being concordant with overall genomic variation. Although neutral loci are commonly used to infer evolutionary history of populations and make inferences about overall variation (see Howes and Lougheed 2007), it is still relatively unknown whether the trends in putatively neutral loci are reflected by quantitative-trait variation found in genes for physiological, morphological, or life history traits that are likely important for the adaptive potential of populations (Merilä and Crnokrak 2001, Reed and Frankham 2001, Eckert et al. 2008). However, the identification adaptive genes and determining the effects of genetic and environment factors on these functional traits are liable to be complex. These results showing significant population structure and limited connectivity to outside populations for the Kenai population provide a working hypothesis for the potential effects on genetic diversity until data regarding both selectively neutral and functional diversity are available to provide greater resolution on the processes responsible for the distribution of genetic diversity among populations within south-central Alaska.

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Table 1. Estimates of genetic diversity of the three moose populations sampled in Anchorage and Kenai, including; average number of alleles, allelic richness, observed and expected heterozygosities (H_o/H_e), inbreeding coefficient (F_{IS}), and sample size calculated from nine microsatellite loci.

		Kenai Peninsula		
	Anchorage	GMU 15A	GMU 15C	Overall Kenai
No. Alleles	4.67	3.67	3.44	4.00
No. Private Alleles	10	1	2	3
Allelic Richness	4.59	3.67	3.44	3.78[1]
H_o (SD) /	0.55 (0.02)/	0.43 (0.02)/	0.47 (0.02)/	0.45 (0.02)/
H_e (SD)	0.56 (0.06)	0.45 (0.07)	0.48 (0.05)	0.47 (0.06)
F_{IS}	0.007	0.056	0.031	0.043

n	65	49	49	98

[1] Allelic richness based on smallest sample size of 65. Within Kenai Peninsula based on sample size of 49.

Table 2. Estimates of observed and expected heterozygosity, number of alleles per locus for nine autosomal nuclear microsatellite loci assayed in three moose populations in south central Alaska. All loci were in Hardy-Weinberg equilibrium.

			Kenai Peninsula			
					Overall Kenai (98)	**All populations**
Locus		**Anchorage (65)**	**GMU 15A (49)**	**GMU 15C (49)**		**(165)**
NVHRT22	H_o/H_e[1]	0.69/0.76	0.49/0.54	0.57/0.53	0.53/0.53	0.60/0.68
	N_a[2]	6	5	4	6	6
NVHRT21	H_o/H_e	0.49/0.50	0.55/0.46	0.39/0.45	0.47/0.45	0.48/0.48
	N_a	5	3	2	3	5
RT1	H_o/H_e	0.49/0.46	0.27/0.29	0.39/0.38	0.31/0.34	0.38/0.40
	N_a	2	2	2	2	2
RT5	H_o/H_e	0.54/0.52	0.18/0.21	0.25/0.32	0.21/0.26	0.34/0.40
	N_a	4	3	3	3	4
RT30	H_o/H_e	0.55/0.58	0.69/0.67	0.74/0.72	0.71/0.70	0.65/0.66
	N_a	5	4	4	4	5
BM203	H_o/H_e	0.20/0.20	0.37/0.41	0.51/0.50	0.44/0.46	0.34/0.38
	N_a	5	3	4	4	6
BM2830	H_o/H_e	0.46/0.49	0.37/0.43	0.41/0.41	0.39/0.42	0.42/0.45
	N_a	2	2	2	2	2
BM888	H_o/H_e	0.63/0.65	0.22/0.26	0.20/0.27	0.21/0.27	0.38/0.46
	N_a	4	4	3	4	4
BL42	H_o/H_e	0.91/0.84	0.71/0.81	0.80/0.75	0.76/0.79	0.82/0.83

	N_a	9	6	7	8	12
Overall Loci	H_o/H_e	0.55/0.56	0.43/0.45	0.47/0.48	0.45/0.47	0.49/0.53
	N_a	4.67	3.67	3.44	4.00	5.11

[1] H_o = heterozygosity observed. H_e = heterozygosity expected.

[2] N_a = number of alleles.

Table 3. Pairwise and overall values of F_{ST} and R_{ST} calculated from nine microsatellite loci. Significant values are marked with an asterisk

	F_{ST}	R_{ST}
Anchorage		
– Kenai GMU 15A	0.094*	0.014
– Kenai GMU 15C	0.092*	0.028
Kenai GMU 15A		
– Kenai GMU 15C	0.001	0.000
Overall	0.071*	0.016

Table 4. Short-term (proportion of individuals with migrant origin, m) calculated in BayesAss and recent (number of migrants per generation N_em) estimated in MIGRATE for Moose populations in south-central Alaska calculated from nine microsatellite loci. Parameter estimates are listed for each population pair, as well as, the directionality of dispersal between population pairs (source vs. sink). The 95% confidence intervals are in parentheses.

	Microsatellites					
	Short-term gene flow (m)			Recent gene flow (N_em)		
	Immigration	Emigration	Direction	Immigration	Emigration	Direction
Anchorage						
– Kenai GMU 15A	0.013	0.008	–	2.56	0.99	Sink
	(0.00–0.04)	(0.00–0.02)		(1.97–3.29)	(0.74–1.32)	
– Kenai GMU 15C	0.019	0.009	–	2.78	1.08	Sink
	(0.00–0.05)	(0.00–0.03)		(2.20–3.48)	(0.78–1.47)	
Kenai GMU 15A						

– Kenai GMU 15C	0.278	0.069	–	1.18	3.29	Source
	(0.13–0.43)	(0.00–0.25)		(0.89–1.54)	(2.63–4.07)	

Table 5. Analysis of historical fluctuations in population demography of moose populations in south central Alaska from nine microsatellite loci tested using the infinite allele model (IAM), stepwise mutation model (SMM), and two-phase model of mutation (TPM).

	Microsatellites		
	IAM	SMM	TPM
Anchorage	Eq	Eq	Eq
Kenai Unit 15A	Eq	Eq	Eq
Kenai Unit 15C	**Het exc**	Eq	Eq

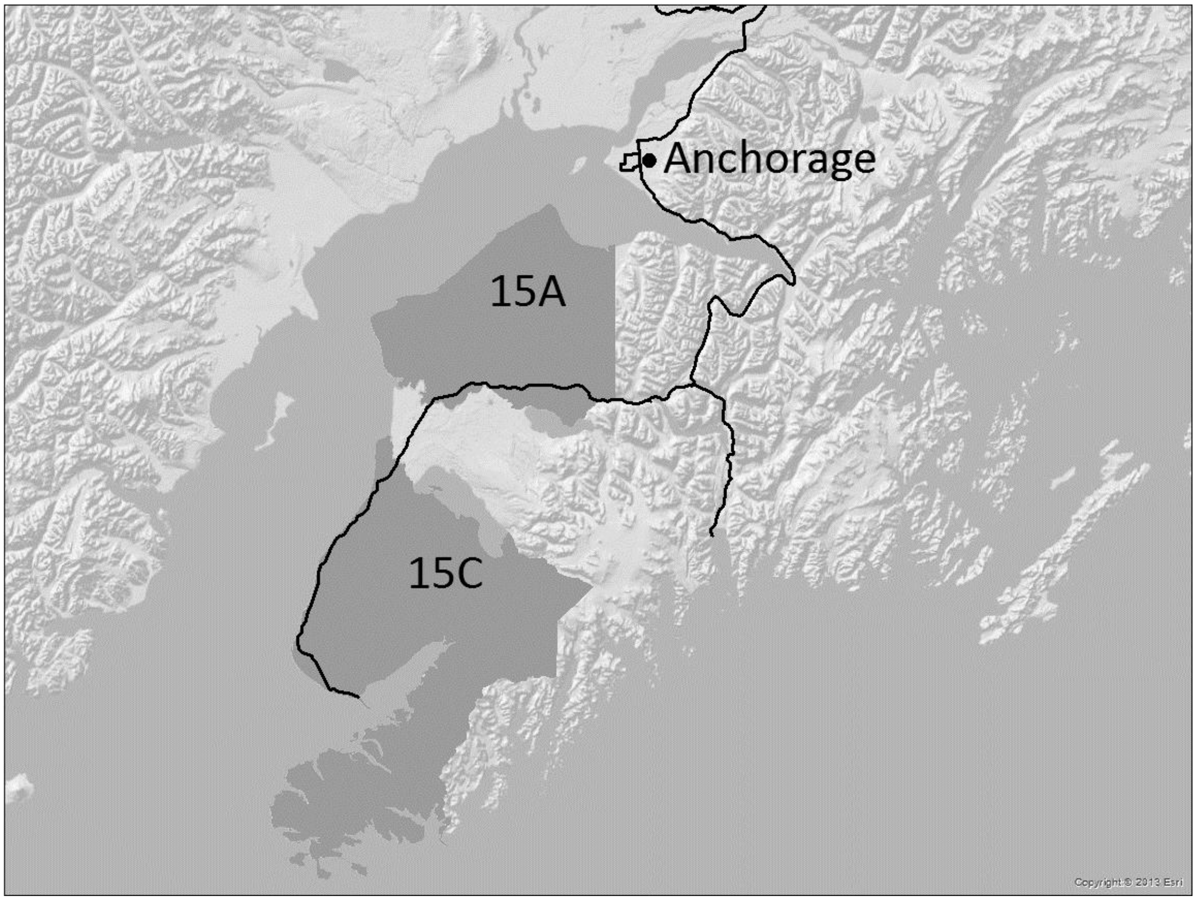

Figure 1. Sampling areas for three moose populations in south-central Alaska; Anchorage and Eagle River, Game Management Unit (GMU) 15A (northwest Kenai Peninsula) and GMU15C (southwest Kenai Peninsula)..

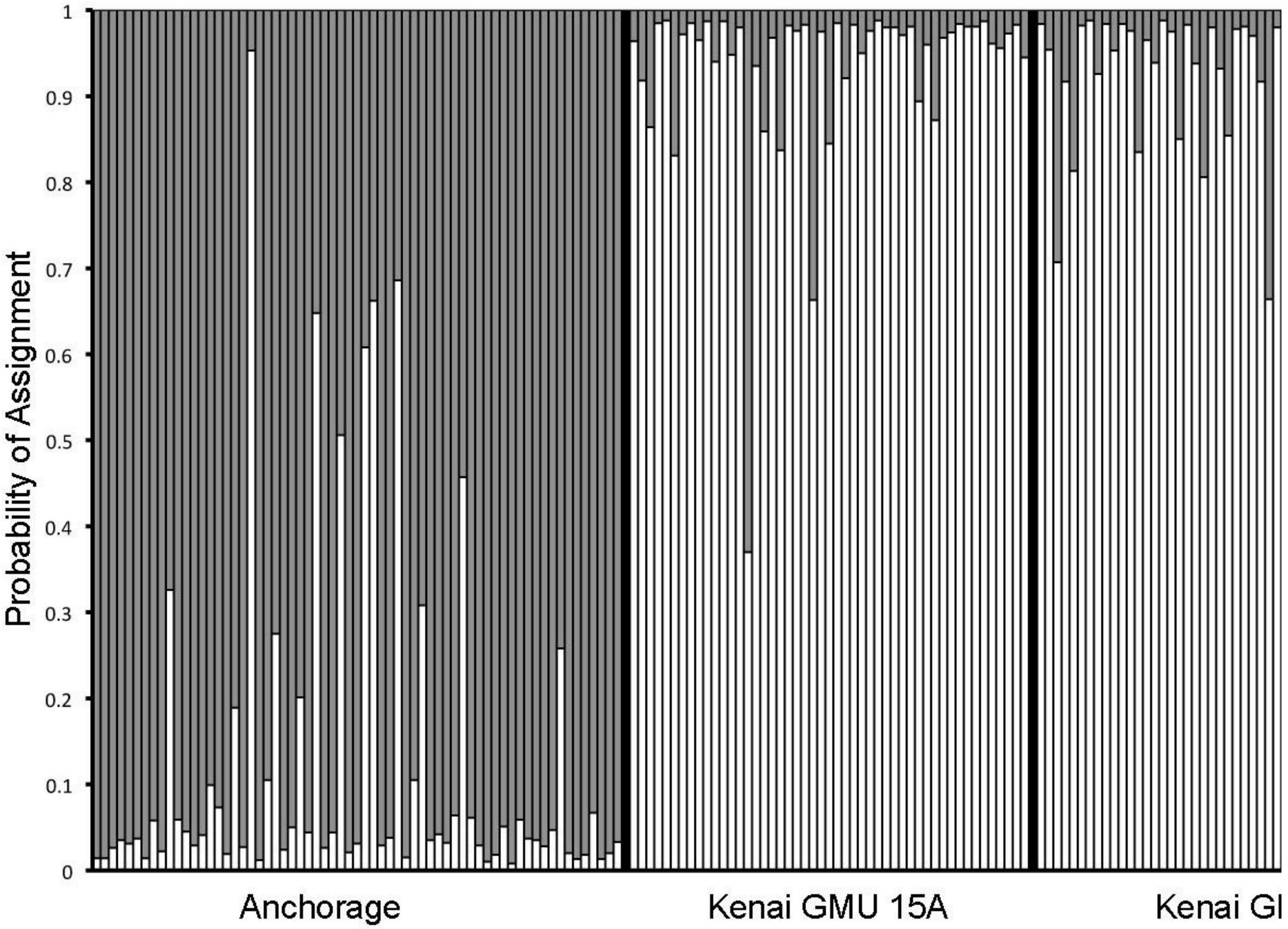

Figure 2. Structure analysis showing posterior probability of assignment of individuals to each ($K = 2$) genetic cluster. White bar represents the estimated probability of assignment to cluster one and grey bar is the estimated probability of assignment to cluster two.

Appendix D

A Genetic Discontinuity in Moose (Alces alces) in Alaska corresponds with fenced transportation infrastructure

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ABSTRACT

The strength and arrangement of movement barriers can impact the connectivity among habitat patches. Anthropogenic barriers (e.g. roads) are a major source of habitat fragmentation that can disrupt these resource networks and can have a major influence on the spatial genetic structure of populations. Using microsatellite data, we evaluated whether observed genetic structure of moose (*Alces alces*) populations were associated with human activities (e.g. roads) in the urban habitat of Anchorage and rural habitat on the Kenai Peninsula, Alaska. We found evidence of a recent genetic subdivision of the Anchorage moose population that corresponds to a major highway and military infrastructure, whereas we did not detect genetic subdivision on the Kenai Peninsula where such human-induced barriers are absent. We hypothesize that this subdivision is due to restrictions in gene flow due to alterations to the highway (e.g. moose-proof fencing with one-way gates) and a significant increase in traffic volume over the past 30 years. This study illustrates the potential rapid effects anthropogenic barriers can have on wildlife populations and the need for genetic assessments to determine the effects on genetic connectivity among habitat patches in conjunction with behavioral and ecological data.

Keywords *Alces alces*, Anthropogenic barrier, Fragmentation, Roads, Genetic spatial structure

Introduction

Dispersal is a fundamental behavior of wildlife that is influenced by many ecological processes. Landscape features such as mountains, rivers, and roads have been shown to influence dispersal as well as seasonal or daily movement patterns within established home ranges (Riley et al 2006; Millions and Swanson 2007; Long et al. 2010). The strength and arrangement of potential barriers to movement determines the degree of connectivity among habitat patches and can ultimately influence population densities and other demographic processes (Delany et al. 2010; Long et al. 2010; Hepenstrick et al. 2012). Spatial distribution of genetic variation relative to landscape features can provide valuable insight into the effects of potential barriers to effective dispersal (i.e. gene flow) and help predict how future alterations to the landscape may impact a population (Coulon et al. 2006; Row et al. 2010; Coster and Kovach 2012).

Human activities can strongly impact animal communities. Urban infrastructures, especially roads, have been shown to be a major contributor to the fragmentation of wildlife habitats (Gerlach and Musolf 2000; Miller and Hobbs 2002; Riley et al. 2006; Balkenhol and Waits 2009; Selva et al.2011; Schuster et al. 2013). Habitat alteration by roads and other anthropogenic developments can modify daily or seasonal movement patterns, disrupt social structure, and increase mortality due to vehicle collisions, potentially leading to barrier effects (Trombulak and Frissell 2000; Jaeger et al. 2005; Clark et al. 2010; Holdo et al. 2011). These movement barriers can affect wildlife populations by restricting access to high quality resources and increasing mortality risk (Fahrig and Rytwinski 2009). In addition, barriers can reduce functional connectivity among habitat patches, subdivide populations and lead to negative genetic effects (e.g. loss of genetic diversity; Hepenstrick et al. 2012). Roads and other human developments are already known to restrict gene flow for small-bodied species such as amphibians (Reh and Seitz 1990; Noel et al. 2007) and insects (Keller and Largiader 2003); however, it is becoming more evident that human activity can also influence species with greater dispersal capabilities (Noss et al. 1996; Leveau 2013; Unfried et al. 2013). Genetic techniques that incorporate spatial information as well as the dispersal ability of species, not only help characterize patterns of genetic structure, but also provide insight into the influence of habitat fragmentation on the distribution of genetic diversity of wildlife populations.

Moose (*Alces alces*) are a valuable game species across Alaska that are particularly well adapted to living in the early successional habitat found in urban settings (Bangs et al. 1985; Loranger et al. 1991; Collins and Helm 1997; Bjørneraas et al. 2012). Habitat patches are scattered across these urban areas, frequently concentrating moose in parks, greenbelts, and other open spaces near human development (Garrett and Conway 1999). The close proximity of wildlife habitats to human communities increases the frequency of negative wildlife-human interactions (e.g. vehicle collisions). Along with hunting, vehicle-collisions are a major source of human-caused mortality in south-central Alaska, and from 2005-2009 accounted for 62% of known human-caused death in the cities of Anchorage, Wasilla, and Palmer, and at least 32% of deaths on the the Kenai Peninsula (Carnahan 2010; Morton 2012). In addition, most vehicle-related deaths involve calves or cows, which can have a detrimental effect on the current growth and future reproductive performance of a population (Del Frate and Spraker 1991). In addition to habitat fragmentation due to roads and other infrastructure, human-caused mortality (via vehicle collisions or hunting) may also affect genetic structure of the population (Nussey et al. 2005; Allendorf et al. 2008; Frantz et al. 2008).

Using microsatellite loci, we assessed moose population genetic structure in two areas in Alaska with contrasting levels of anthropogenic disturbances (high disturbance in Anchorage and low disturbance in Kenai Peninsula). These two regions differ in habitat (forage quality and composition) and history of recent habitat changes due to either human activities (e.g. roads and fences in

Anchorage) or natural disturbances (e.g. bark beetle, *Dendroctonus rufipennis*, infestation and forest fires on the Kenai Peninsula). We aimed to determine (1) whether there is genetic structure within each area and (2) if structure is present, whether is it associated with any potential dispersal barriers. We hypothesized that the moose population in and near Anchorage has greater genetic subdivision due to greater levels of anthropogenic habitat fragmentation. In addition, we predicted any spatial genetic structure would be associated with human disturbances, in particular the Glenn Highway, as illustrated in other ungulate species (Wang and Schreiber 2001; Epps et al. 2005; Kuehn et al. 2007; Hepenstrick et al. 2012). Understanding the distribution of genetic diversity and how it is related to habitat fragmentation in urban environments can inform mitigation strategies to reduce the potential impacts of fragmentation by roads and other landscape features on moose populations.

Methods

Study area and genetic sampling

Our study was conducted in two geographic areas in south-central Alaska; one population in Anchorage encompassing the Joint Base Elmendorf-Richardson (JBER) and Chugach State Park, and a population from western Kenai Peninsula (Game Management Unit (GMU) 15C; Figs. 1, 2). JBER encompasses about 300 km^2, which provides important habitat for moose that remain in the area year-round at a current estimated density of 0.97 moose/km^2 (Farley unpub. data). Undeveloped land on and adjacent to JBER is composed of mixed forests of birch (*Betula papyrifera*) and white spruce (*Picea glauca*) with more recently disturbed areas containing balsam popular (*Populus balsamifera*), willow (*Salix spp*.), birch, and aspen (*P. tremuloides*). Shrublands with high percentages of willows and other woody browse (Bennet 1983; Rothe et al. 1983) provide the highest quality of forage for moose on JBER (Welch 2012). The Glenn Highway, which bisects JBER and serves as the principal access to Anchorage, is heavily utilized by freight as well as by commuters to Anchorage with an estimated annual average daily traffic (AADT) of 54,201 vehicles in 2012 (Yan 2012). To minimize vehicle collisions, moose-proof fencing with one-way gates, additional lighting, and an underpass designed for moose passage were installed in 1987 (McDonald 1991). However, this underpass (3 m wide x 3.2 m high) does not meet the current minimum height recommendations for moose (18.3 m wide x 5.5 m high; Center for Environmental Excellence by the American Association of State Highway and Transportation Officials 2009). As the Alaskan moose can stand over 2 m at the shoulder, this is especially pertinent in winter where snow overflow can significantly reduce the underpass height. Therefore due to the lack of an appropriately sized underpass, along with the fencing and traffic density, moose movements across the highway are restricted (Farley et al. 2012).

On the Kenai Peninsula, GMU 15C comprises over 6,300 km^2 of the southwest portion of the Kenai Peninsula and contains approximately 90% of the moose population found north of Kachemak Bay (core area: 3,032 km^2). The current population density of 1.06 moose/km^2 (McDonough unpub. data) is similar to Anchorage. Unlike Anchorage, however, moose habitat in this area is not strongly bisected by roads, as the only major highway is located along the coast. GMU 15C is characterized by well-defined river drainages, variable elevation (range in core area: 0–762 m), and continuous forests of white spruce and mixed forest of white and Lutz (*Picea glauca* x *P. sitchensis*) spruce, birch, and black cottonwood (*Populus trichocarpa*). Between 1987 and 2003, over 4,290 km^2 of forest (mainly within GMU 15C) was infested with spruce bark beetle, which changed the vegetation composition to early successional grasses and forbes in the lowlands and late successional species in the mountains due to high spruce mortality and subsequent salvage logging (Boucher and Mead 2006).

Home range size and centroid calculations

Between March 2009 and November 2012, Alaska Department of Fish and Game (ADF&G) biologists deployed 25 radio collars with GPS and VHF capabilities on adult female moose within and in close proximity to JBER land. GPS locations were collected either every 30 minutes or every 60 minutes. In addition, 49 VHF collars were deployed on the Kenai Peninsula with location data collected once a month via fixed wing aerial (telemetry) surveys from March to December 2012. We used the minimum convex polygon method (MCP; Mohr 1947) to delineate moose home ranges and centroid locations. We generated MCPs for each moose using the genmcp (generate minimum convex polygon) tool in Geospatial Modeling Environment (GME), version 0.7.1.0 (Beyer 2009) and centroids using the "Calculate Geometry" option in ArcGIS v. 10.0 (ESRI, Inc. Redlands, CA). Although our calculation of home range may underestimate the range size for the Kenai due to sampling regime (Girard et al. 2002; Mills et al. 2006), we were only interested in assessing gross scale movements to provide a level of uncertainty around the centroid coordinates for the program GENELAND (see below). We used home range sizes to calculate an upper limit on the maximum potential movement an individual was capable of during the year for the uncertainty index. The Anchorage moose population had a mean home range size of 55 km^2 (range: 27–83 km^2) for individuals with at least 11 months of location data; therefore we assumed on average an individual would be within 7.5 km of their center of activity. The Kenai Peninsula moose exhibited a greater range of yearly movement, with a mean home range size of 106 km^2 (0.7–334 km^2) and an uncertainty index of 10.3 km around the centroid position.

Genetic sampling

We collected ear-plugs and blood from the adult GPS or VHF collared female moose (Anchorage *n* = 25 and Kenai Peninsula *n* = 49; Fig. 1). To increase the sample size on the western side of the Glenn Highway in Anchorage (Fig. 2), we supplemented our dataset with muscle tissue taken from 15 hunter-killed female moose from the same area during the winter of 2011–2012. Anchorage samples are archived at the Molecular Ecology Laboratory, U.S. Geological Survey, Anchorage, Alaska, and Kenai Peninsula samples at the ADF&G in Homer, Alaska. All animal capturing and genetic sampling were conducted under Division of Wildlife Conservation ACUC approval (# 2012-07, 2013-21, and 90-05) and under the University of Alaska Fairbanks IACUC approval (# 14885 and 182744).

Molecular techniques

We extracted genomic DNA from blood and muscle tissue samples using a "salting out" procedure described by Medrano et al. (1990), with modifications described in Sonsthagen et al. (2004). We quantified genomic DNA concentrations using fluorometry and diluted to 50 ng mL^{-1} working solutions. Individuals were screened at seventeen microsatellite loci. Thirteen autosomal loci were found to be polymorphic, of which we selected ten with dinucleotide repeat motifs for further analysis: BL42, BM888, BM203, BM2830 (Bishop et al. 1994), NVHRT21, NVHRT22, NVHRT34 (Røed and Midthjell 1998), RT1, RT5, and RT30 (Wilson et al. 1997). Polymerase chain reaction (PCR) amplification and electrophoresis followed protocols described in Roffler et al. (2012). For quality control purposes, ten percent of the samples were amplified and genotyped in duplicate at all loci.

Data analysis

To infer the number of subpopulations and assign individual samples to these subpopulations, we analyzed microsatellite allelic frequency and sample spatial location data using two different approaches implemented in R 3.0.2 (R Development Core Team 2011): (1) Bayesian clustering using the program GENELAND 4.0.3 (Guillot et al. 2005a,b; Guillot and Santos 2009) and (2) multivariate ordination method using a spatial principal components analysis (sPCA) with the *adegenet* (Jombart 2008; Jombart and Ahmed 2011) and *ade4* (Dray and Dufour 2007) packages.

GENELAND can incorporate geographical information to detect spatial delineation of genetic discontinuities, where the number of population units is treated as an unknown parameter. We set the maximum number of populations (K) at five and used a matrix of genotypes and spatial coordinates for each individual with an uncertainty index (described above). Allelic frequencies were drawn from independent Dirichlet distributions and allowed for correlated allelic frequencies and null alleles (recommended whether or not the dataset contains null alleles; Guillot 2008). As recent ecological events often result in weak genetic differentiation, the correlated allelic frequency model has been shown to have greater power to detect subtle differentiation when compared to other clustering programs (Latch et al. 2006). However, this model is more sensitive to departure from model assumptions (e.g. presence of isolation-by-distance IBD); therefore we tested for IBD using a Mantel Test with Isolation by Distance Web Service 3.23 (Jensen et al. 2005) as well as tested for Hardy-Weinberg (HWE) and linkage disequilibrium (LE) in FSTAT ver. 2.9.3 (Goudet 1995).

GENELAND was run for 1 million Markov chain Monte Carlo iterations (thinning = 100, burn in = 1,000) and repeated ten times to ensure consistency across runs. Alternate values for location uncertainty that encompass the movement capabilities of all individuals based on home range sizes (all populations: 0 km, 2.5 km, 5 km, 7.5 km, 10 km, and for Kenai population only: 15 km and 20 km) did not substantially alter the results. Failure to account for null alleles in the model slightly reduced consistency in inferring K across runs and in assigning individuals (Guillot et al. 2008), but for the Kenai population only. The number and geographic location of clusters within the Anchorage population did not vary across models; therefore, we only considered runs allowing for null alleles. Individuals were assigned to subpopulations based on their probability of population membership, using the default threshold of 50% assignment probability. We also visually inspected the distribution of individual assignment probabilities to determine areas of potential admixture using a more stringent criterion of 70% assignment probability.

Unlike the Bayesian clustering methods, sPCA makes no assumptions regarding HWE or LE that accounts for spatial autocorrelation issues such as neighbor mating and sample distribution, and therefore provides a complementary approach to Bayesian approaches (Schwarz and McKelvey 2009; Rudledge et al. 2010). A sPCA was run with the spca function in *adegenet* library using a Delaunay's triangulation (Upton and Fingleton 1985) to corroborate any genetic structure found in the program GENELAND. A sPCA defines synthetic variables (principal components) that optimize the product of genetic variability and Moran's Index to summarize the spatial patterns of genetic structure at global and local scales. To select the number of principal components to interpret, we considered the proportion of the total variance explained as well as the distribution among eigenvalues in a screeplot. We identified underlying spatial patterns by plotting the lagged principal component values with the s.value function in the *ade4* package.

We calculated genetic diversity (number of alleles, inbreeding coefficient (F_{IS}), observed and expected heterozygosities) within each subpopulation (as determined by the default 50% threshold and stricter 70% criterion GENELAND assignment) and population differentiation (F_{ST}) in FSTAT. Because the upper possible F_{ST} value for a set of microsatellite loci is usually < 1.0 (Hedrick 2005), we used RECODEDATA, version 1.0 (Meirmans 2006), to calculate the uppermost limit of F_{ST} for our data set. We also computed overall estimator of actual differentiation (D_{est}; Jost 2008) in SMOGD (Crawford 2010) between each subpopulation. All genetic diversity estimates and population differentiation measures were similar for each population assignment criterion (50% vs. 70%); therefore, we reported the default 50% threshold to allow for the inclusion of all individuals.

Results

Multilocus genotypes were collected from 89 unique individuals and each individual had a unique genotype. There was no evidence of IBD within each sampling area (Anchorage $r = 0.06$ $P = 0.19$; GMU 15C $r = -0.06$ $P = 0.18$). All loci and populations were at HWE (Ps > 0.14) and in LE (Ps > 0.03 with Bonferroni adjusted P-value for 5% level at 0.001). The clustering analysis in GENELAND revealed that the Anchorage moose population was subdivided into two subpopulations. The genetic subpopulations were separated by the Glenn Highway and JBER infrastructure when using the default 50% threshold of population assignment (Fig. 2A). Using a more stringent population criteria, admixed individuals (< 70% assignment probability) were primarily located on undeveloped land in-between the two subpopulations along the highway, suggesting that this area is a zone of contact. In contrast, no genetic sub-structuring was observed on the Kenai Peninsula or within Anchorage without spatial priors.

In the sPCA for the Anchorage population, only the first global component (eigenvalue = 0.107, variance = 0.282, Moran's Index of 0.378) appeared to be informative (Fig. 2B). Similar to the Bayesian analysis, sPCA revealed that Anchorage moose are split into two genetic clusters with the Glenn Highway as an apparent barrier (Fig 2B). As with results from GENELAND, individuals along the highway comprise both groups, with some individuals intermediate (e.g. not well differentiated from either group). The first global component for Kenai Peninsula (eigenvalue = 0.04) was not distinct from the other eigenvalues (second component eigenvalue = 0.03). Strong structuring should be reflected in extreme eigenvalues with an abrupt decrease in eigenvalues, indicating a boundary between true patterns (e.g. relevant biological signal) and non-interpretable structure (Jombart 2013). The lack of either in the Kenai dataset suggests lack of global structure.

Overall, the Anchorage/JBER population had a higher observed heterozygosity ($t_{\mathrm{df}\,=\,87} = 18.85$; $P < 0.001$) and number of alleles ($t_{\mathrm{df}\,=\,87} = 2.19$; $P = 0.03$) than the Kenai Peninsula (Table 1). The total number of alleles for each locus ranged from two to nine in Anchorage and two to seven on the Kenai Peninsula. The average standard genetic diversity measures between subpopulations in Anchorage as defined by the 50% threshold in GENELAND were similar for most loci to each other and to the overall population (Table 1). The two Anchorage subpopulations (east and west side of the highway) exhibited low but significant genetic differentiation after correcting for multiple comparisons using permutation in

FSTAT (F_{ST} = 0.025, P-value = 0.01). The maximum possible F_{ST} for our microsatellite data set is 0.487, therefore our F_{ST} accounts for 5.1% of variation observed. D_{est} ranged from –0.031 to 0.279 across loci with an overall value of 0.005.

Discussion

Human-induced habitat fragmentation, in particular transportation infrastructure, can have large ecological impacts, including influencing the fine-scale genetic structure within species (Balkenhol and Waits 2009; Hale et al. 2013; Hartmann et al. 2013; Schuster et al. 2013; Sotiropoulos et al. 2013). Our results indicated that moose occupying urban Anchorage habitats exhibit weak but significant genetic structure, while the more rural population on the Kenai population showed no population subdivision. Diversity measures between the two subpopulations suggest that this separation has only occurred recently and/or that only a slight reduction in gene flow has occurred (Latch et al. 2011). Although the genetic discontinuity appears to depart only slightly from panmixia, it is likely that the major highway and associated infrastructure is restricting local movements as the boundary between the urban subpopulations for both the GENELAND and sPCA coincide with the only major highway in Anchorage.

Roads can exert a strong barrier effect on wildlife populations by modifying behavior in the form of general road-avoidance (Laurian et al. 2012) or isolating formerly connected populations by the altering migration routes or limiting dispersal capabilities (Hartmann et al. 2013; Seiler et al. 2003). In general, moose in Anchorage do not appear to avoid roadways, as evident by the large number of minor highway and road crossings (Farley et al. 2012), and the spatial distribution of genetic structure did not appear to associate with any of these types of roads. Conversely, the distribution of genetic variation appears to be associated with the only major highway in the city. In 1987, a portion of the Glenn Highway was modified to reduce moose-vehicle collisions. Although this strategy appears to have been effective in reducing road mortality (McDonald 1991), the sole underpass to facilitate wildlife movement across the highway is drastically undersized for moose and rarely used (Farley 2012). Therefore, moose must cross the highway while avoiding traffic and find a way around the exclusion fencing. In situations where crossing attempts decrease to a small number of individuals, exclusion fencing can decrease genetic connectivity (Balkenhol and Waits 2009). A recent telemetry study has shown that highway crossings are not as frequent as previously reported (McDonald 1991), as only 68 crossings by 14 female collared moose were recorded over a 2-year span, with the majority of crossings (~68%) involving only two females (Farley et al. 2012). These findings are in agreement with the general notion that wider roads and higher traffic volume will have a stronger effect on wildlife populations (Clevenger and Waltho 2005; Jaarsma et al. 2006). In fact, it has been hypothesized that highways with AADT levels greater than 10,000 will become impassable to most species (Bellis and Graves 1978; Mueller and Berthoud 1997). The Glenn Highway certainly exceeds this level; traffic volumes have increased by 63% since the highway alterations to an estimated AADT level of 49,214 during peak traffic hours (6 AM-10 PM; Yan 2012). Although non-peak traffic hours could provide more opportunities to cross, the traffic volume during these hours (~5,000 AADT) may still be sufficiently high to represent an effective barrier (Mueller and Berthoud 1987; Alexander et al. 2005). Although the highway and fencing are not impenetrable barriers, increasing traffic volumes and an inadequate underpass to facilitate crossings suggest the highway has become a major impediment to movement (see McDonald 1991; Farley et al. 2012), and ultimately gene flow, facilitating the observed genetic subdivision on either side of the highway.

Genetic discontinuities due to low genetic divergence can be difficult to detect over ecological time (Hedrick 1999; Waples and Gaggiotti 2006; Latch et al. 2011). However, anthropogenic barriers have apparently promoted population subdivision in a variety of taxa with varying dispersal capabilities in a relatively short time frame (Epps et al. 2005; Holderegger and Di Giulio 2010; Lee et al. 2012), even within one generation (Landguth et al. 2010). It is difficult to determine exactly when the Glenn

Highway became a barrier to moose movement, because genetic and movement data are not available for the period before road modifications in 1987. Given the generation time of moose (c. 7 years; Galliard 2007), genetic subdivision could have occurred either within 4 generations with the widening and fencing of highway in 1987, or within the last 10 generations, when the highway was first completed in 1945. Given the apparent decline in crossings from 1987 to present, it is possible that this fine-scale genetic pattern has occurred very recently as human developments are known to restrict movement and influence home range boundaries in other moose populations soon after exposure (Seiler et al. 2003; Wattles and DeStefano 2013). In addition, rapid genetic subdivision due to human-made barriers, in particular, fenced highways (e.g. desert bighorn sheep, *Ovis canadensis nelsoni*, Epps et al. 2005 and roe deer, *Capreolus capreolus*, Wang and Schreiber 2001; Kuehn et al. 2007; Hepenstrick et al. 2012), has been observed in other ungulate species (but see Finnegan et al. 2012), supporting the hypothesis that road effects can be observed within a small time frame even in species with long generation times.

Conclusion

Our study further highlights that anthropogenic barriers have the potential to rapidly impact female genetic structure. The pattern of spatial allelic variation in Anchorage is consistent with decreased connectivity resulting from a barrier effect within an urban environment. Although insufficient time may have passed for fitness-relevant effects to become apparent (Hepenstrick et al. 2012), neutral markers suggest the highway and fencing have impeded gene flow strongly enough to promote genetic subdivision. Although recent telemetry data also suggest that the highway is restricting movement (Farley et al. 2012), crossing and periodic location data shortly after the installation of highway fencing indicated no such decrease in crossings or habitat use (McDonald 1991). However, observed movement patterns might be a poor surrogate for gene flow (Riley et al. 2006). Changes in behavior associated with a human-made barrier points to the need for periodic monitoring of genetic diversity of populations associated with barriers, as impacts (behavioral or genetic) may not necessarily be observed immediately. This study highlights the value of genetic inferences on spatial structure in conjunction with behavioral and ecological data on assessing the consequences of habitat alteration and conservation strategies.

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Table 1. Estimates of genetic diversity of female moose for Anchorage/Joint Base Elmendorf-Richardson (JBER) population and inferred subpopulations from GENELAND in Anchorage and Kenai Peninsula Game Management Units (GMU), including; average number of alleles, observed and expected heterozygosities (H_o/H_e), inbreeding coefficient (F_{IS}), and sample size (n).

	Anchorage/JBER			Kenai Peninsula
	Total	West	East	GMU 15C
Avg. no. Alleles	4.10	3.60	3.90	3.20
H_o/H_e	0.52/0.52	0.52/0.50	0.51/0.52	0.42/0.43
F_{IS}	0.010	-0.039	0.029	0.031
n	40	19	21	49

FIGURE LEGENDS

Figure 1. Moose individual sampling locations (black circles) in south-central Alaska; Anchorage and western Kenai Peninsula north of Kachemak Bay (shaded dark grey: Game Management Unit 15C).

Figure 2. Spatial Bayesian clustering in GENELAND and spatial principal components analysis (sPCA) of female moose in Anchorage including the Joint Base Elmendorf-Richardson (JBER) and Chugach State Park. Major roads are indicated by thick black line, main secondary roads are thick grey lines and small residential roads are light grey. Star indicates the location of the Anchorage weigh station where traffic volume was estimated at 54,201 vehicles per day in 2012. (A) GENELAND analysis suggests two distinct clusters for moose in Anchorage (black and white circles) with map of posterior probability of belonging to western subpopulation (insert). (B) Projection of the individual lagged scores of the first spatial principal component positioned by its spatial coordinates. The color of the square (black or white) corresponds to the sign of the score and the area is proportional to the absolute value of the score; therefore large squares indicate large differentiation with smaller squares indicating smaller differences.

Appendix E

Movement Patterns and Use of the Landscape by Female Moose on Joint Base Elmendorf-Richardson, AK

Proposal for Thesis

Presented to the Faculty of

Colorado State University

In Partial Fulfillment of the Requirements

For the Degree of

Master of Science, Rangeland Ecosystem Science

David Battle

February 2009

(Updated June 2013)

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Introduction

Objectives

This work will rank the habitat found in JBER moose home ranges by behavior patterns and movement characteristics exhibited by moose in the habitat. Behaviors will be identified from data collected by tri-axial accelerometers attached to GPS collars worn by the moose. Movement characteristics will include parameters of speed and direction calculated from the GPS generated travel path. Data collection will include the following projects:

4. The behaviors of browsing, grazing, walking, standing, and lying will be identified from unique signatures recorded by tri-axial accelerometers worn by free-ranging moose. Preliminary data have been collected during tests with captive animals.

5. Behavior data interpreted from tri-axial accelerometer information will be summarized across each animal's home range, then across all animals. I will identify whether specific behaviors are strongly associated with discrete habitat types and if the behaviors occur in similar proportions across the home ranges, irrespective of habitats.

6. Movement characteristics including turning angle, speed, angular deviation and density of locations will be calculated across each animal's home range. Values will be summed for all animals and used to characterize habitat type as to movement characteristics.

7. The potential path areas (PPA; ref??) used by moose during winter (defined as Dec-Feb) and during summer (defined as June –Aug) will be determined for each moose, then summed by moose by season. Important areas or routes will be identified by season.

Research calculating the nutritional value of JBER habitats has recently been completed (Welch 2012). This project will complement that work by using movement characteristics and accelerometer readings to determine use of the landscape. Graves et al. (2007) showed that animal movement characteristics can be used to determine landscape functionality. My project will rank the habitat types found in the moose home ranges by behaviors and movement characteristics and identify those habitat types important to moose. Finally, the potential path areas identified for each moose will be used to identify possible movement corridors which likely maintain habitat connectivity.

These data on behaviors, movement characteristics, and potential connectivity will assist JBER wildlife managers if they need to direct moose movements through habitat and landscape modifications.

Site description

Methods

Data collection: Habitat Classes, Animal Locations, and Activity

1. Habitat Classes

A large body of habitat data exists for Fort Richardson and Elmendorf (e.g., Carlson, 2008; Davis and Gibson, 2006; Jorgensen et al, 2003). Welch (2012) took the 54 habitat types identified on JBER by Jorgensen et al (2003) and condensed them down to eight habitat classes. Moose home ranges will be determined from location data and will be overlaid on these eight habitat classes.

2. Animal Locations

Between March 2009 and March 2012, biologists from the Alaska Department of Fish and Game (ADF&G) deployed radio collars with GPS and VHF capabilities on 27 adult female moose within and in close proximity to the JBER reservation. In some instances, moose were collared on adjacent lands in order to better characterize seasonal distribution and movement patterns, in cases where there was a high likelihood these moose also use the JBER reservation. Thirty two radio collars were used during the project. Eighteen of these radio collars collected GPS locations once every 30 minutes, with the other twelve collecting locations once every hour. Radio collars were marked with highly visible numbers to permit visual identification of individual animals from a distance. All captures were conducted according to State of Alaska approved institutional animal care and use policies.

During the study collared animals were located periodically by ground and/or aerial relocation, using VHF receivers, in order to assess health, functionality of the radio collar, and presence/absence of calves. An effort was made to recapture all collared moose each October/November, and again each March, in order to download GPS locations from each collar. However, as captures were conducted from the ground, some moose could not be recaptured during all capture periods. All but six collars were removed at the end of the study, and efforts continue to retrieve those six.

Animal locations were collected and variables describing movement characteristics will be calculated, including: density, speed, bearing, and sinuosity.

3. Animal Activity

General daily activity budgets for moose will be estimated using data collected from tri-axial accelerometers in each GPS collar. These accelerometers detect changes in acceleration in any of three planes of motion, giving an estimate of an animal's activity level. Data are recorded as active seconds per minute.

Data Analysis: Utilization of the Landscape

Moose movement rates and home range size can vary widely between seasons (Hundertmark, 1997). Additionally, landscape features of the fragmented urban environment found on JBER and in Anchorage can affect animal movement. For example, Dussault, et. al. (2007) found that moose movement rates during movement steps crossing a highway were an average of three times faster than steps preceding or following a crossing step. Accordingly, I will examine differences in movement among individuals, seasons, and the effect of manmade landscape features.

Moose movement paths will be estimated as straight lines between successive GPS locations at < 6 hour intervals. Home range and movement estimators employed may include the Brownian Bridge Movement Model (BBMM) (Horne, et al., 2007), Potential Path Area (PPA) (Long and Nelson, 2012), Minimum Convex Polygon (MCP) (Mohr, 1947), and/or Kernel Density Estimator (KDE) (Silverman, 1986). This will allow me to identify high use areas, and evaluate home range, the existence of movement corridors, and the effect of impediments to travel on movement patterns.

Moose movements will be compared to random distribution of points in an approach similar to Graves et al. (2006). If appropriate I will also compare the distribution of moose locations to simulated random walk procedures as in Bartumeus et al. (2005).

Objective 1. Where are areas of high and low use located on JBER? Are there specific corridors on JBER that moose utilize to move between high use areas?

Movement characteristics (density of locations, speed, and angular deviation between locations derived from GPS data, as in Bruggeman et al. 2007 and Graves et al. 2007) will be used to classify sections of moose home ranges and to investigate area and seasonal patterns.

Density of locations will be calculated as x locations/x m cell/time period. Movement speed across the landscape will be calculated from GPS locations. Angular deviation will be calculated by determining the length and bearing of each path.

I would like to test for the presence of moose movement corridors, as that is a paramount objective for this study from the funding agency (Department of Defense). However the terms “movement corridor” or “travel corridor” have been defined differently by various authors. Forman (1995) stated that corridors have vegetation that provides better food or cover than the surrounding habitat matrix, are composed of patches that are longer than wide, and are often aligned to a habitat feature such as a river that may form a natural travel route. Graves et al (2007) delineated movement corridors used by brown bears on the Kenai Peninsula using movement characteristics alone. They defined “highly functional corridors” as places where animals exhibit large amounts of rapid and highly directional movement and “minimally functional corridors” as areas where animals exhibit long, rapid, and infrequent movements. Defining corridors using movement characteristics eliminates the assumption that all habitat factors to which animals respond can be correctly identified.

Landscape Use Classifications

Similar to Graves et al. (2007), I will classify sections of moose home ranges into categories based on movement characteristics: density, speed, and turning angle (or sinuosity). The terms “high” and “low” with respect to each of these movement characteristics will be established by mining movement data and establishing threshold criteria for each characteristic.

1. High use areas contain enough resources to meet many or all of an animal’s needs. I expect movement patterns of moose in high use areas to be dense (because animals spend a lot of time there), slow (because animals often stop to eat and rest in these areas) and sinuous (because animals are searching for food). Areas where moose exhibit a high density of GPS locations, slow movement, and high amounts of sinuous movement will be classified as high use areas.

2. Low use areas contain enough resources to support some use by moose, but considerably less than high use areas. Areas with slow movements and high amounts of sinuous movement, but few GPS locations, will be classified as low use areas.

3. Non-use areas are within a moose’s home range, but have few resources to attract moose. Areas that occur within moose home ranges, but have very few locations or no locations will be classified as non-use areas.

4. Corridors. I will define corridors to be areas which moose utilize to move between high use areas, as described above. In most cases, corridors will be longer than wide, indicating that the areas on either side will be low use or non-use areas, or that moose movements are constrained by impediments to travel. Note that in some instances, the corridor itself may be a high use area, in which case it should display the same characteristics as other high use areas (high density of locations, slow speed, and high amounts of sinuous movement), but will be significantly longer than wide, and may be the only patch of habitat by which moose are able to access another high use area. Other corridors may not have the resources to function as high use areas, but may be used primarily for travel, rather than feeding or resting. I expect moose moving through these areas to exhibit high amounts of very directional, rapid movement. These areas will be classified as “travel corridors”. Travel corridors with dense locations (moose use them frequently) will be classified as primary travel corridors, and those with fewer locations (moose rarely use them) will be classified as secondary travel corridors.

5. Non-sampled. In order to distinguish non-use areas from areas where no research animals are present, I will classify areas outside all collared moose home ranges as non-sampled.

Landscape Use Classification	**Density**	**Speed**	**Turning Angle**
High Use Area	High	Low	High

Low Use Area	Low	Low	High
Primary Travel Corridor	High	High	Low
Secondary Travel Corridor	Low	High	Low
Non-Use Area (within home ranges)	--	--	--
Non-Sampled (outside home ranges)	--	--	--

Figure 1. Movement characteristics used to identify Landscape Use Classifications.

Objective 2. Can data from tri-axial accelerometers imbedded in GPS collars be used to differentiate specific behaviors (browsing, grazing, walking, standing, lying), behavior categories (feeding, travelling, resting), or simply active vs. inactive behaviors in moose?

Accelerometer data will be correlated with animal behaviors as in Naylor and Kie (2004). The authors predicted elk activity budgets for various activities by constructing a model incorporating activity sensor data. I collared three captive moose held by the Alaska Dept of Fish and Game and recorded focal animal observations of specific behaviors for each collared moose. Data from the observations are being correlated with the activity data from each animal's collar, allowing me to calibrate activity readings to observed behaviors. I developed five datasets in order to test whether readings from this type of accelerometer can be used to differentiate specific behaviors (browsing, grazing, walking, standing, lying), behavior categories (feeding, travelling, resting), or simply active vs. inactive behaviors.

I am still evaluating whether all the moose activities listed above can be reliably deduced from the simplistic activity data. Out of the five datasets, the highest accuracy was achieved through applying threshold criteria to the Active/Inactive dataset. Using a threshold of 0 active seconds per minute (0=Inactive, >0=Active), while there was some individual variation among research subjects, the accelerometers were found to correctly classify Active behavior 92.29% of the time, and Inactive behavior 90.64% of the time.

Objective 3. Are certain areas on JBER associated with specific behaviors, or are areas used for feeding, resting, and traveling in similar proportions (i.e., are moose traveling back and forth between bedding and feeding areas connected by travel corridors, or do they tend to bed and feed in the same area?)?

Accomplishing this objective will involve combining movement and activity data. Simply put, I will quantify the amount of time spent engaged in different behaviors in each high use area. Comparison of location data with activity information will enable me to determine the dominant behavior exhibited in each segment of a moose's home range, and ascertain whether high use areas are primarily used for active (feeding and/or traveling) or inactive (bedding) behaviors.

In order to account for very short behaviors which may throw off interpretations of accelerometer readings (e.g., vigorous head shaking due to insect harassment, which would produce high readings in an otherwise inactive period), I will use an approach similar to Moen's Neighboring Minutes Method (Moen, 1996), in which activity readings during the minutes neighboring a focal minute are taken into account when classifying the focal minute as active or inactive. Inactive points will be assumed to represent a bedding event, and will be defined as locations with a mean activity value <1.0 active seconds per minute for the five minute interval around each point. Active points will be assumed to represent feeding and/or traveling behavior, and will be defined as locations with a mean activity value ≥1.0 active seconds per minute for the five minute interval around each point. The amount of time spent engaged in active and inactive behaviors in each landscape use classification will be quantified.

Tasks Already Completed

March 2009	Initial moose captures and collaring; seven collars deployed
October 2009	Twelve additional moose captures, five recaptures, data downloaded
January 2010	One moose recapture, data downloaded
March 2010	Eleven recaptures, data downloaded
October 2010	Accelerometer testing on three captive moose
November 2010	Eight recaptures, data downloaded
March 2011	Eight recaptures, data downloaded, six collars removed
October 2011	One recapture, collar removed
March 2012	Eight additional collars (with automatic drop-off mechanisms) deployed on moose north of Eagle River
October 2012	Recover dropped collars, download data

Ongoing Tasks

Work that was ongoing throughout the project included: manual (hand-held receiver) telemetry location of subjects and deployment of remote cameras in order to assess health/calving status; habitat assessment of movement patterns using existing US Army GIS data; calibration of radio collars for activity data using captive moose; and analysis of activity and movement data. In addition, six collars are still deployed, and efforts continue to recover them. Since these portions of the work have been ongoing throughout the project, they are not included in a set timeline.

Tasks Associated with each Objective

Data analysis will involve bringing together data on GPS locations; behavior (feeding, resting, travelling; or active/inactive, based on both accelerometer readings and movement characteristics); classification of movement patterns (through the measurement of density, speed, and angular deviation); and pre-existing data on vegetation class, including “disturbed areas” such as manmade obstacles to moose movements.

I will categorize landscape use classifications (high use areas, low use areas, non-use areas, and movement corridors) based on movement characteristics. (Objective 1).

I will quantify percentage of each vegetation class that is located within each landscape use classification. (Objective 1).

I will develop datasets from accelerometer trials on captive moose in order to test whether readings from this type of accelerometer can be used to differentiate specific behaviors (browsing, grazing, walking, standing, lying), behavior categories (feeding, travelling, resting), or simply active vs. inactive behaviors. (Objective 2).

I will determine how much time is spent engaged in each behavior (feeding, resting, travelling; or active/inactive) for each vegetation class and landscape use classification, and examine data for differences in seasonal use patterns. (Objective 3).

I will analyze movement patterns and prepare graphic representations in order to better visualize seasonal use of the landscape, and identify the existence of any movement corridors and impediments to moose movements on JBER lands. (All objectives).

Estimated Work Plan for Analysis

July 2013	Calculate density, speed, angular deviation and attempt to detect patterns
October 2013	Define landscape use classifications
November 2013	Finish movement analysis
December 2013	Finish writing Movement Analysis chapter
January 2014	Accelerometer chapter--add descriptive statistics, finish analysis
February 2014	Finish writing Accelerometer chapter
March 2014	Finish writing Introductory chapter
April 2014	Finish all writing
Summer 2014	Expected graduation date

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Appendix F: Black bear and wolf handling

ANIMAL	STATUS	Field Age	SPECIES	Sex	COMMENTS
1	DEAD (VEHICLE)	Adult	BLACK BEAR	M	Adult male, captured by barrel trap 5/23/09 on Elmendorf, struck and killed by truck near Eagle river on highway on 6/18/09
2	DROPPED	Adult	BLACK BEAR	F	Adult female captured Antennae fields 3 June 09 and near mad bull airstrip 7-8-09; collar replaced in den 2 April 2010; collar dropped as scheduled on 1 June 2011
3	NOT COLLARED	Sub adult	BLACK BEAR		Yearling captured Grady rd and Ship creek June 9 2009, tattooed but not collared, no ear tags
4	DROPPED	Adult	BLACK BEAR	F	Adult female with 2 Coy, captured Grady rd and family camp, collared 6/10/2009 12:30; collar replaced in den April 6 2010; collar dropped as scheduled on 1 June 2011
5	DEAD (NATURAL)	Sub adult	BLACK BEAR	M	small male, collared 19 june 2009; near Madbull airstrip, may have been hit by car near main gate died in woods likely hit on 7/21/2009
6	DEAD (DLP)	Adult	BLACK BEAR	M	small male, collared June 20, 2009 south Cole FR barrel trap, shot in/near Euklutna July 25, 2009
7	NOT COLLARED	Sub adult	BLACK BEAR		Sub adult female first captured June 25, 2009 at Ship creek by Grady rd and Family camp, given right orange ear tag 972, not tattooed or collared, recaptured 20 June 2012 breaking into campers, had 3 coy, she was euthanized
8	MIA	Adult	BLACK BEAR	F	Mad bull SE, Adult female orange left 08, orange right 977 collared 10-Jul-09 12:45; soon was MIA

Appendix F: Black bear and wolf handling, cont.

ANIMAL	STATUS	Field Age	SPECIES	Sex	COMMENTS
9	DROPPED	Sub adult	BLACK BEAR	F	Sub adult female at Mahon Trap FRA, small arms complex left orange 17,right orange 985 collared 20-Jul-09 18:38 collar dropped as scheduled on Oct 15, 2010,recovered
10	DROPPED	Sub adult	BLACK BEAR	F	adult (3-4) female, left yellow 296,right yellow 297 collared 23-Jul-09 13:38; collar recovered 500m S Arctic valley Rd, 500m E. Biathlon range, July 2011
11	DROPPED	Adult	BLACK BEAR	M	captured at Moose run golf course young (adult)male Aug 4 2009 148.62 15:35 appeared dropped/mort July 2010, recovered nr Birchwood airport on Peters ck, as a shed
12	DROPPED	Adult	BLACK BEAR	M	Barrel capture Mahon range 6-11-2010;146.6400 lone male, adult, collar shed behind small arms complex, recovered
13	DROPPED	Adult	BLACK BEAR	M	barrel capture (need location) on Elmendorf;June 11 2010 148.610 lone adult male,collar recovered approx 4 mi upstream hwy and Peters ck
14	DROPPED	Adult	BLACK BEAR	M	Adult male in Mahon range barrel trap June 17,2010; collar dropped as scheduled1 June 2011 upstream highway/Peters ck crossing, approx 2 miles, S side
15	DROPPED	Adult	BLACK BEAR	F	subadult (3-4yrs) barrel trapped 6/29/2011NE Cherry hill housing,Elmendorf. Collared with vhf and released; collar recovered in den; recaptured Government hill area June 27, 2013,collared with Lotek camera collar
16	DROPPED	Adult	BLACK BEAR	M	Collared June 1, 2012 near Oceanview Dr, on Jarvi street given Lotek camera collar, went MIA around July 5, collar retrieved from Fire Island, dropped as scheduled July 4,2012
17	DROPPED	Sub adult	BLACK BEAR	M	Captured barrel trap Anchorage 7/20/2012,subadult Male, Given Lotek camera Collar, recovered Hillside, dropped as scheduled on August 30 2012

Appendix F: Black bear and wolf handling, cont.

ANIMAL	STATUS	Field Age	SPECIES	Sex	COMMENTS
18	DROPPED	Adult	BLACK BEAR	F	Adult sow 3 COY, free range dart July 23 2012 Anchorage hillside, Lotek camera collar;fall 2012 denned wearing collar, den held 5 bears, on Seward hwy east Mchugh creek recaptured July 2013 upper hillside
20	NOT COLLARED	Yearling	BLACK BEAR	M	Captured Anchorage August 21, 2012, moved to Euklutna L ear 039 Green, R ear 965 Orange,
21	DROPPED	Adult	BLACK BEAR	M	Collared with LOTEK camera collar 8/3/2012 collar dropped on schedule (Sept 15, 2012) and recovered.
22	DROPPED	Sub adult	BLACK BEAR	F	captured prospect heights, O Malley, July 1,2013, collared with Lotek camera collar, dropped as scheduled (8/20/2013) and recovered.
23	Dead	Adult	BLACK BEAR	F	captured culvert trap near/on UAA campus Mallard lane relocated to Euklutna area killed ADFG 2014
24	NOT COLLARED	Sub adult	BLACK BEAR	M	captured July 12,2013 8531 ANC, AK barrel trap
25	NOT COLLARED	Adult	BLACK BEAR	F	culvert trap at JBER antennae field July 14, 2013
26	NOT COLLARED	Adult	BLACK BEAR	F	captured 8531 Leo Street, Anchorage AK, had 4 coy
27	NOT COLLARED	Adult	BLACK BEAR	M	captured Ship ck, Elmendorf, behind ammo dump Given pink ear streamers
28	NOT COLLARED	Adult	BLACK BEAR	M	captured behind JBER ammo dump on ship creek. Left ear pink streamer, right green ear tags green

Appendix F: Black bear and wolf handling, cont.

ANIMAL	STATUS	Field Age	SPECIES	Sex	COMMENTS
29	Dead	Adult	BLACK BEAR	F	bear trapped in garbage truck in Whittier, darted in Anchorage same day (Sept 13, 2013), released Arctic valley road shed collar within 24 hrs; killed by hunter
1000	DROPPED/MORT?	Adult	WOLF	F	Ft. Richardson Wolf, grey, captured nr Biathlon range, June 23, 2009 lactating female
1001	DROPPED	Subadult	WOLF	F	captured by leg hold Feb 3 2010,IBPC Ft. Richardson collar dropped as scheduled
1002	DEAD (VEHICLE)	Adult	WOLF	M	killed by car at weigh station on Glen hwy Sept 9, 2010 near Ft.Richardson gate
1003	DEAD (HUNTER)	Sub adult	WOLF	F	shot by K. Lingofelt on Ft. Richardson Jan. 14, 2011 while moose hunting
1004	DEAD (CONTROL)	Adult	WOLF	M	killed by mgmt. biologists Feb. 7, 2011 in JBER snare
1005	DEAD (CONTROL)	Adult	WOLF f	M	Shot by mgmt. biologists Feb 12, 2011
1006	DEAD (CONTROL)	Sub adult	WOLF	M	killed by mgmt. biologists Feb. 24, 2011 in JBER snare
1007	DEAD (CONTROL)	ADULT	WOLF	M	killed by mgmt. biologists Feb. 26, 2011 in JBER snare
1008	DEAD (CONTROL)	Sub Adult	WOLF	M	killed by mgmt. biologists Feb. 28, 2011 in JBER snare
1009	DEAD (CONTROL)	ADULT	WOLF	F	killed by mgmt. biologists March 7, 2011 in JBER snare

Appendix G Black bear locations and home ranges

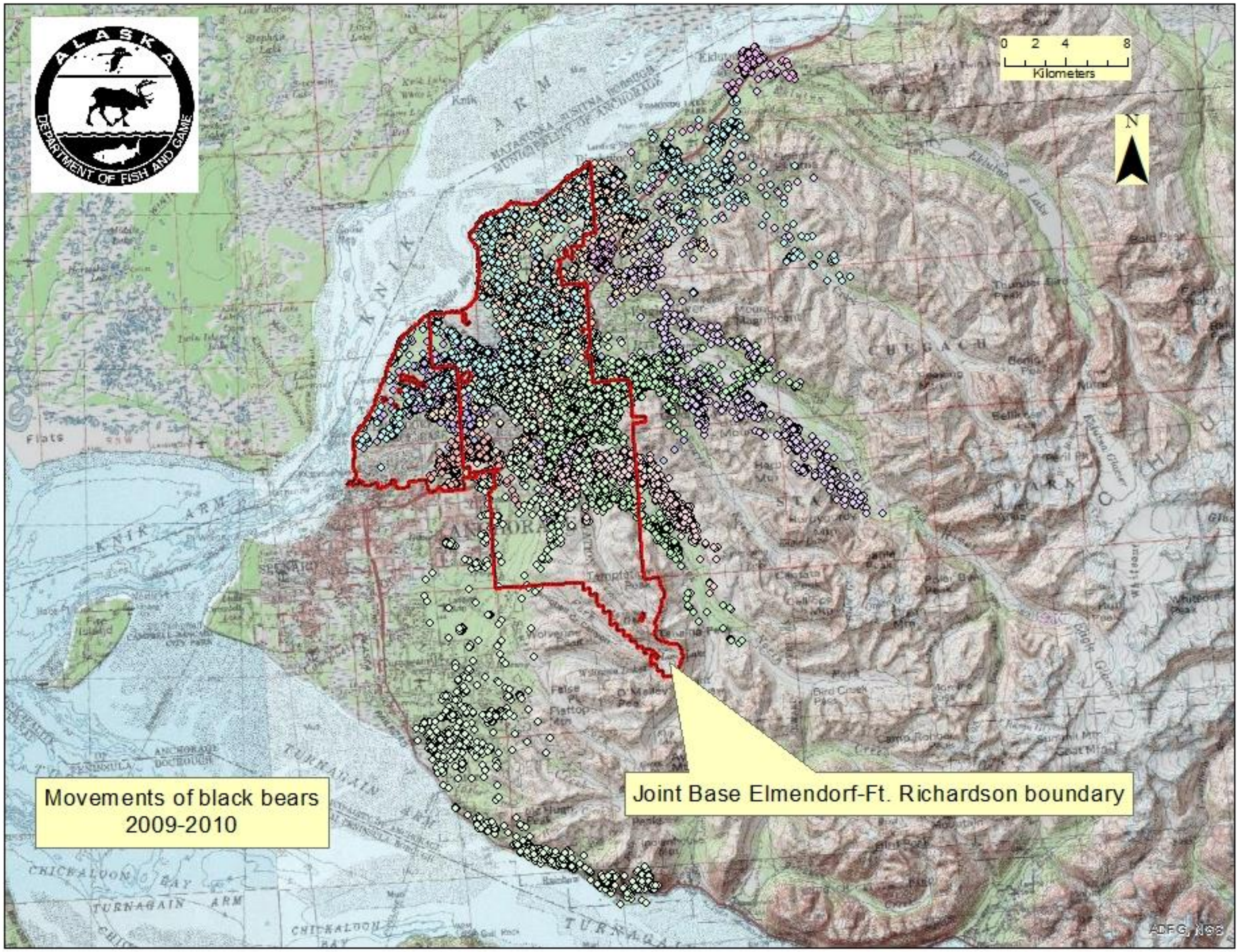


Figure 1. Locations of black bears collared for study. Resource Selection Function analyses are ongoing.

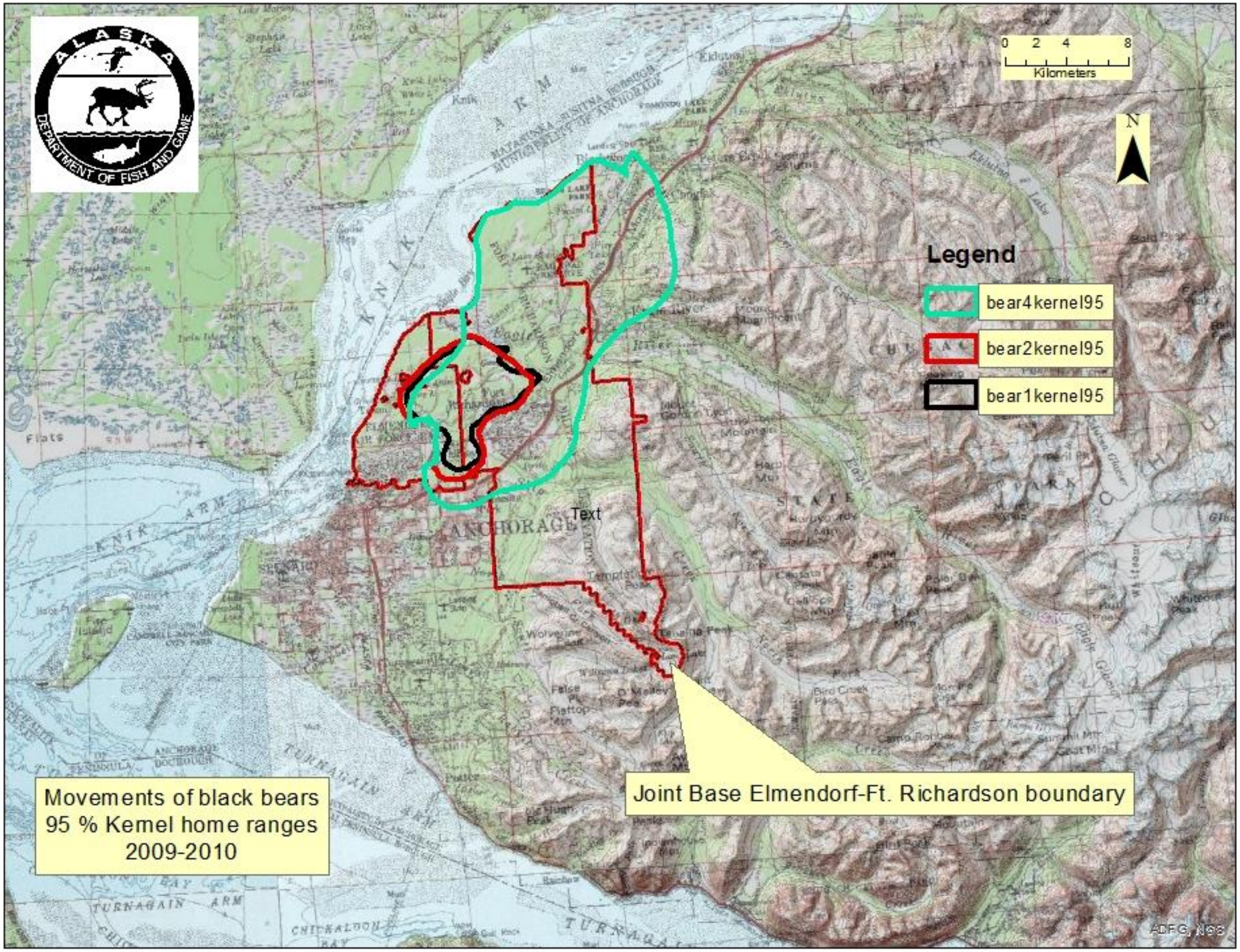
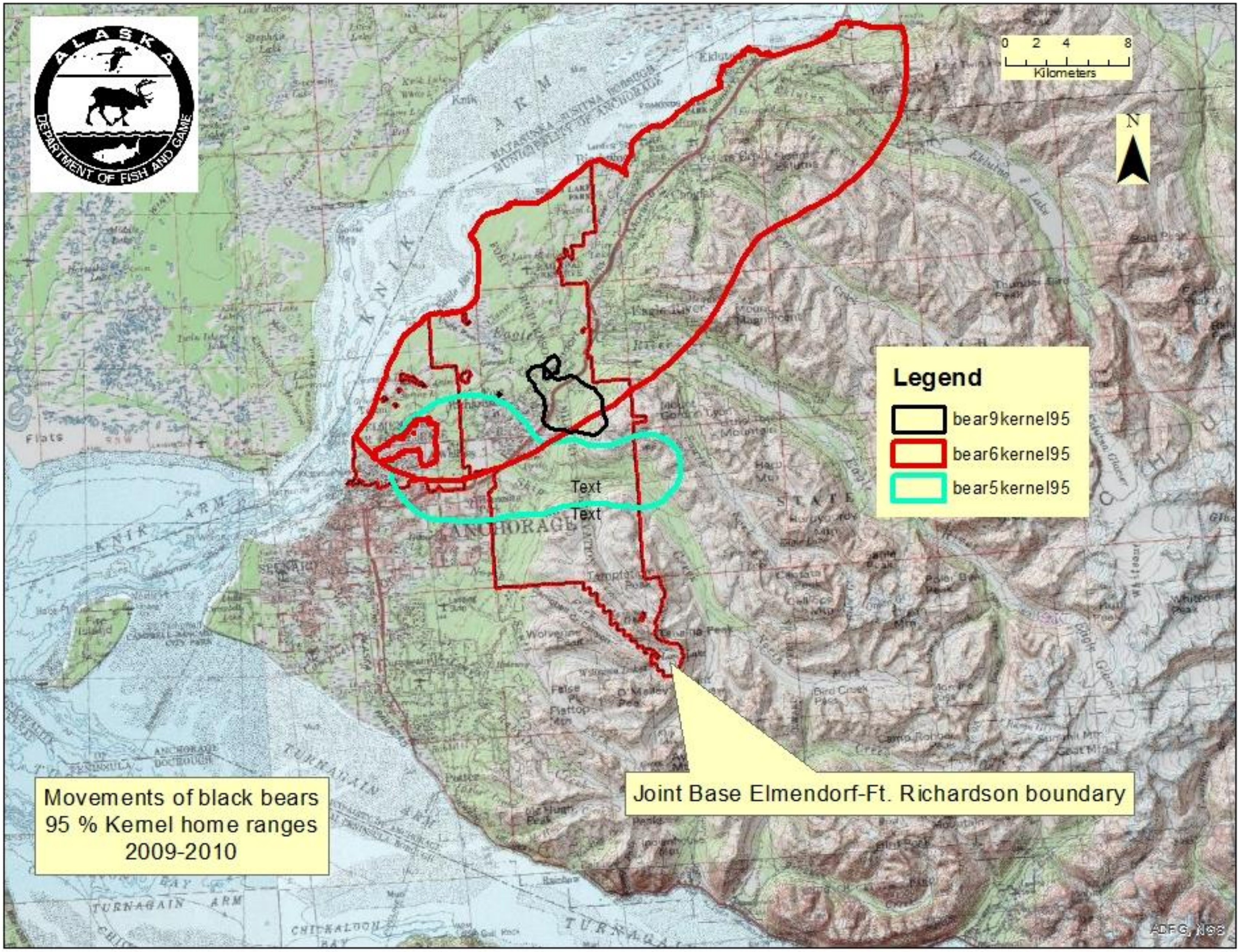
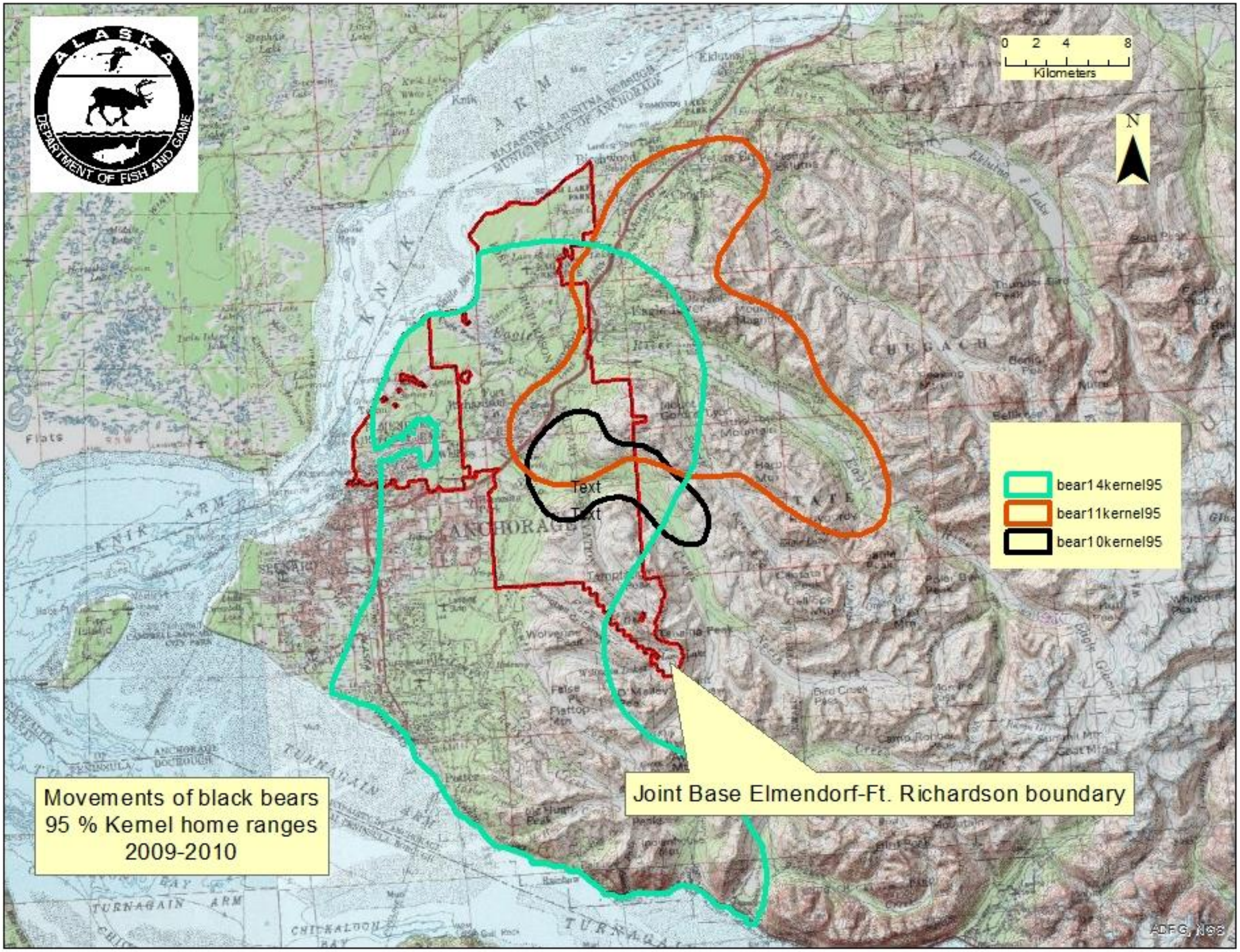


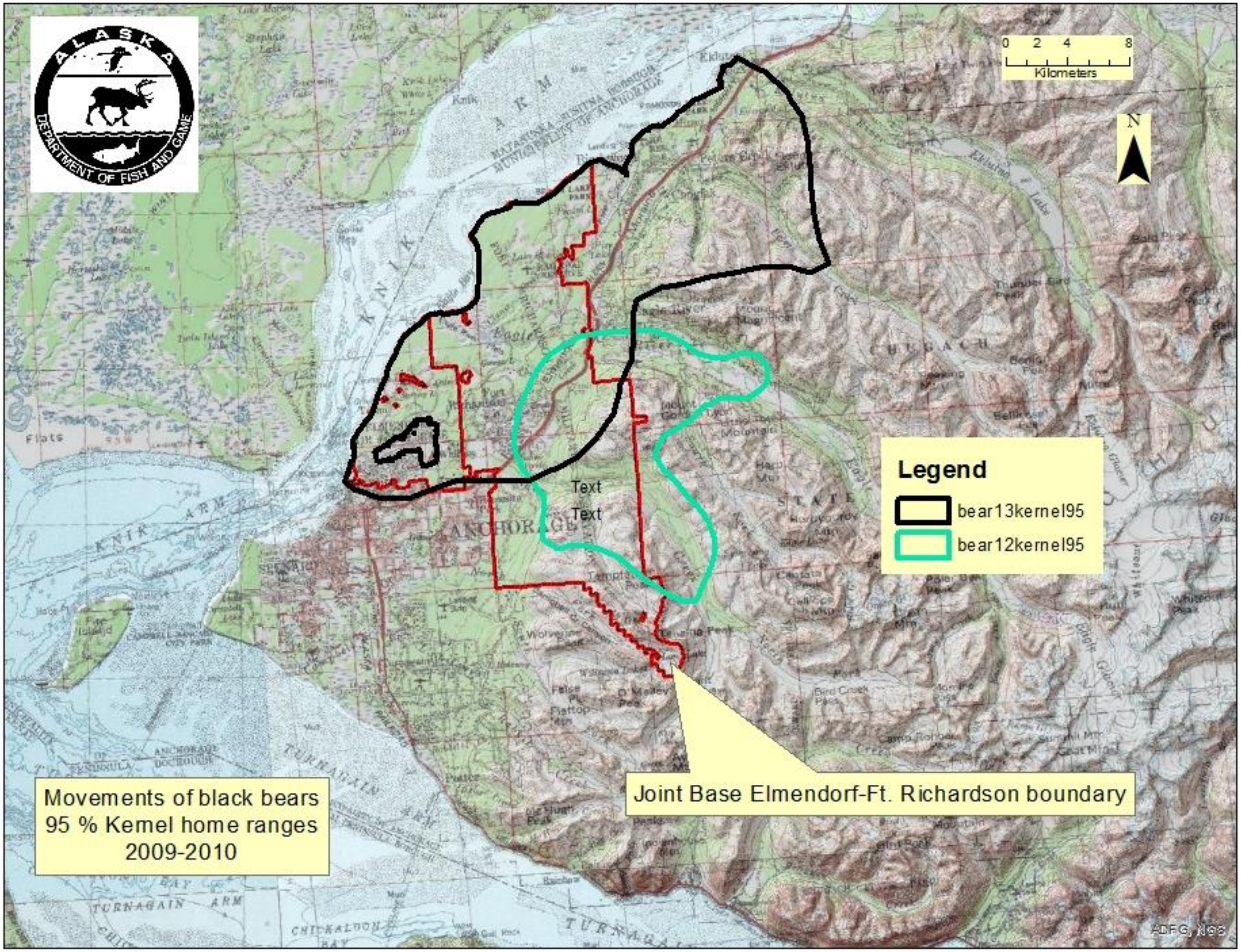
Figure 2. 95% kernel home ranges for black bears 1,2, and 4.


ALASKA
DEPARTMENT OF FISH AND GAME
0 2 4 8
Kilometers
N
Legend
bear9kernel95
bear6kernel95
bear5kernel95
Text
Text
Joint Base Elmendorf-Ft. Richardson boundary
Movements of black bears
95 % Kemel home ranges
2009-2010
ADFG, NGS



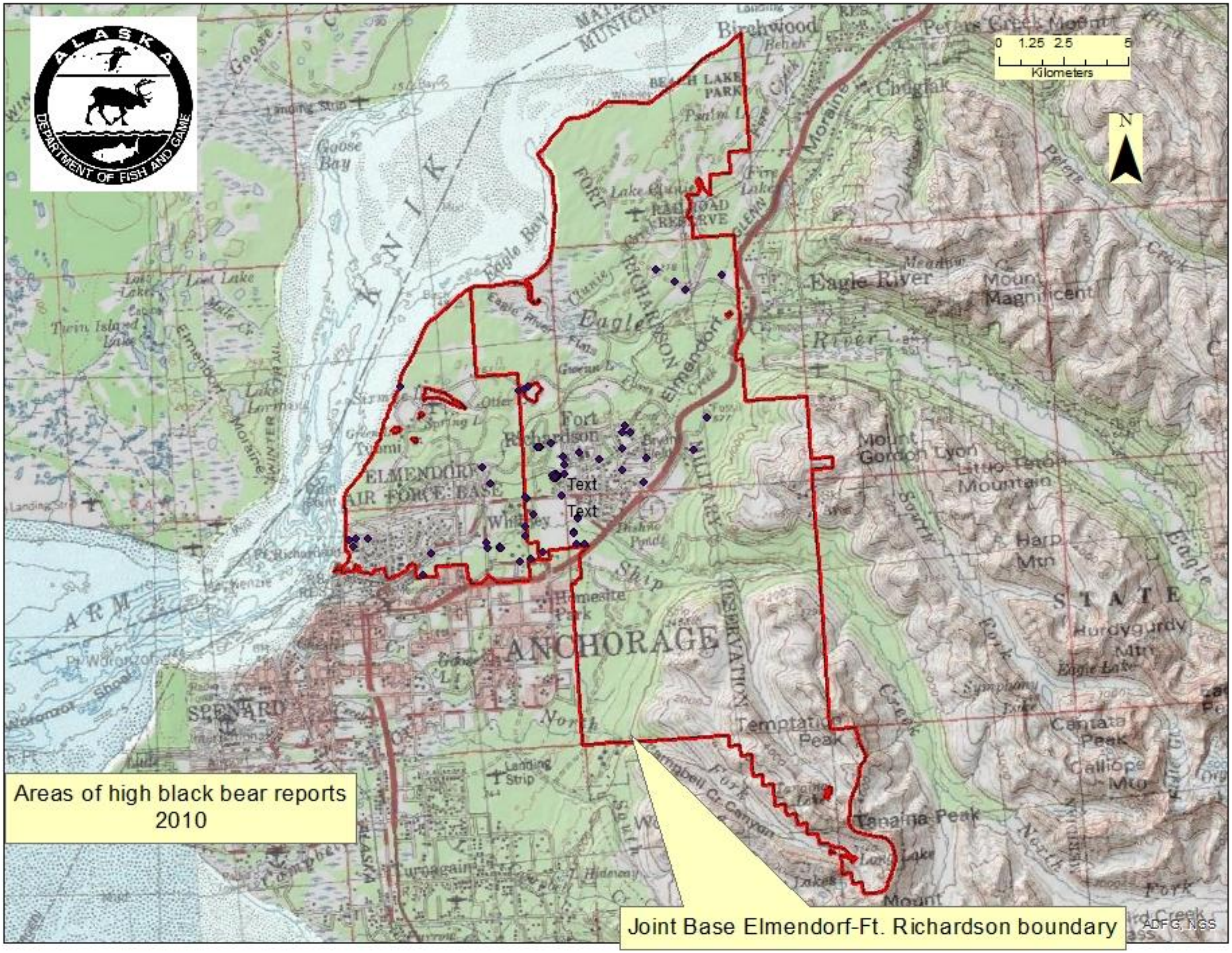
Movements of black bears
95 % Kernel home ranges
2009-2010

Joint Base Elmendorf-Ft. Richardson boundary



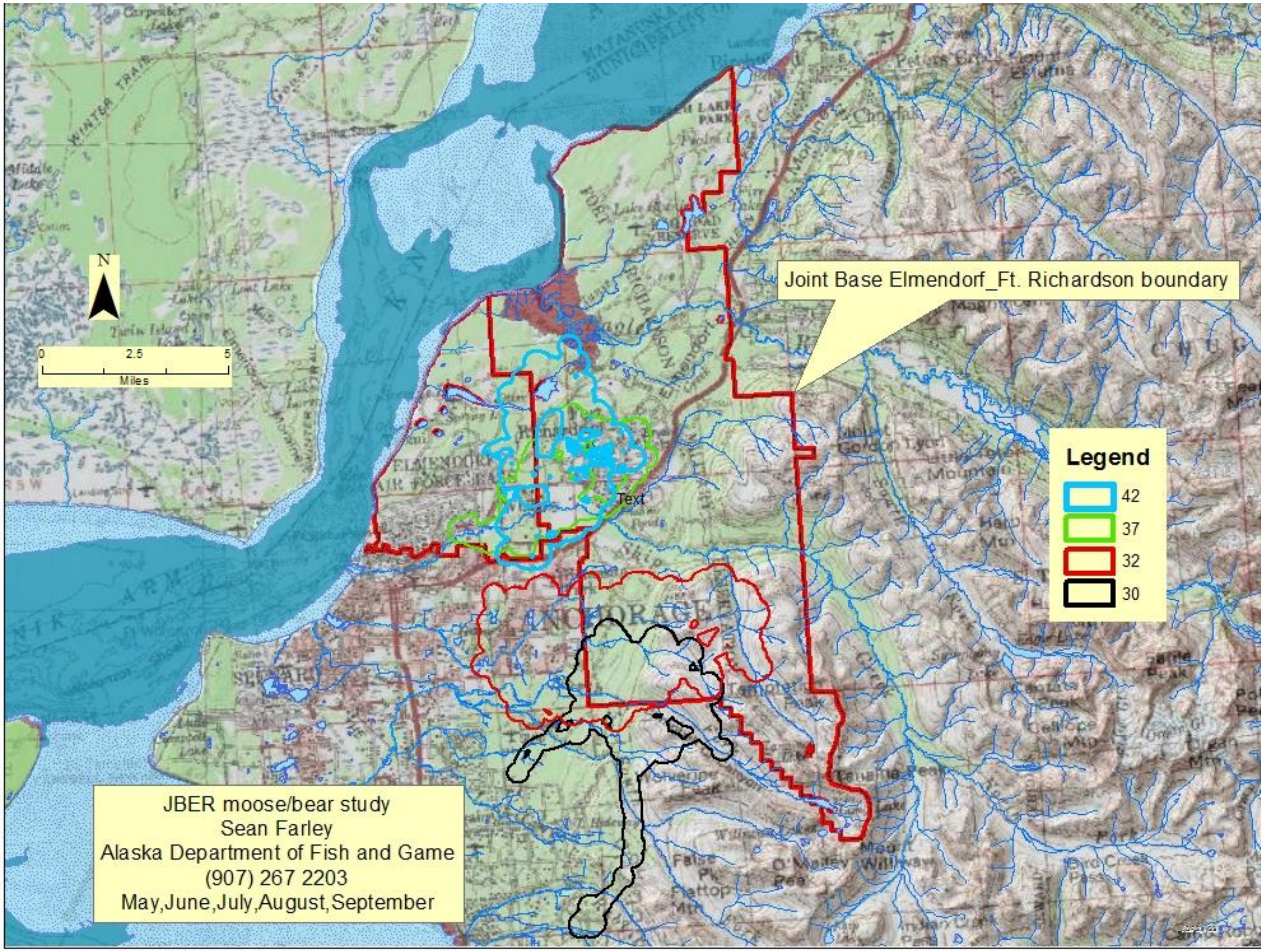
Movements of black bears
95 % Kemel home ranges
2009-2010

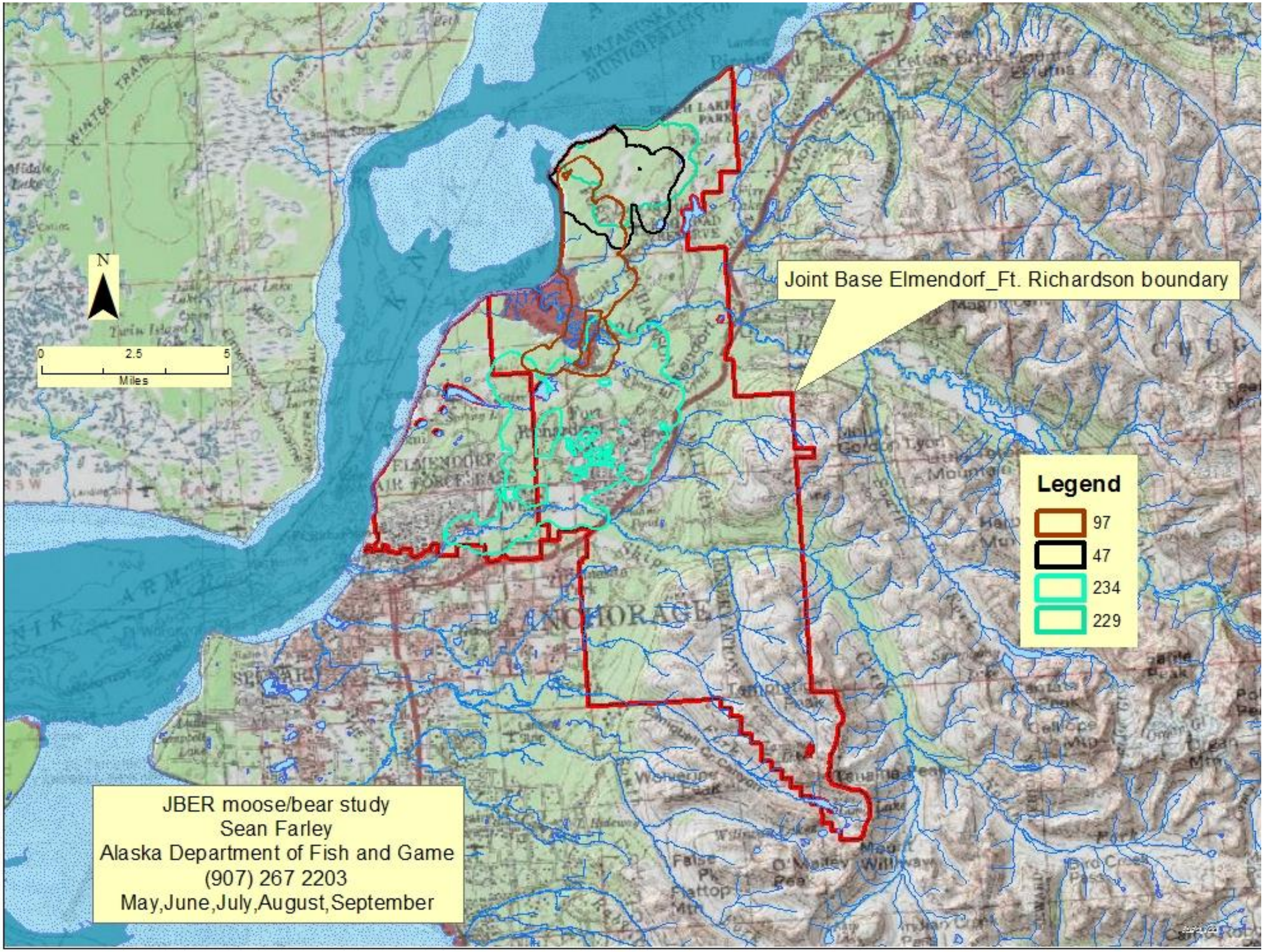
Joint Base Elmendorf-Ft. Richardson boundary

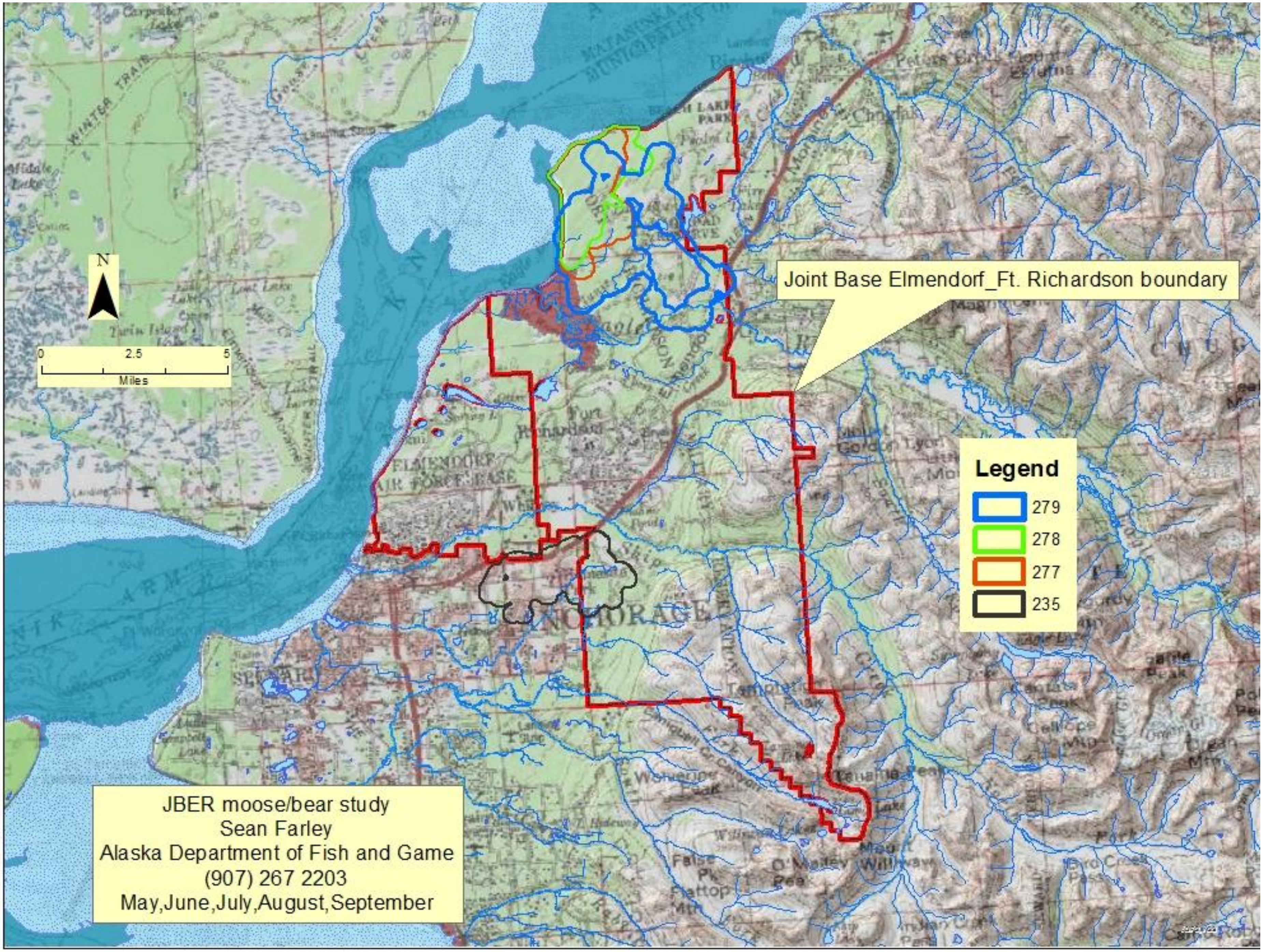


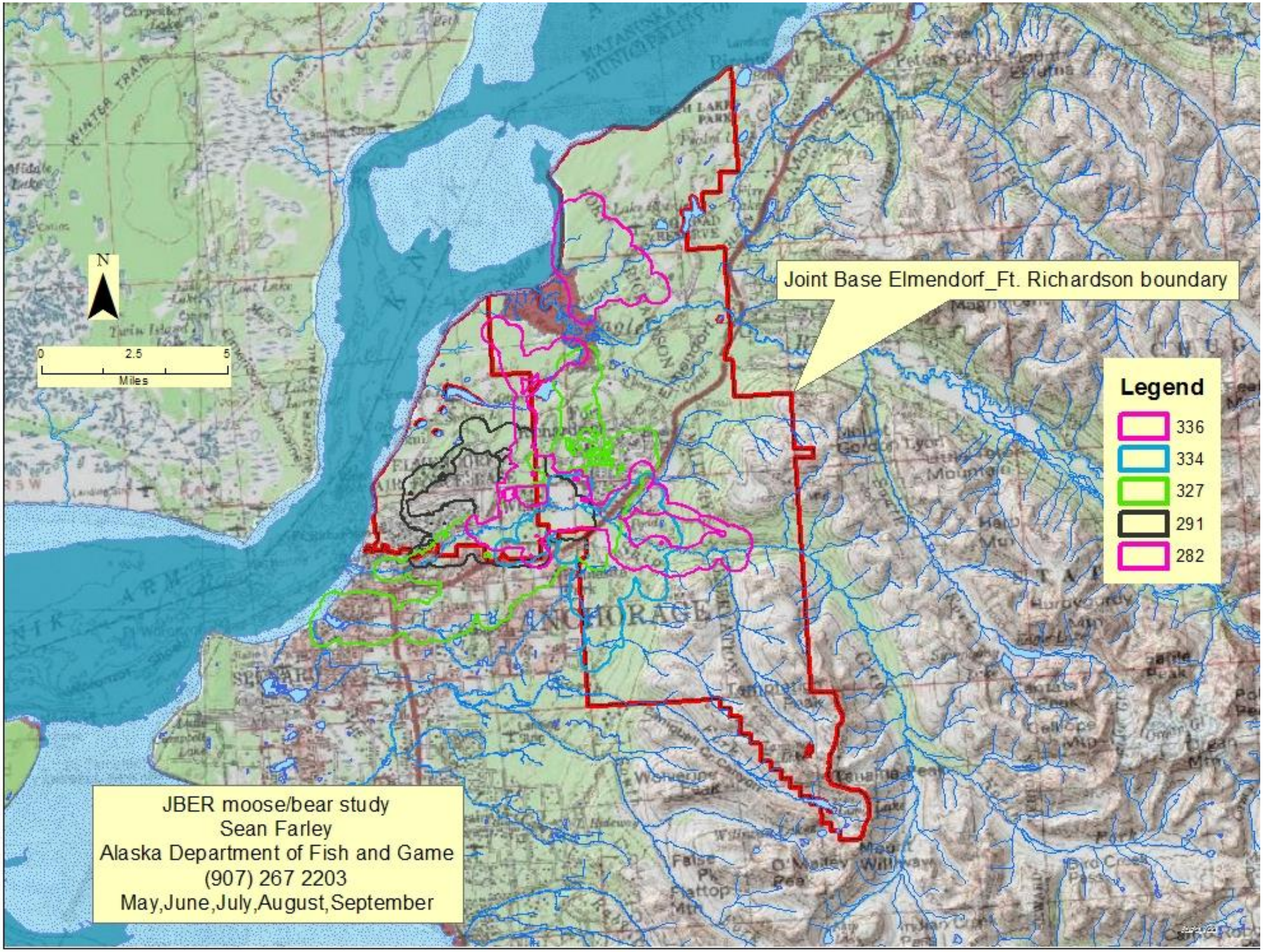
Areas of high black bear reports 2010

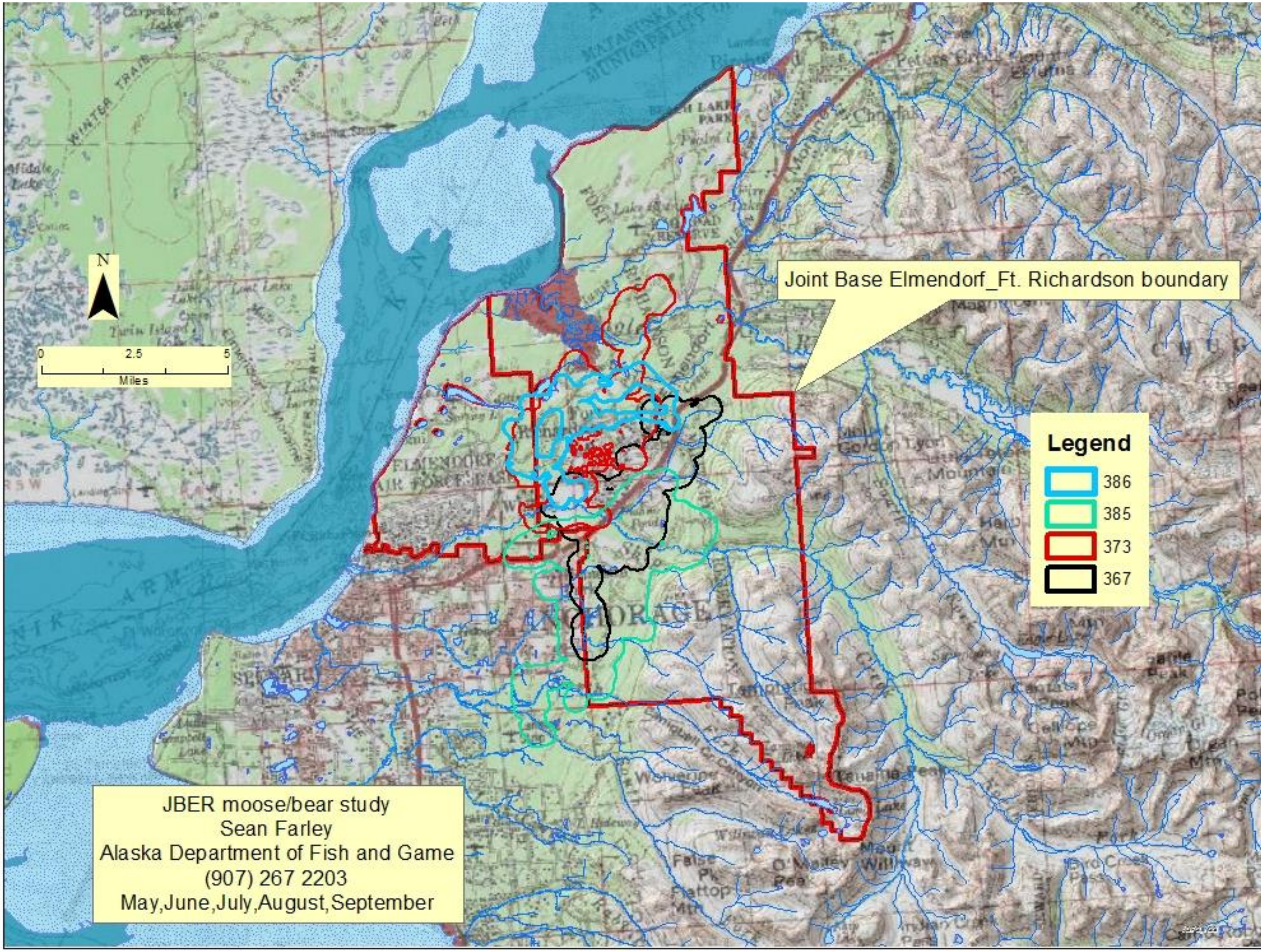
Appendix H Moose home ranges determined by potential path area




Joint Base Elmendorf_Ft. Richardson boundary
Legend
97
47
234
229
N
0
2.5
5
Miles
ANCHORAGE
ELMENDORF AIR FORCE BASE
JBER moose/bear study
Sean Farley
Alaska Department of Fish and Game
(907) 267 2203
May,June,July,August,September


Joint Base Elmendorf_Ft. Richardson boundary
Legend
279
278
277
235
N
0
2.5
5
Miles
JBER moose/bear study
Sean Farley
Alaska Department of Fish and Game
(907) 267 2203
May,June,July,August,September
ELMENDORF AIR FORCE BASE
ANCHORAGE


Joint Base Elmendorf_Ft. Richardson boundary
Legend
336
334
327
291
282
N
0
2.5
5
Miles
JBER moose/bear study
Sean Farley
Alaska Department of Fish and Game
(907) 267 2203
May,June,July,August,September
ANCHORAGE



Joint Base Elmendorf_Ft. Richardson boundary

JBER moose/bear study
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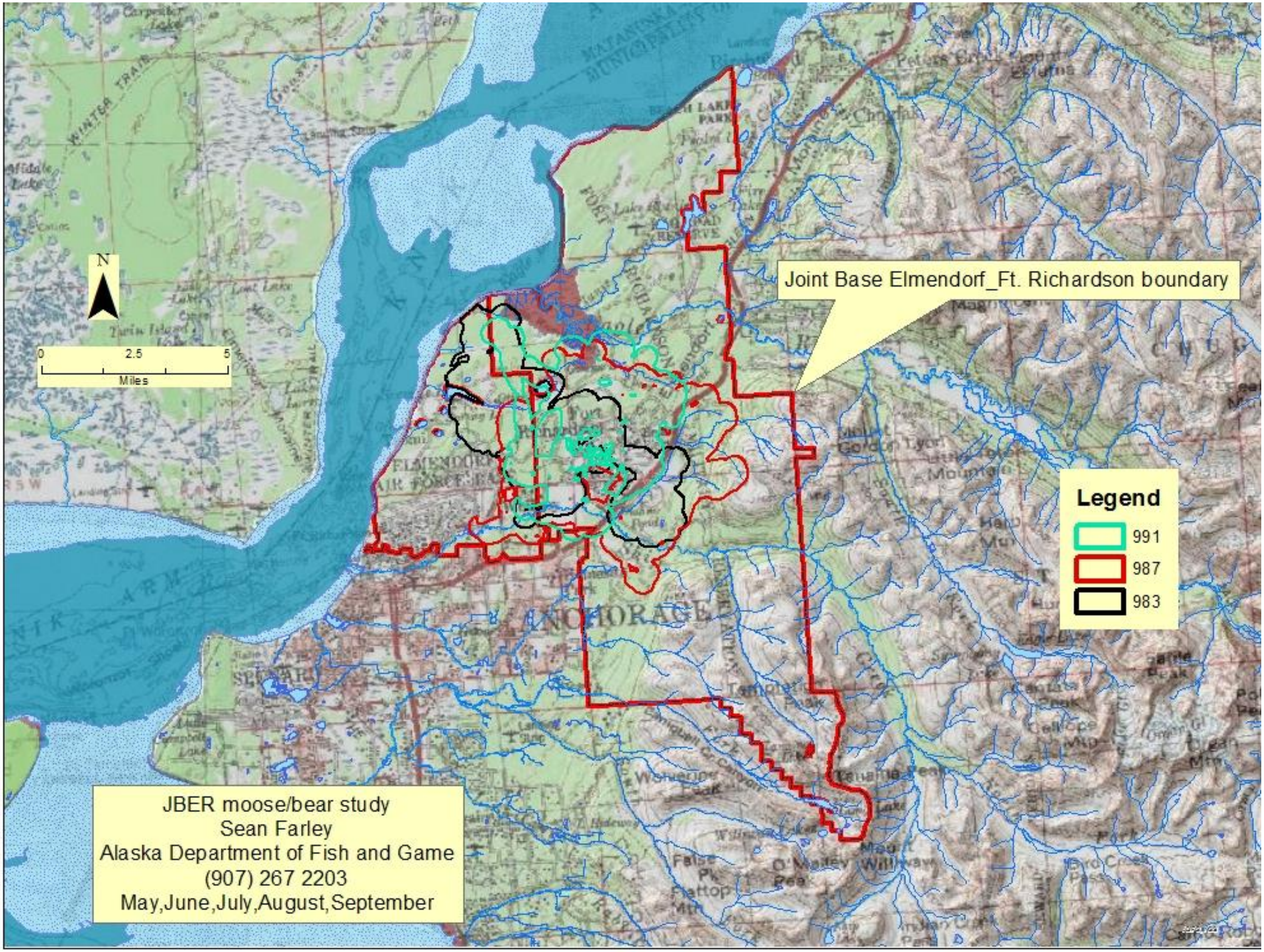
May,June,July,August,September


Joint Base Elmendorf_Ft. Richardson boundary
Legend
991
987
983
N
0
2.5
5
Miles
JBER moose/bear study
Sean Farley
Alaska Department of Fish and Game
(907) 267 2203
May,June,July,August,September