NUTRITIONAL ECOLOGY OF MOOSE IN AN URBAN LANDSCAPE

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A

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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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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.

1.7 Literature Cited

Andersen, R., J. D. C. Linnell, and R. Langvatn. 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. Biological Conservation 77:169-176.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative Wildlife Nutrition. Springer-Verlag, Heidelberg, Germany.

Child, K. N., S. P. Barry, and D. A. Aitken. 1991. Moose mortality on highways and railways in British Columbia. Alces 27:41-49.

Crête, M., and P. A. Jordan. 1982. Production and quality of forage available to moose in southwestern Quebec. Canadian Journal of Forest Research 12:151-159.

Dussault, C., Réhaume Courtois, J.-P. Ouellet, and I. Girard. 2005. Space use of moose in relation to food availability. Canadian Journal of Zoology 83:1431-1437.

Dussault, C., J. P. Quellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. Journal of Wildlife Management 71:2338-2345.

Etzenhouser, M. J., M. K. Owens, D. E. Spalinger, and S. B. Murden. 1998. Foraging behavior of browsing ruminants in a heterogeneous landscape. Landscape Ecology 13:55-64.

Garrett, L. C., and G. A. Conway. 1999. Characteristics of moose-vehicle collisions in Anchorage, Alaska, 1991–1995. Journal of Safety Research 30:219-223.

Gibson, C., and K. Jung. 2005. Historical census statistics on population totals by race, 1790 to 1990, and by Hispanic origin, 1970 to 1990, for large cities and other urban places in the United States. U.S. Census Bureau Population Division Working Paper No. 76, Washington D.C., USA. .

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.

Neumann, W., G. Ericsson, and H. Dettki. 2009. Does off-trail backcountry skiing disturb moose? European Journal of Wildlife Research 56:513-518.

Northern Economics Inc. 2006. The Value of Alaska Moose. Anchorage, Alaska.

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

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management 48:474-488.

Rea, R. V., K. N. Child, D. P. Spata, and D. Macdonald. 2010. Road and rail side vegetation management implications of habitat use by moose relative to brush cutting season. Environmental Management 46:101-9.

Regelin, W. L., C. C. Schwartz, and A. W. Franzmann. 1985. Seasonal energy metabolism of adult moose. Journal of Wildlife Management 49:388-393.

Renecker, L. A., and R. J. Hudson. 1985. Estimation of dry matter intake of free-ranging moose. Journal of Wildlife Management 49:785-792.

Renecker, L. A., and R. J. Hudson. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Canadian Journal of Zoology 64:322-327.

Renecker, L. A., and R. J. Hudson. 1988. Seasonal quality of forages used by moose in the aspen-dominated boreal forest, central Alberta. Holarctic Ecology 11:111-118.

Risenhoover, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis. Michigan Tech University., Houghton.

Saether, B.-E., and R. Andersen. 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68:993-999.

Schwartz, C. C., M. E. Hubbert, and A. W. Franzmann. 1988. Changes in body composition of moose during winter. Alces 24:178-187.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1987. Seasonal weight dynamics of moose. Swedish Wildlife Research, Suppl 1:301-310.

Shipley, L. A. 2010. Fifty years of food and foraging in moose: lessons in ecology from a model herbivore. Alces 43:1-13.

Sinnott, R. 2008. Unit 14C moose management report. Pages 189–1206 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2005–30 June 2007 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska.

Støen, O.-G., W. Neumann, G. Ericsson, J. E. Swenson, H. Dettki, J. Kindberg, and C. Nellemann. 2010. Behavioural response of moose *Alces alces* and brown bears *Ursus arctos* to direct helicopter approach by researchers. Wildlife Biology 16:292-300.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345-1354.

U.S. Census Bureau. 2010. 2010 Census Data. <http://2010.census.gov/2010census/data>. Accessed 12 Jan 2012.

U.S. Department of Defense. 2012. Joint Base Elmendorf-Richardson Overview. <http://www.militaryinstallations.dod.mil>Accessed March 13, 2012.

Vivas, H. J., and B.-E. Saether. 1987. Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: An experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology 56:509-520.

Wallmo, O. C., L. H. Carpenter, W. L. Regelin, R. B. Gill, and D. L. Baker. 1977. Evaluation of deer habitat on a nutritional basis. Journal of Range Management 30:122-127.

Weixelman, D. A., R. T. Bowyer, and V. Van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. Alces 34:213-238.

Young, D. D. 2008. Unit 20B moose. Pages 348–372 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2005–30 June 2007 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska

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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[1] Welch, J.H., P.S. Barboza, S.D. Farley and D. E. Spalinger. Nutritional value of habitat for an urban ungulate: moose (*Alces alces*) in Anchorage Alaska. Prepared for Journal of Wildlife Management

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 lupus*) 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 +14°C 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 -20° 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

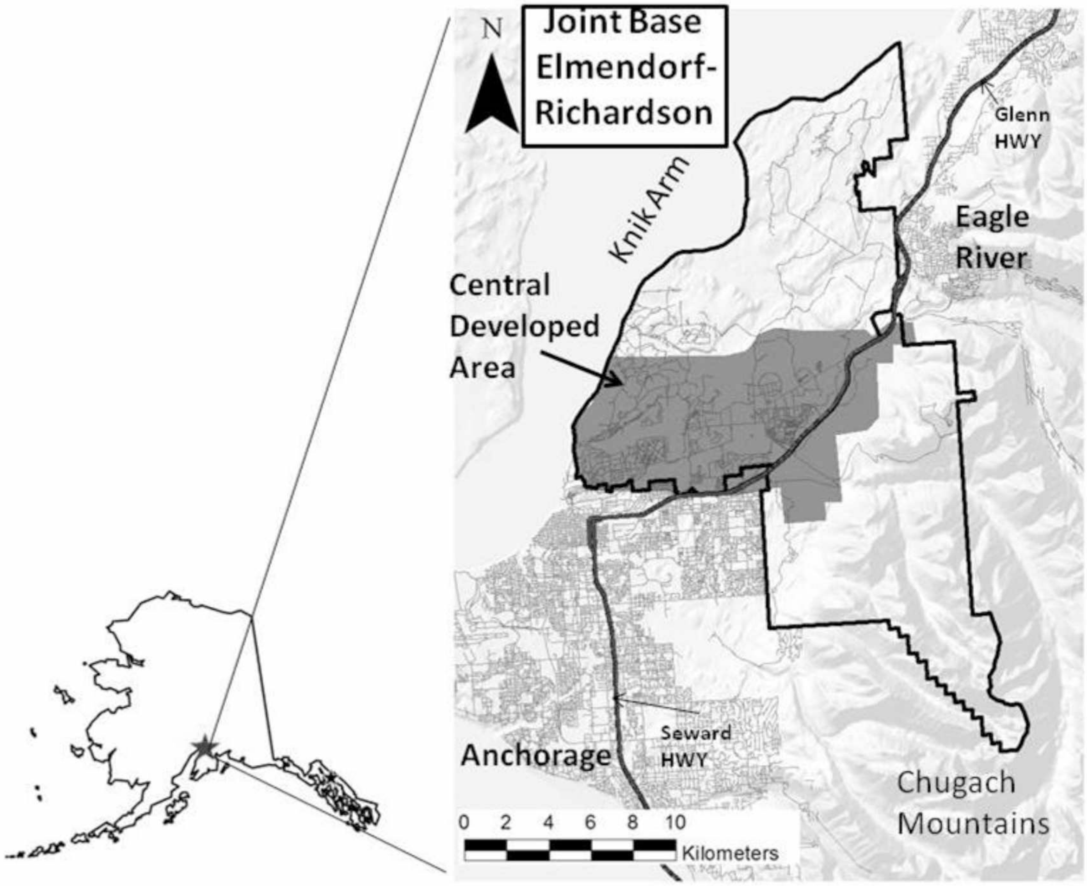

Figure 2.1. Study area for female moose on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

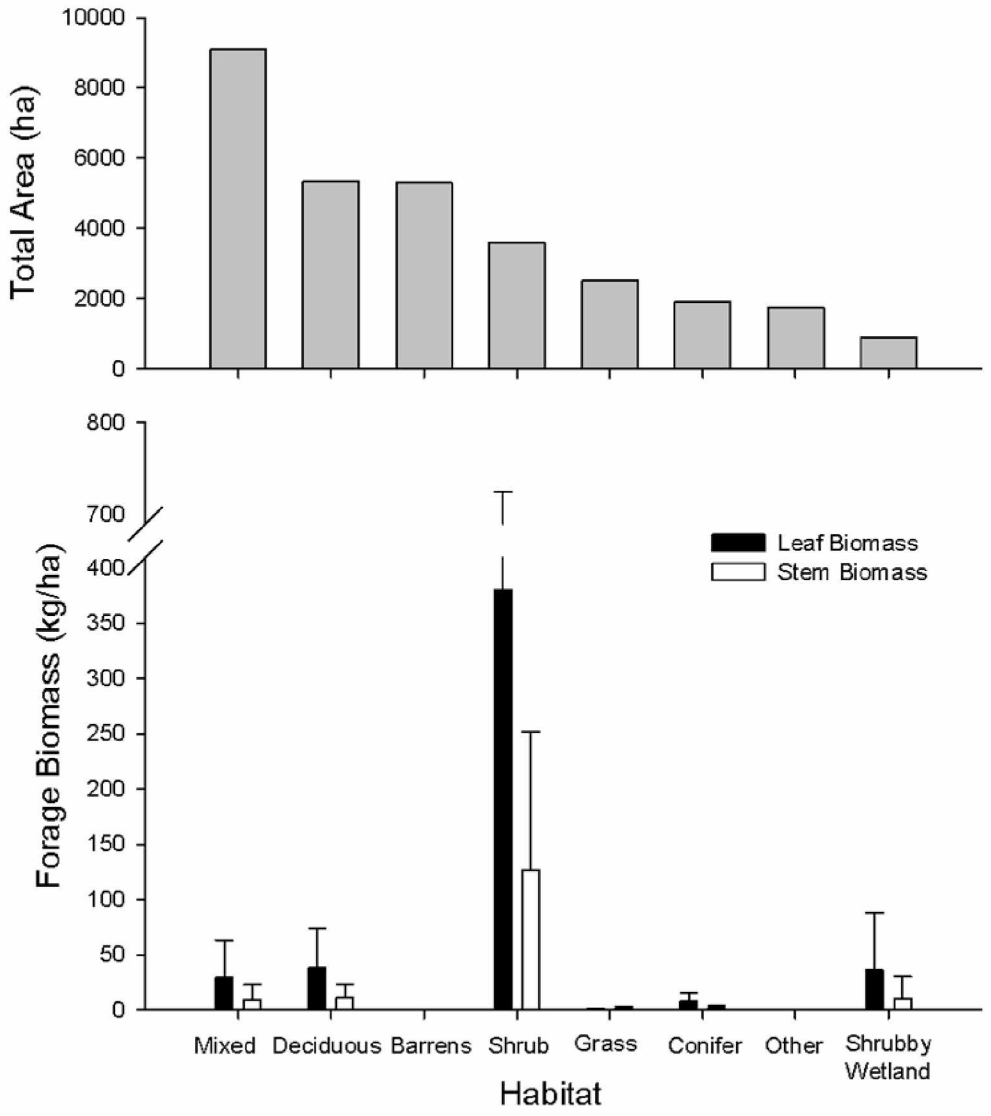

Figure 2.2. Metrics of habitat classes for moose on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA. Barrens include upland tundra as well as areas cleared for operations such as gravel pits and parking lots. "Other" areas include water bodies and fenced areas that exclude moose. A. Total 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).

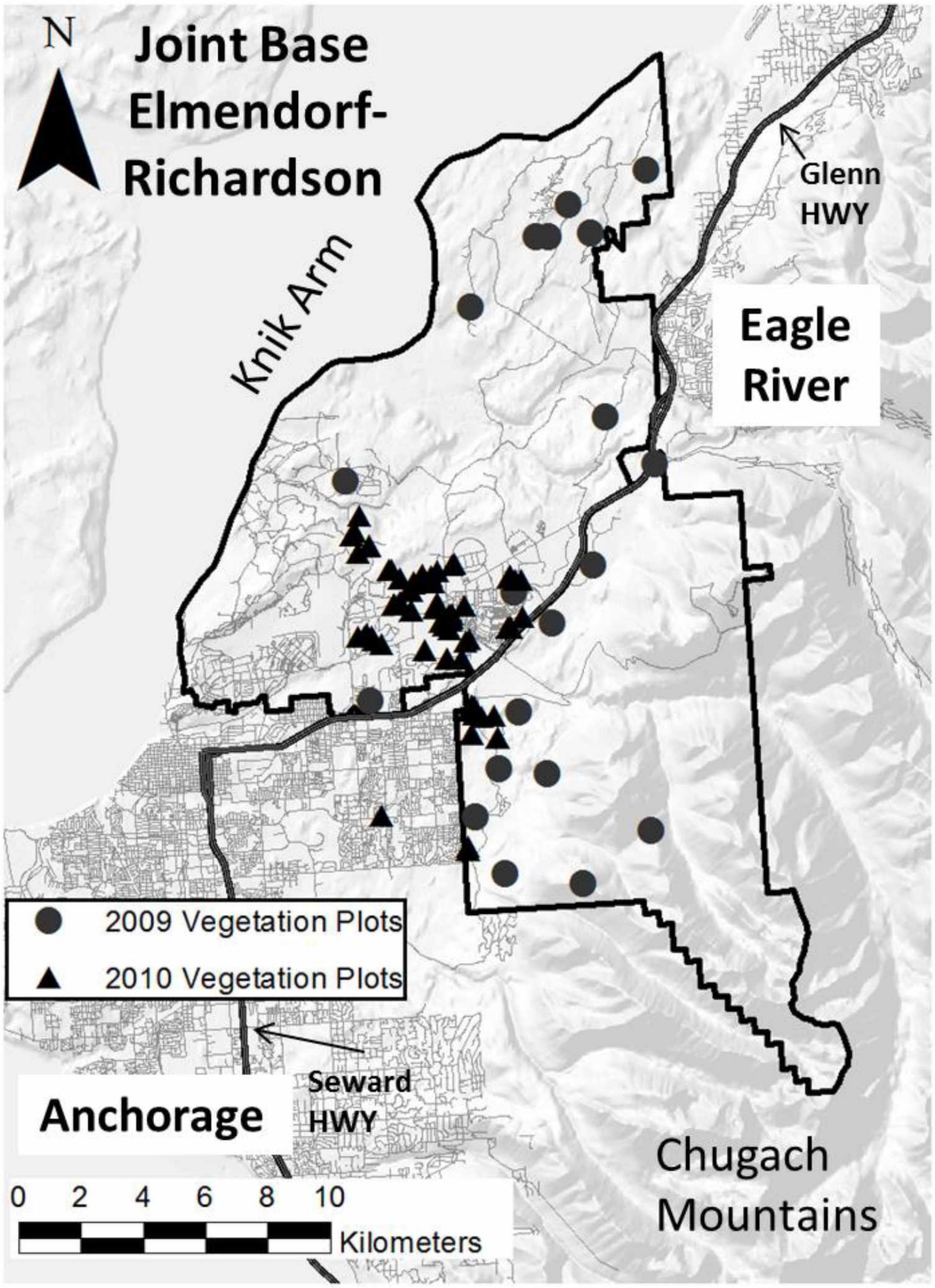

Figure 2.3. Vegetation plots for forage collections in 2009 and 2010 on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

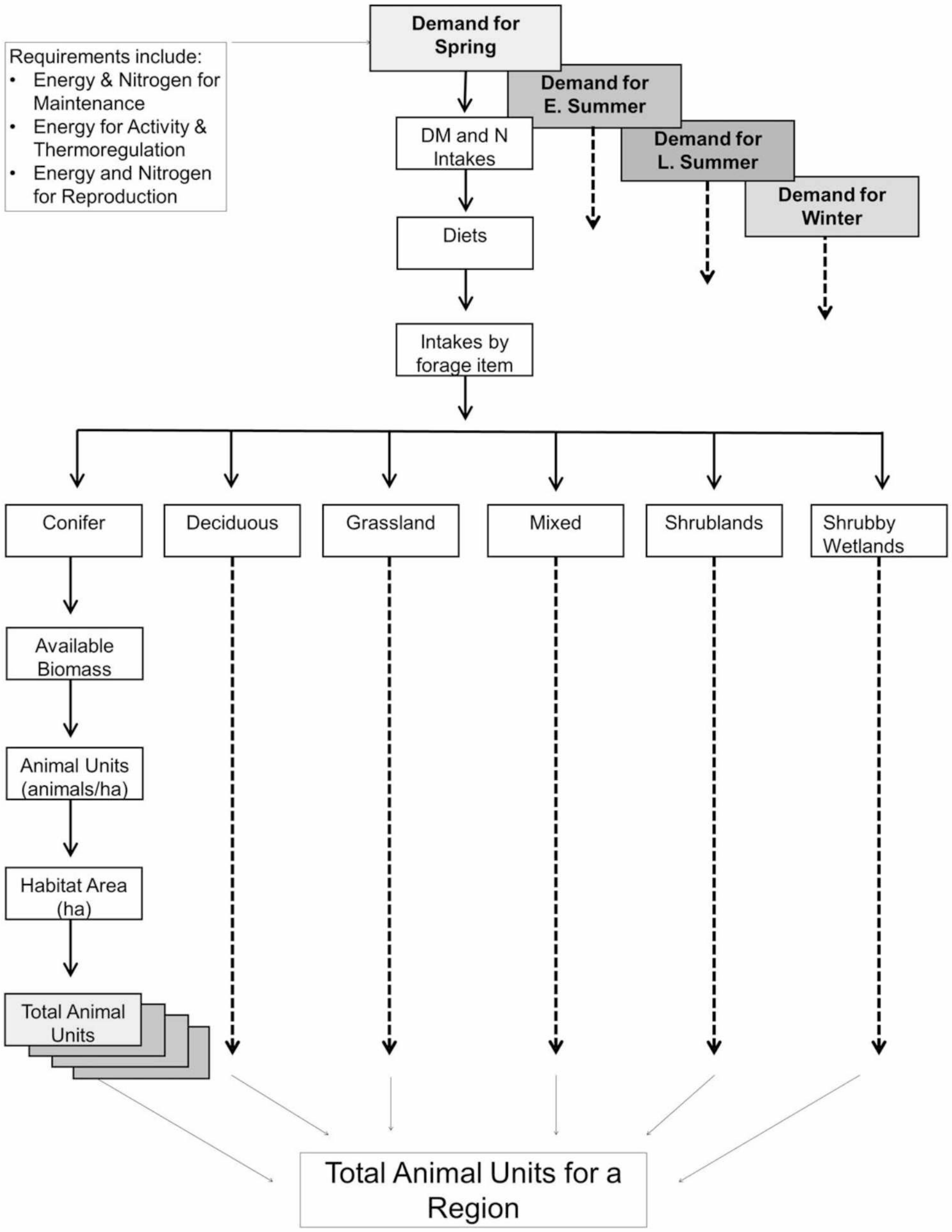

Figure 2.4. Scheme for modeling the nutritional demands of moose to project animal units for each habitat class and area on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA.

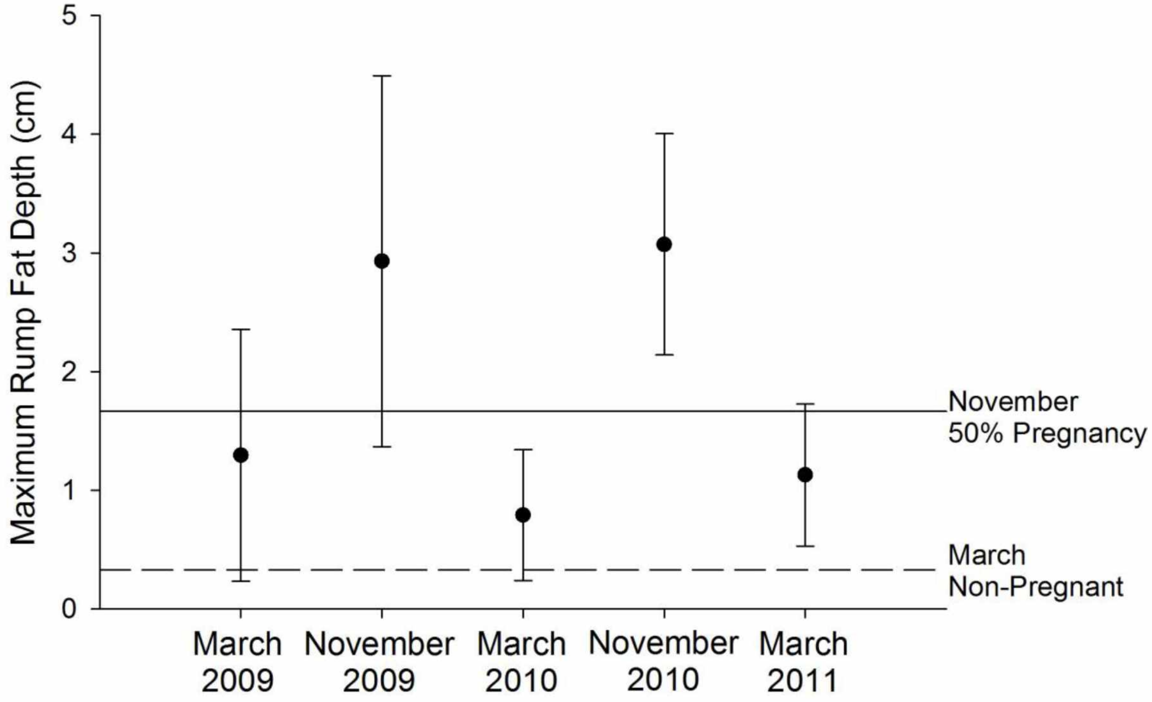

Figure 2.5. Subcutaneous fat stores measured by ultrasound of female moose captured on Joint Base Elmendorf-Richardson near Anchorage, Alaska, USA. Solid line indicates a fat depth (1.66 cm) that corresponds with a 50% probability of pregnancy in November (Testa and Adams 1998). Dashed line indicates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

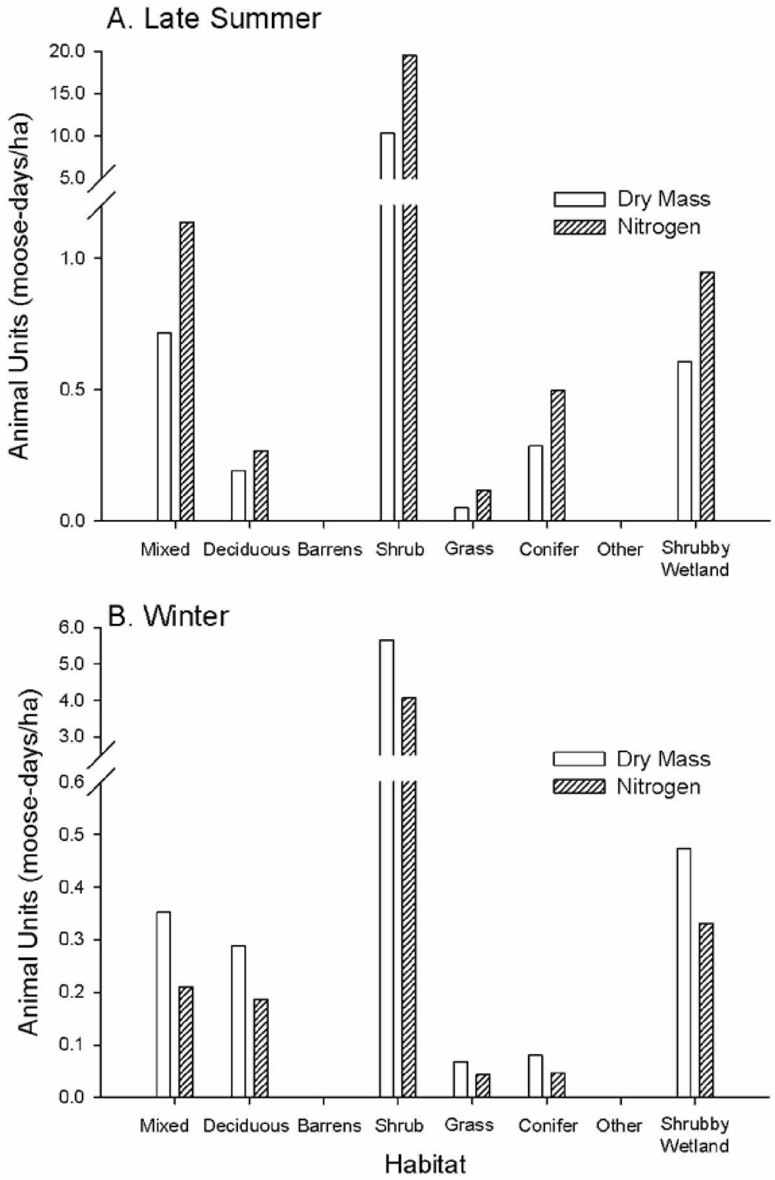

Figure 2.6. Seasonal estimates of animal units (moose – days/ha) for each class of habitat on Joint Base Elmendorf-Richardson near Anchorage, AK. Estimates are based on the utilizable dry mass (open bars) and Nitrogen of forages that were projected by a nutritional model for a reproductive female moose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

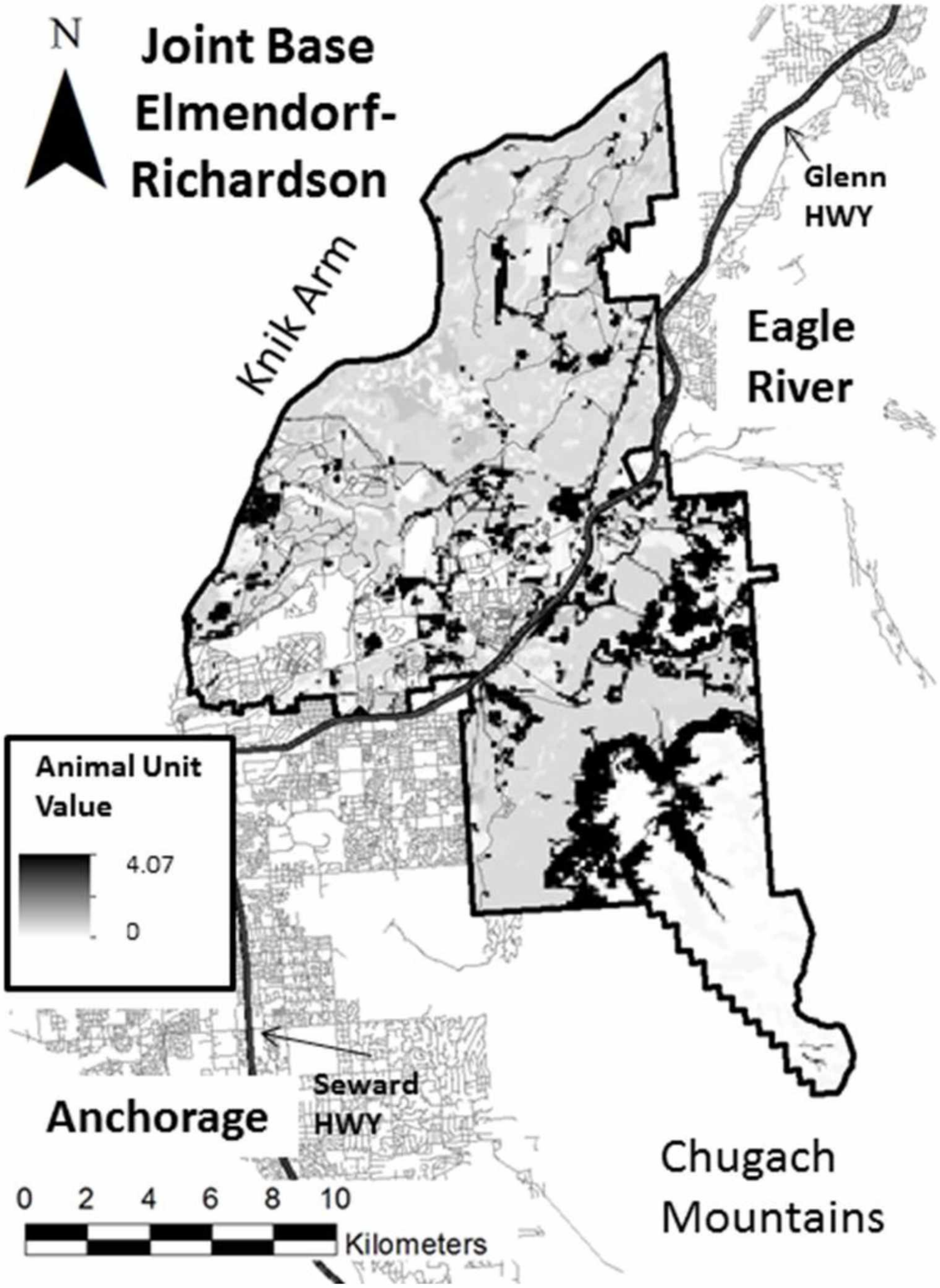

Figure 2.7. Winter distribution of animal units (AU; moose-days/ha) for Joint Base Elmendorf-Richardson near Anchorage, AK projected by the nutritional model for utilizable Nitrogen. Estimates are based on reproductive female moose of 428 kg in January.

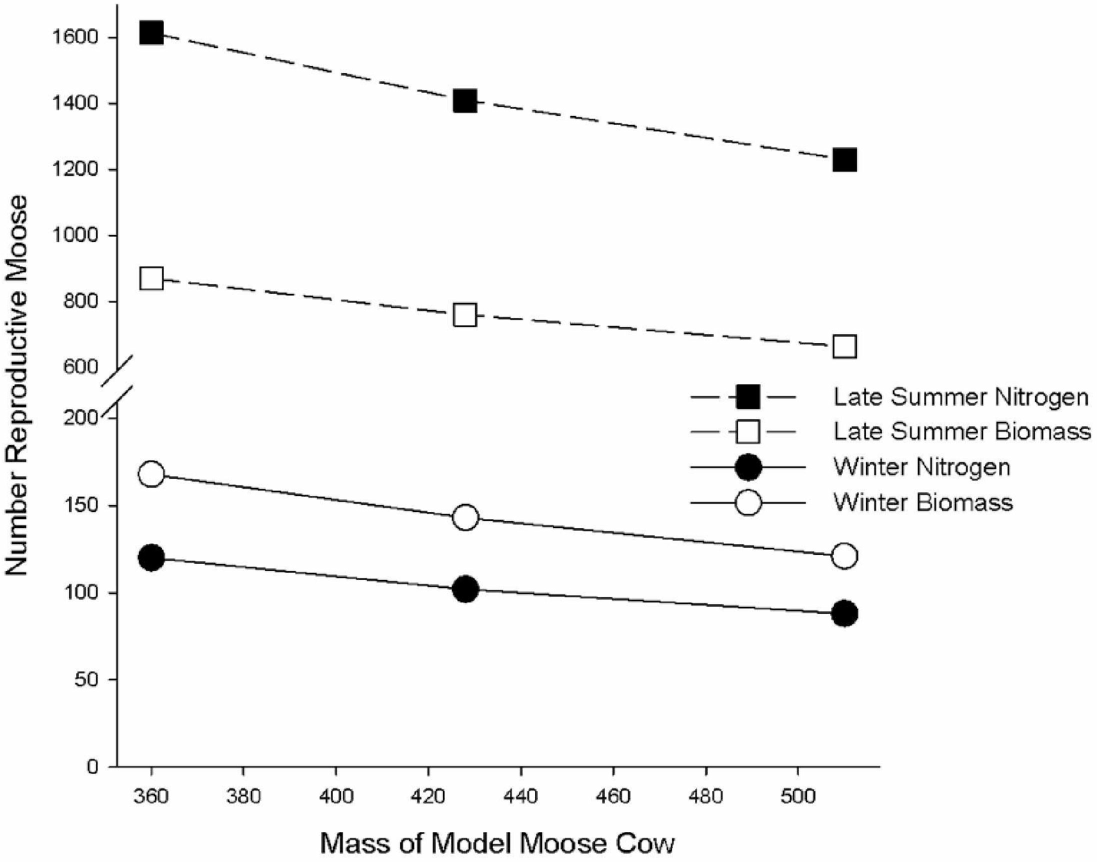

Figure 2.8. Number of reproductive female moose that can be supported by habitats on Joint Base Elmendorf-Richardson near Anchorage, AK. Numbers are projected by the nutritional model from the utilizable dry mass and Nitrogen in forage starting with a body mass of 360, 428 or 510 kg in January. Estimates 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.

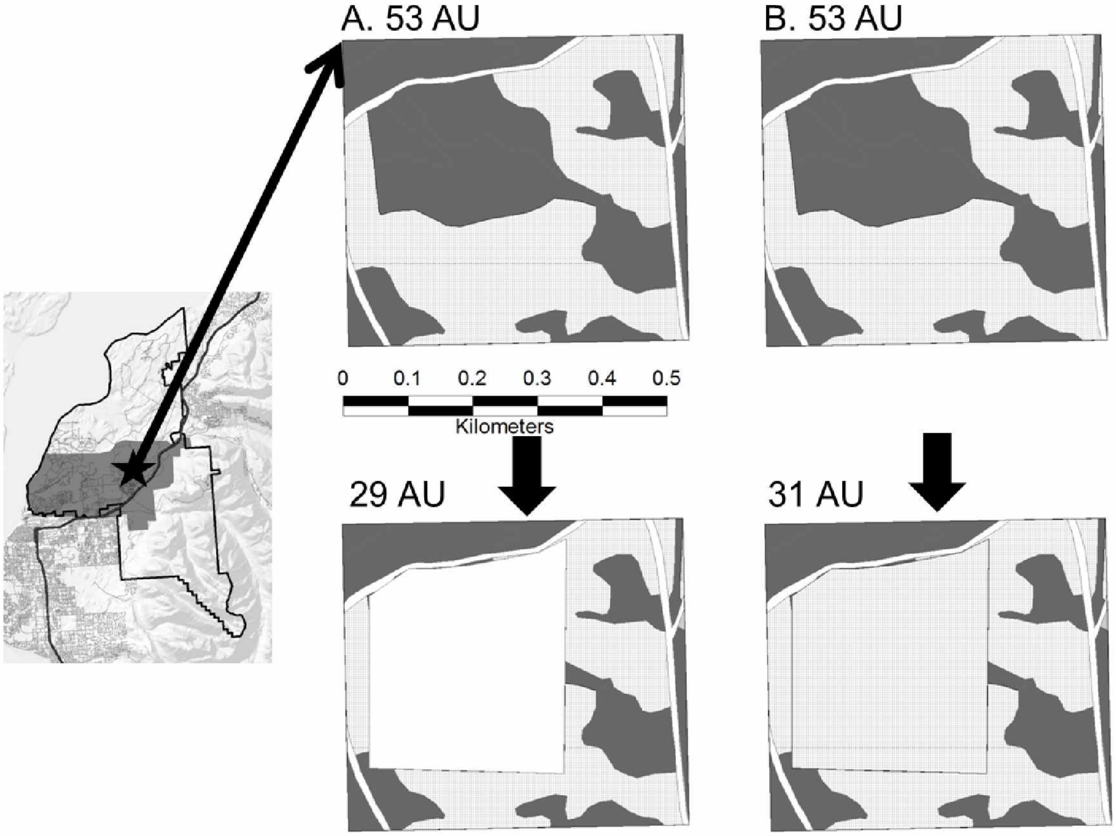

Figure 2.9. Projected winter animal units (AU; moose-days/ha) supported by a 25 ha parcel. Light shading indicates mixed forest (valued at 0.24 AU), dark shading indicates shrublands (valued at 4.07 AU), and white indicates barrens and roads (valued at 0 AU). If a 10 ha section is fenced (A), total AU 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

2.10 Literature Cited

Alaska Climate Research Center. 2012. Anchorage Climatological Data. <http://climate.gi.alaska.edu/climate/Location/TimeSeries/Anchorage.html>. Accessed 20 Feb 2012.

Ballard, W. B., J. S. Whitman, and D. J. Reed. 1991. Population dynamics of moose in south-central Alaska. Wildlife Monographs 3-49.

Barboza, P. S., and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. Journal of Mammalogy 81:473-489.

Barboza, P. S., and T. R. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer. Alces 37:275-292.

Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer-Verlag, Heidelberg, Germany.

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

Bertram, M. R., and M. T. Vivion. 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66:747-756.

Blaxter, K. L. 1989. Energy metabolism in animals and man. Cambridge University Press, Cambridge.

Boertje, R. D. 1984. Seasonal diets of the Denali Caribou Herd, Alaska. Arctic 37:161-165.

Boertje, R. D., K. A. Kellie, C. T. Seaton, M. A. Keech, D. D. Young, B. W. Dale, L. G. Adams, and A. R. Aderman. 2006. Ranking Alaska moose nutrition: signals to begin liberal antlerless harvests. Journal of Wildlife Management 71:1494-1506.

Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79:1332-1344.

Cameron, R. D., W. T. Smith, R. G. White, and B. Griffith. 2005. Central arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. Arctic 58:1-9.

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

Côté, S. D., T. P. Rooney, J. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

Danks, Z. D., and W. F. Porter. 2010. Temporal, spatial, and landscape habitat characteristics of moose–vehicle collisions in western Maine. Journal of Wildlife Management 74:1229-1241.

Ferguson, S. H., A. R. Bisset, and F. Messier. 2000. The influences of density on growth and reproduction in moose *Alces alces*. Wildlife Biology 6:31-39.

Franzmann, A. W., and C. C. Schwartz. 1983. Moose productivity and physiology. Federal aid in wildlife restoration final report. Alaska Department of Fish and Game. Juneau, Alaska.

Franzmann, A. W., and C. C. Schwartz. 1985. Moose twinning rates: a possible population condition assessment. Journal of Wildlife Management 49:394-396.

Gasaway, W. C., R. D. Boertje, R. O. Stephenson, D. V. Grangaard, D. G. Kelleyhouse, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 4-59.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelations of wolves, prey, and man in interior Alaska. Wildlife Monographs 1-50.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body composition and nutrient reserves of arctic caribou. Canadian Journal of Zoology 74:136-146.

Goering, H. K., and P. J. Van Soest. 1970. Forage fiber analysis (apparatus, reagents, procedures, and some applications). USDA Agricultural Research Service, Washington, D. C.

Hamilton, G. D., P. D. Drysdale, and D. L. Euler. 1980. Moose winter browsing patterns on clear-cuttings in northern Ontario. Canadian Journal of Zoology 58:1412-6.

Harveson, P., R. Lopez, B. Collier, and N. Silvy. 2007. Impacts of urbanization on Florida Key deer behavior and population dynamics. Biological Conservation 134:321-331.

Heard, D., S. Barry, G. Watts, and K. Child. 1997. Fertility of female moose (*Alces alces*) in relation to age and body condition. Alces 33:165-176.

Hebblewhite, M., and E. H. Merrill. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445-3454.

Hjeljord, O., N. Hovik, and H. B. Pedersen. 1990. Choice of feeding sites by moose during summer, the influence of forest structure and plant phenology. Holarctic Ecology 13:281-292.

Hjeljord, O., F. Sundstøl, and H. Haagenrud. 1982. The nutritional value of browse to moose. Journal of Wildlife Management 46:333-343.

Hubbert, M. E. 1987. The effect of diet on energy partitioning in moose. Dissertation, University of Alaska Fairbanks, USA. .

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Jorgenson, M. T., J. E. Roth, S. F. Schlentner, E. R. Pullman, M. Macander, and C. H. Racine. 2003. An ecological land survey for Fort Richardson, Alaska. Cold Regions Research and Engineering Laboratory. Hanover, New Hampshire, USA.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.

Krebs, C. J. 1999. Ecological methodology. Second edition. Addison-Wesley, California.

Laurian, C., C. Dussault, J. Quellet, R. Courtois, M. Poulin, and L. Breton. 2008. Behavior of moose relative to a road network. Journal of Wildlife Management 72:1550-1557.

McArt, S. H., D. E. Spalinger, W. B. Collins, E. R. Schoen, T. Stevenson, and M. Bucho. 2009. Summer dietary nitrogen availability as a potential bottom-up constraint on moose in south-central Alaska. Ecology 90:1400-11.

McCullough, D. R., K. W. Jennings, N. B. Gates, B. G. Elliott, and J. E. Didonato. 1997. Overabundant deer in California. Wildlife Society Bulletin 25:478-483.

Miquelle, D. G., J. M Peek, and V. Van Ballenberghe. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 3- 57.

Moen, A. N., and R. A. Moen. 1998. Metabolic ratios for estimating energy metabolism in moose. Alces 34:181-187.

Natural Resources Conservation Service. 2012. Alaska Snowpack Reports. <http://www.wcc.nrcs.usda.gov/cgibin/snow_rpt.pl?state=alaska>. Accessed 5 Jan 2012.

Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215-238 in Robert J. Hudson and Robert G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, FL.

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

Oldemeyer, J. L. 1982. Estimating production of paper birch and utilization by browsers. Canadian Journal of Forest Research 12:52-57.

Ouellet, J.-P., D. C. Heard, S. Boutin, R. Mulders, and J. P. Quellet. 1997. A comparison of body condition and reproduction of caribou on two predator-free arctic islands. Canadian Journal of Zoology 75:11-17.

Parker, K. L., P. S. Barboza, and T. R. Stephenson. 2005. Protein conservation in female caribou: effects of decreasing diet quality during winter. Journal of Mammalogy 86:610-622.

Pastor, J., and K. Danell. 2003. Moose-vegetation-soil interactions: a dynamic system. Alces 39:177-192.

Peltier, T. C., P. S. Barboza, and J. E. Blake. 2003. Seasonal hyperphagia does not reduce digestive efficiency in an arctic grazer. Physiological and Biochemical Zoology 76:471-483.

Poole, K. G., R. Serrouya, and K. Stuart-Smith. 2007. Moose calving strategies in interior montane ecosystems. Journal of Mammalogy 88:139-150.

Reese, E. O., and C. T. Robbins. 1994. Characteristics of moose lactation and neonatal growth. Canadian Journal of Zoology 72:953-957.

Regelin, W. L., C. C. Schwartz, and A. W. Franzmann. 1985. Seasonal energy metabolism of adult moose. Journal of Wildlife Management 49:388-393.

Regelin, W. L., C. C. Schwartz, and A. W. Franzmann. 1987. Effects of forest succession on nutritional dynamics of moose forage. Swedish Wildlife Research Supplement 1 247-263.

Renecker, L. A., and R. J. Hudson. 1985. Estimation of dry matter intake of free-ranging moose. Journal of Wildlife Management 49:785-792.

Renecker, L. A., and R. J. Hudson. 1988. Seasonal quality of forages used by moose in the aspen-dominated boreal forest, central Alberta. Holarctic Ecology 11:111-118.

Renecker, L. A., and R. J. Hudson. 1989. Ecological metabolism of moose in aspen-dominated boreal forests, central Alberta. Canadian Journal of Zoology 67:1923-1928.

Renecker, L. A., and R. J. Hudson. 1992. Habitat and forage selection of moose in the Aspen-dominated boreal forest, Central Alberta. Alces 28:189-201.

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

Robbins, C. T. 1993. Wildlife feeding and nutrition. Second edition. Academic Press, San Diego, California, USA.

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

Schwartz, C. C., M. E. Hubbert, and A. W. Franzmann. 1988a. Energy requirements of adult moose for winter maintenance. Journal of Wildlife Management 52:26-33.

Schwartz, C. C., and K. J. Hundertmark. 1993. Reproductive characteristics of Alaskan moose. Journal of Wildlife Management 57:454-468.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1984. Seasonal dynamics of food intake in moose. Alces 20:223-244.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1987a. Seasonal weight dynamics of moose. Swedish Wildlife Research, Supplement 1 301-310.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1987b. Protein digestion in moose. Journal of Wildlife Management 51:352-357.

Schwartz, C. C., W. L. Regelin, and A. W. Franzmann. 1988b. Estimates of digestibility of birch, willow, and aspen mixtures in moose. Journal of Wildlife Management 52:33-37.

Schwenk, W. S., and A. M. Strong. 2011. Contrasting patterns and combined effects of moose and insect herbivory on striped maple (*Acer pensylvanicum*). Basic and Applied Ecology 12:64-71.

Searle, K. R., and L. A. Shipley. 2008. The comparative feeding behaviour of large browsing and grazing herbivores. Pages 117-148 in I. J. Gordon and H. H. T. Prins, editors. The ecology of browsing and grazing. Springer-Verlag, Heidelberg, Germany.

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

Shipley, L. A., S. Blomquist, and K. Danell. 1998. Diet choices made by free-ranging moose in northern Sweden in relation to plant distribution, chemistry, and morphology. Canadian Journal of Zoology 76:1722-1733.

Singleton, V. L., R. Orthofer, and R. M. Lamuela-Raventos. 1999. Analysis of total phenols and other oxidation substrates and antioxidants by means of Folin-Cioalteu reagent. Methods in Enzymology 299:152-178.

Sinnott, R. 2004. Unit 14C moose management report. Pages 183–199 *in* C. Brown, editor. Moose management report of survey and inventory activities 1 July 2001–30 June 2003 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska.

Sinnott, R. 2006. Unit 14C moose management report. Pages 181–198 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2003–30 June 2005 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska.

Sinnott, R. 2008. Unit 14C moose management report. Pages 189–1206 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2005–30 June 2007 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska.

Spaeth, D. F., R. T. Bowyer, T. R. Stephenson, P. S. Barboza, and V. Van Ballenberghe. 2002. Nutritional quality of willows for moose: effects of twig diameter and age. Alces 38:143-154.

Spalinger, D. E., W. B. Collins, T. A. Hanley, N. E. Cassara, and A. M. Carnahan. 2010. The impact of tannins on protein, dry matter, and energy digestion in moose (*Alces alces*). Canadian Journal of Zoology 88:977-987.

Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. The American Naturalist 140:325-348.

Stephenson, T. R., V. Van Ballenberghe, J. M. Peek, and J. G. MacCracken. 2006. Spatio-temporal constraints on moose habitat and carrying capacity in coastal Alaska: vegetation succession and climate. Rangeland Ecology & Management 59:359-372.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1993. Ultrasonic fat measurements of captive yearling bull moose. Alces 29:115-123.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717-722.

Stolter, C., P. Niemelä, J. P. Ball, R. Julkunen-Tiitto, A. Vanhatalo, K. Danell, T. Varvikko, and J. U. Ganzhorn. 2009. Comparison of plant secondary metabolites and digestibility of three different boreal coniferous trees. Basic and Applied Ecology 10:19-26.

Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345-1354.

Testa, J. W., E. F. Becker, and G. R. Lee. 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. Journal of Mammalogy 81:162-168.

Thompson, I. D., and R. W. Stewart. 2007. Management of moose habitat. Pages 377–402 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American moose. Second edition. University Press of Colorado, Boulder, Colorado.

Tilley, J. M. A., and R. A. Terry. 1963. A two-stage technique for the in vitro digestion of forage crops. Grass and Forage Science 18:104-111.

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

Wam, H. K., O. Hjeljord, and E. J. Solberg. 2010. Differential forage use makes carrying capacity equivocal on ranges of Scandinavian moose (*Alces alces*). Canadian Journal of Zoology 88:1179-1191.

Wam, H. K., and O. Hjeljord. 2010. Moose summer and winter diets along a large scale gradient of forage availability in southern Norway. European Journal of Wildlife Research 56:745-755.

Weixelman, D. A., R. T. Bowyer, and V. Van Ballenberghe. 1998. Diet selection by Alaskan moose during winter: effects of fire and forest succession. Alces 34:213-238.

Western Regional Climate Center. 2011. WRCC Homepage. http://www.wrcc.dri.edu. Accessed 5 July 2009.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

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
<u>Baseline Energy Demands</u>					
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
<u>Reproductive Energy Demands</u>					
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
<u>Seasonal Energy Demands</u>					
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
<u>Seasonal Nitrogen Demands</u>					
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 (%)
<u>*Woody Browse Species (Shrubs)*</u>				
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**
<u>*Non-Shrub*</u>				
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 87° (18° SD) to 70° (15° 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 infrastructure and may use areas near development for protection from predators

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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

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 °C 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 (87° ± 18°) compared to winter (70° ± 15°; $F = 12.70$; 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

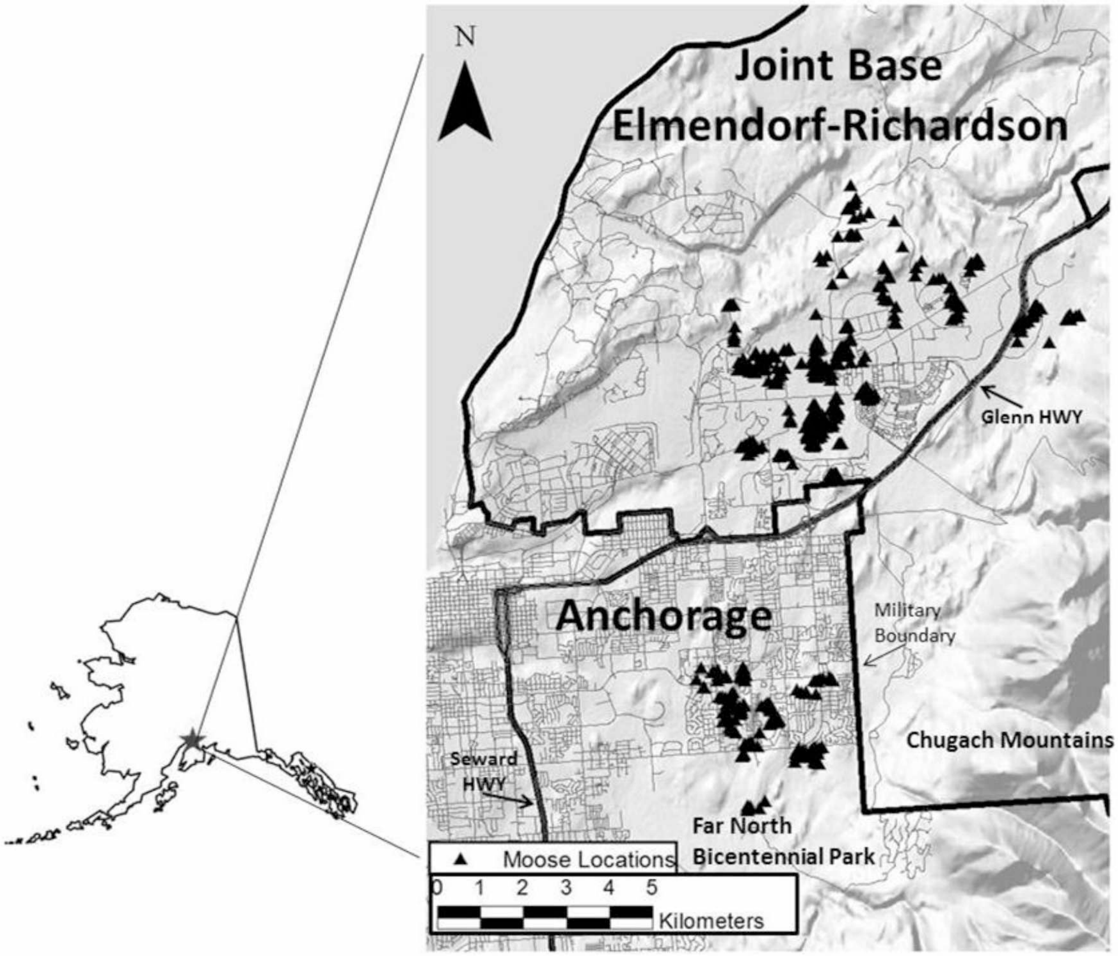

Figure 3.1. Study area for female moose foraging in Anchorage and Joint Base Elmendorf-Richardson, Alaska, USA. Black triangles indicate moose locations used in our analysis

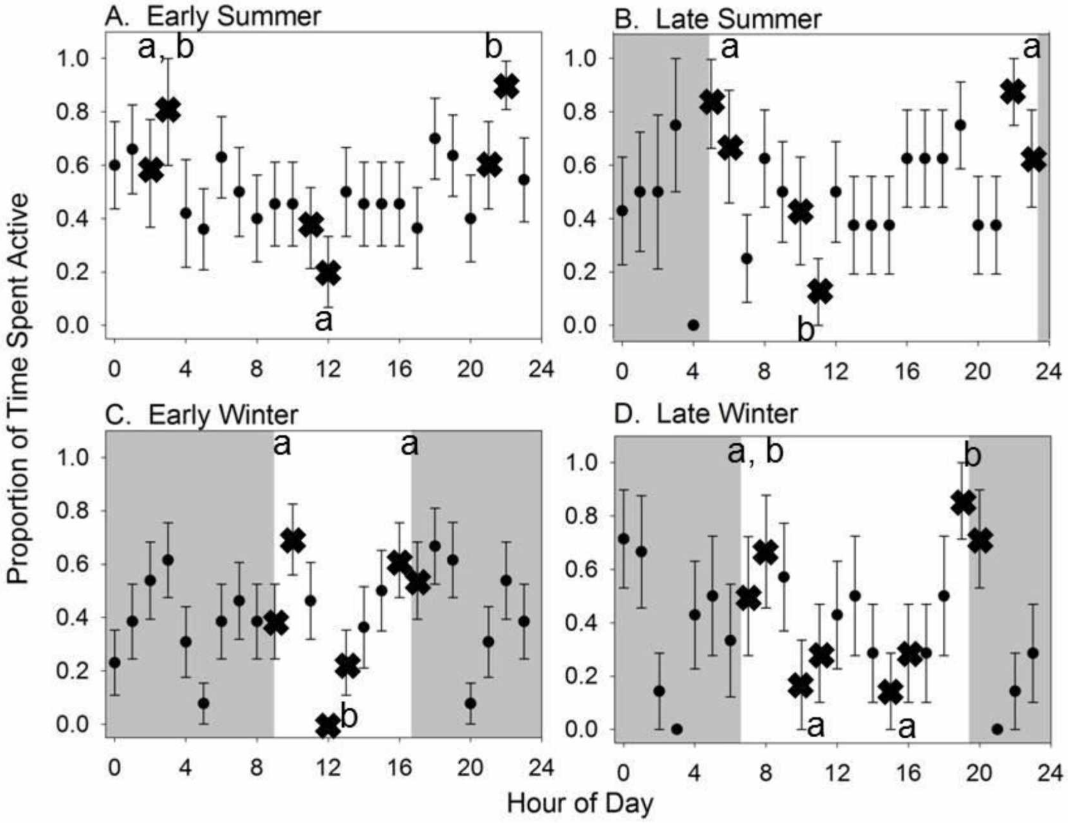

Figure 3.2. Mean (± 1 SE) proportion of time spent active by hour of day for moose in Anchorage and Joint Base Elmendorf-Richardson, AK. Shading edge represents the mean start and end for civil twilight during the respective season. Early summer lacks a civil twilight period due to long days. Bold crosses 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.

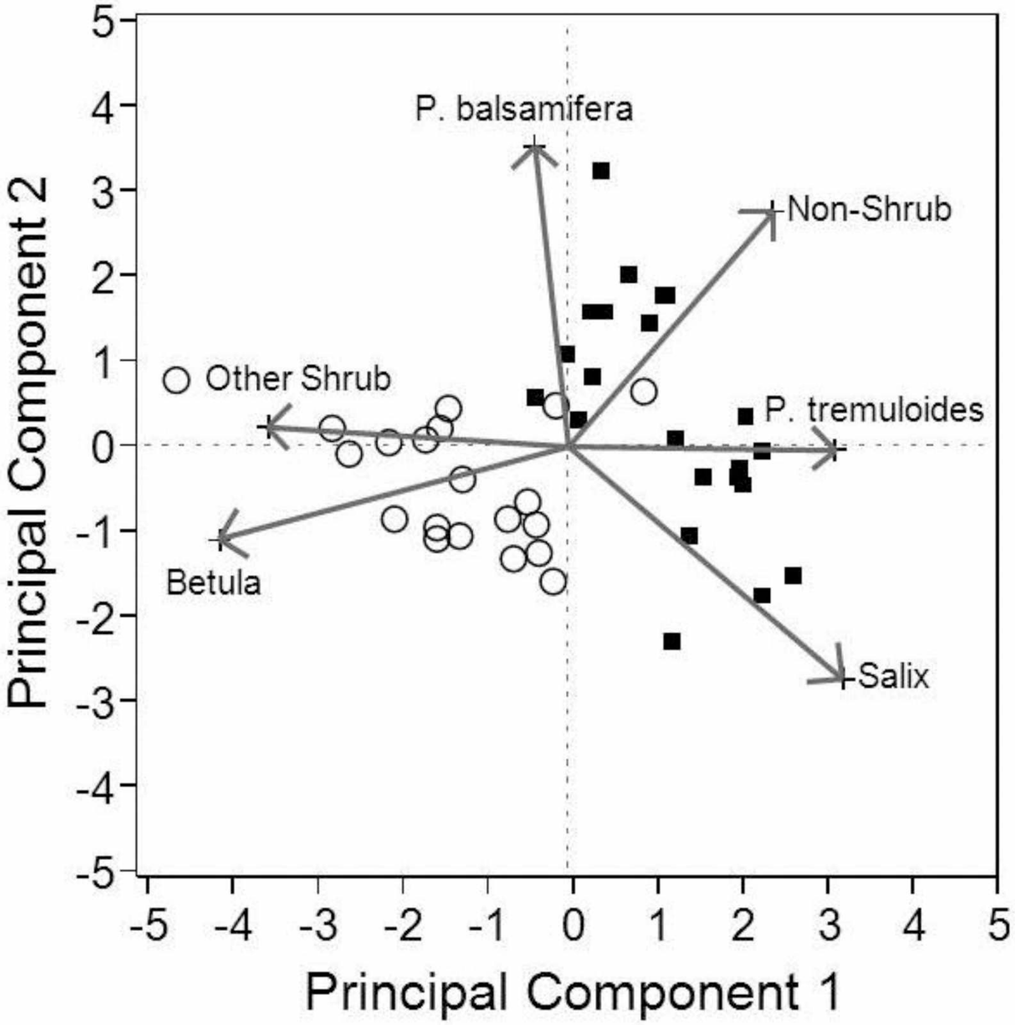

Figure 3.3. Biplot of principal component analysis of diet composition for moose in Anchorage, Alaska during summer (black squares) and winter (open circles). Principal component 1 (PC 1) explained 43.9% of the variance in diets while principal component 2 (PC 2) explained 22.6% of the variance in diets. 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.

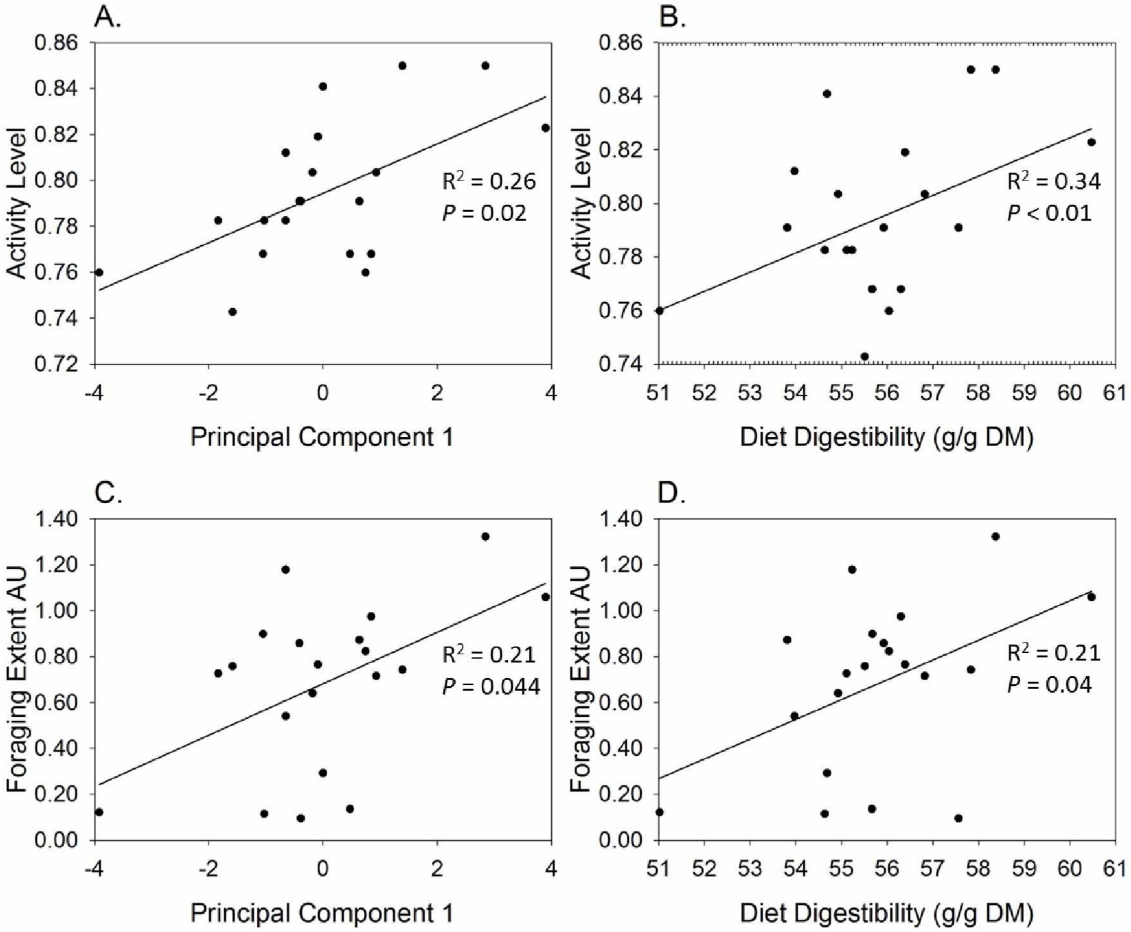

Figure 3.4. Winter relationships between diet, activity level, and mean AU value of foraging extent for adult female moose in Anchorage, AK. Activity level was 4th root transformed for normality. Principal component 1 (PC 1) was derived from winter diet composition. Eigenvector values for PC 1 were *Betula 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

3.9 Literature Cited

ALASKA CLIMATE RESEARCH CENTER. 2012. Anchorage Climatological Data. <http://climate.gi.alaska.edu/climate/Location/TimeSeries/Anchorage.html>. Accessed Feb 2012.

ANDERSEN, R., J. D. C. LINNELL, and R. LANGVATN. 1996. Short term behavioural and physiological response of moose *Alces alces* to military disturbance in Norway. Biological Conservation 77:169-176.

BELANT, J. L., J. A. PAYNTER, K. E. STAHLNECKER, and V. VAN BALLENBERGHE. 2006. Moose distribution relative to human development in a National Park. Alces 42:33-39.

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

BOERTJE, R. D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic 37:161-165.

DE JAGER, N. R., J. PASTOR, and A. L. HODGSON. 2009. Scaling the effects of moose browsing on forage distribution, from the geometry of plant canopies to landscapes. Ecological Monographs 79:281-297.

DUNGAN, J. D., L. A. SHIPLEY, and R. G. WRIGHT. 2010. Activity patterns, foraging ecology, and summer range carrying capacity of moose (*Alces alces shirasi*) in Rocky Mountain Park, Colorado. Alces 46:71-87.

DUSSAULT, C., R. COURTOIS, J. P. OUELLET, and I. GIRARD. 2005. Space use of moose in relation to food availability. Canadian Journal of Zoology 83:1431-1437.

GAUTESTAD, A. O., and I. MYSTERUD. 2010. Spatial memory, habitat auto-facilitation and the emergence of fractal home range patterns. Ecological Modelling 221:2741-2750.

GILSDORF, J. M., S. E. HYGNSTROM, K. C. VERCAUTEREN, E. E. BLANKENSHIP, and R. M. ENGEMAN. 2004. Propane exploders and electronic guards were ineffective at reducing deer damage in cornfields. Wildlife Society Bulletin 32:524-531.

HARVESON, P., R. LOPEZ, B. COLLIER, and N. SILVY. 2007. Impacts of urbanization on Florida Key deer behavior and population dynamics. Biological Conservation 134:321-331.

JIANG, Z., AND R. J. HUDSON. 1996. Digestive responses of wapiti *Cervus elaphus canadensis* to seasonal forages. Acta Theriologica 41:415-423.

KRAUSMAN, P. R., L. K. HARRIS, C. L. BLASCH, K. K. G. KOENEN, and J. FRANCINE. 2004. Effects of military operations on behavior and hearing of endangered Sonoran pronghorn. Wildlife Monographs 1-41.

LAWLER, J. P., A. J. MAGOUN, C. T. SEATON, C. L. GARDNER, R. D. BOERTJE, J. M. VER HOEF, and P. A. DEL VECCHIO. 2005. Short-term impacts of military overflights on caribou during calving season. Journal of Wildlife Management 69:1133-1146.

LECHNER, I., P. S. BARBOZA, W. COLLINS, J. FRITZ, D. GÜNTHER, B. HATTENDORF, J. HUMMEL, K. SÜDEKUM, and M. CLAUSS. 2010. Differential passage of fluids and different-sized particles in fistulated oxen (Bos primigenius f. taurus), muskoxen (Ovibos moschatus), reindeer (*Rangifer tarandus*) and moose (*Alces alces*): rumen particle size discrimination is independent from contents. Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology 155:211-22.

McDonald, M. G. 1991. Moose movements and mortality associated with the Glenn Highway expansion, Anchorage, AK. Alces 27:208-219.

Mårell, A., J. P. Ball, and A. Hofgaard. 2002. Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. Canadian Journal of Zoology 80:854-865.

Moen, R., J. Pastor, and Y. Cohen. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78:505-521.

Neumann, W., G. Ericsson, and H. Dettki. 2009. Does off-trail backcountry skiing disturb moose? European Journal of Wildlife Research 56:513-518.

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

Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. The Journal of Wildlife Management 48:474-488.

Person, S. J., R. E. Pegau, R. G. White, and J. R. Luick. 1980. In vitro and nylon-bag digestibilities of reindeer and caribou forages. The Journal of Wildlife Management 44:613-622.

Peterson, M. N., R. R. Lopez, E. J. Laurent, P. A. Frank, N. J. Silvy, and J. Liu. 2005. Wildlife loss through domestication: the case of endangered key deer. Conservation Biology 19:939-944.

Quinn, G. P., and M. J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

REESE, E. O., and C. T. ROBBINS. 1994. Characteristics of moose lactation and neonatal growth. Canadian Journal of Zoology 72:953-957.

REGELIN, W. L., C. C. SCHWARTZ, and A. W. FRANZMANN. 1985. Seasonal energy metabolism of adult moose. Journal of Wildlife Management 49:388-393.

RENECKER, L. A., and R. J. HUDSON. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. Journal of Wildlife Management 53:296-302.

RISENHOOVER, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis. Michigan Tech University, Houghton, MI.

SAETHER, B. E., and R. ANDERSEN. 1990. Resource limitation in a generalist herbivore, the moose *Alces alces*: ecological constraints on behavioural decisions. Canadian Journal of Zoology 68:993-999.

SCHWARTZ, C. C., M. E. HUBBERT, and A. W. FRANZMANN. 1988. Changes in body composition of moose during winter. Alces 24:178-187.

_____, W. L. REGELIN, and A. W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. Alces 20:223-244.

_____, _____, and A. W. FRANZMANN. 1987. Seasonal weight dynamics of moose. Swedish Wildlife Research, Supplement 1 301-310.

STØEN, O. G., W. NEUMANN, G. ERICSSON, J. E. SWENSON, H. DETTKI, J. KINDBERG, and C. NELLEMANN. 2010. Behavioural response of moose *Alces alces* and brown bears *Ursus arctos* to direct helicopter approach by researchers. Wildlife Biology 16:292-300.

TELONICS. 2009. Gen4 GPS Systems Manual. Mesa, Arizona, USA; 1-55.

TESTA, J. W., and G. P. ADAMS. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345-1354.

TINOCO TORRES, R., J. C. CARVALHO, M. PANZACCHI, J. D. C. LINNELL, and C. FONSECA. 2011. Comparative use of forest habitats by roe deer and moose in a human-modified landscape in southeastern Norway during winter. Ecological Research 26:781-789.

ULLREY, D. E., W. G. YOUATT, H. E. JOHNSON, L. D. FAY, and B. E. BRENT. 1967. Digestibility of cedar and jack pine browse for the white-tailed deer. The Journal of Wildlife Management 31:448-454.

UNITED STATES CENSUS BUREAU. 2012. 2010 Census Data. <http://2010.census.gov/2010census/data>. Accessed Jan 2012.

UNITED STATES DEPARTMENT OF DEFENCE. 2012. <http://www.militaryinstallations.dod.mil>. Accessed Feb 2012

VAN BALLENBERGHE, V., and D. G. MIQUELLE. 1990. Activity of moose during spring and summer in interior Alaska. The Journal of Wildlife Management 54:391-396.

VERCAUTEREN, K. C., J. A. SHIVIK, and M. J. LAVELLE. 2005. Efficacy of an animal-activated frightening device on urban elk and mule deer. Wildlife Society Bulletin 33:1282-1287.

VIVAS, H. J., and B. E. SAETHER. 1987. Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: An experimental study of winter foraging behaviour in relation to browse availability. Journal of Animal Ecology 56:509-520.

WEISENBERGER, M. E., P. R. KRAUSMAN, M. C. WALLACE, D. W. DE YOUNG, and O. E. MAUGHAN. 1996. Effects of simulated aircraft noise on heart rate and behavior of desert ungulates. Journal of Wildlife Management 60:52-61.

WHITE, R. G., D. F. HOLLEMAN, C. C. SCHWARTZ, W. L. REGELIN, and A. W. FRANZMAN. 1984. Control of rumen turnover in northern ruminants. Canadian Journal of Animal Science 64:349-350.

ZAR, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

ZOLLNER, P. A., and S. L. LIMA. 1999. Search strategies for landscape-level interpatch movements. Ecology 80:1019-1030.

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.

4.4 Literature Cited

Dungan, J. D., L. A. Shipley, and R. G. Wright. 2010. Activity patterns, foraging ecology, and summer range carrying capacity of moose (*Alces alces shirasi*) in Rocky Mountain Park, Colorado. Alces 46:71-87.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.

Morrison, S. F., G. J. Forbes, and S. J. Young. 2002. Browse occurrence, biomass, and use by white-tailed deer in a northern New Brunswick deer yard. Canadian Journal of Forest Research 32:1518-1524.

Renecker, L. A., and R. J. Hudson. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. Journal of Wildlife Management 53:296-302.

Schwartz, C. C., M. E. Hubbert, and A. W. Franzmann. 1988. Changes in body composition of moose during winter. Alces 24:178-187.

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

Sinnott, R. 2008. Unit 14C moose management report. Pages 189–1206 *in* P. Harper, editor. Moose management report of survey and inventory activities 1 July 2005–30 June 2007 Alaska Department of Fish and Game. Project 1.0. Juneau, Alaska.

Stephenson, T. R., K. J. Hundertmark, C. C. Schwartz, and V. Van Ballenberghe. 1998. Predicting body fat and body mass in moose with ultrasonography. Canadian Journal of Zoology 76:717-722.

Stephenson, T. R. 2003. Physiological ecology of moose: nutritional requirements for reproduction with respect to body threshold conditions. Alaska Department of Fish and Game. Federal aid in wildlife restoration research final performance report, 1 July 1997-30 June 2003. .

Suring, L. H., and C. Sterne. 1998. Winter habitat use by moose in south-central Alaska. Alces 34:139-147.

Telfer, E. S. 1988. Habitat use by moose in southwestern Alberta. Alces 24:14-21.

Testa, J. W., and G. P. Adams. 1998. Body condition and adjustments to reproductive effort in female moose (*Alces alces*). Journal of Mammalogy 79:1345-1354.

Van Ballenberghe, V., and D. G. Miquelle. 1990. Activity of moose during spring and summer in interior Alaska. The Journal of Wildlife Management 54:391-396.