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WALD, ERIC J., Management of an Expanding Moose (*Alces alces*) Population on the Yukon-Kuskokwim Delta, Alaska, PhD, Department of Ecosystem Science and Management, December 2014.

My overall objective of this project was to identify and develop management tools for an expanding moose population in western Alaska. The Yukon-Kuskokwim Delta (YKD) is home to over 40 villages that rely on subsistence resources across the region, and the high demand for resources has prioritized moose management on the Delta. It is critical for wildlife managers to understand not only wildlife ecology, but also the social component to resource management, which often times is the most important factor for success.

I investigate a historical perspective of moose and moose management on the YKD. The historical colonization of moose into Alaska and subsequently into the Yukon-Kuskokwim region is described. I document a case study of the dual-management process for wildlife management in Alaska between the state and federal agencies and how this process worked for moose in the region. Additionally, the success of co-management is documented where the local residents of the region worked with agencies to make resource management decisions such as enacting a short-term moose hunting moratorium that benefited them in the long-term.

I investigated management tools to help better understand the expanding moose population. There was a need to develop an alternative population survey technique for parts of the region that do not receive adequate or reliable survey conditions for the

standard method used in the area. I developed a helicopter-based distance sampling technique that can be used in narrow riparian corridors during low snow years.

Additionally, I developed a method for characterizing and indexing moose browse species within the region. Moose expanding into previously unoccupied habitats could have lasting effects on forage if populations become excessive in localized areas. It is important to characterize the condition of the browse base before the moose population expands and increases in density in order to have a baseline for future comparisons. This project also investigates the effects that snowshoe hares and beavers have on moose browse in the study area. Lastly, I relate a brooming index based on plant architecture to moose twinning rates, a measure of population productivity.

MANAGEMENT OF AN EXPANDING MOOSE (*Alces alces*) POPULATION ON THE YUKON-KUSKOKWIM DELTA, ALASKA

By

Eric J. Wald

A dissertation submitted to the Department of Ecosystem Science and Management
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DEDICATION

Dedicated to my understanding wife, Amy.

The most steadfast support I have had through this entire journey spanning all oscillations of deep lows and soaring highs. You gave me everything. You gave me Alyska.

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This dissertation would not be possible without the support of many friends, family, and colleagues throughout my life and during this epic journey of higher education. This has been an exceedingly long, rutted, and wearisome journey. I started this degree in 2003 and moved to Alaska in 2006 after accepting my dream job, but before finishing my dissertation on moose in the Snowy Range of Wyoming. I thought the opportunity was lost; however, four years later I was asked to return to finish my degree by Larry Munn (an original committee member). Larry saw the potential, perseverance, and abilities in me and wanted me to follow through with what I started. Upon acquiring new moose data in Alaska, I formed my present graduate project with a new committee: Drs. Larry Munn, Jeff Beck, Melanie Murphy, Scott Miller and Rich McCormick. I can't thank you all enough for the opportunity you offered me to get closure on this long overdue project.

My interest in higher thinking was nurtured by family friend and neighbor, Don Paul. While giving me a job one summer helping in his shop, Don mentored me in the science and art of thinking intelligently (i.e., problem solving). He would pose a question, problem or task and then would leave me to think about it on my own terms and time. When he thought the time was right, he would pose the question, "well, what do you think?" I learned a lot that summer. Independent thought is the foundation of science and Don was one of the founders in my scientific career; thank you Don for the time you took to teach. My interest for research and higher education continued into college and was nurtured and developed by my master's committee at South Dakota State

University; Drs. Scott Kronberg, Gary Larson and Carter Johnson. All three of you gave me a great experience and education making it easy to want to continue on for my PhD. You are good friends and mentors.

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Tom Doolittle, my former boss at Yukon Delta NWR, encouraged the use of these moose data for my dissertation work, while Brian McCaffery, Yukon Delta NWR, encouraged me to go back to school and not look back. Additionally, my current supervisor, Dave Payer, has been a staunch supporter of my education and finishing of my degree. Without Dave’s support, this would never have happened. Thanks Dave!

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My parents James and Debbie Wald have been exceedingly encouraging and supportive of my pursuit of education and career. Their greatest gift to me is the hard work ethic that they instilled in my mind, developed by their leading-through-example philosophy. Without lessons learned through hard work my entire life, this project would not have materialized; thank you both and I love you, even if you still think that I am going to school to be a “Game Warden”. Uncle Lawrence (Wald) never wavered in his exhaustive approach to teaching me the love of the outdoors. We had endless weekends of “classroom” time while I grew up hunting the great state of North Dakota and its neighbor to the north, Saskatchewan. I can only hope that my Alyska will be able to have a mentor of the outdoors such as you—thank you.

My very understanding and loving wife, Amy, has been with me through this entire journey and has supported the completion of the process all along. Giving me my baby girl, has been the best gift a man could ask for. Thank you for your love and support—I love you.

Lastly, there are many people directly involved with individual chapters of this dissertation and are acknowledged in those respective chapters. This document is not mine alone, but rather a compilation of efforts derived from an ecosystem of friends, family and colleagues that have influenced my life’s path; I thank you all…!!

Sincerely,
Eric J. Wald

10/29/14: 2:36 am
Laramie, WY

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CHAPTER 1

EXECUTIVE INTRODUCTION

Moose have been an important subsistence resource in Alaska since the late Pleistocene and have recently become an important resource on the Yukon-Kuskokwim Delta (YKD). The recent expansion and establishment of moose into western Alaska was prolonged by confounding factors related to both habitat and human activity. Moose were relatively restricted to the boreal forest of Interior Alaska until habitat changes allowed them to expand their distribution. Fires within the boreal forest created seral stages of habitat matrices and optimal moose forage, opening corridors for westward expansion. Although the habitat on the YKD isn't as extensive as the Interior, it was not a limiting factor in establishing moose on the Delta. Humans have occupied and utilized subsistence resources on the YKD for thousands of years. As shown elsewhere, humans are highly efficient predators that affect wildlife populations through direct utilization (Grayson 2001; Kay 1994, 2007). Coady (1980) was correct in his assessment of a highly mobile human population on the YKD that harvested moose when the opportunity arose. The harvesting of dispersing individual moose did not allow a sustainable moose population to establish in the region.

Dispersing animals can play a key role in repopulating an area that was depleted by hunting (Novaro et al. 2000). Dispersal of most mammal species is related to animal density within the source population (McCullough 1996); therefore, surrounding areas that have higher moose densities are important for dispersing moose to the YKD.

Protected areas are important refugia for the persistence of source populations (Campbell et al. 2011). Creating areas of refugia on the YKD would allow moose populations to establish and become their own self-sustaining source population, which would eventually allow sustainable harvest. These refugia were developed through hunting moratoriums across large areas on the lower Yukon and lower Kuskokwim Rivers. The moratorium on the Yukon was in effect from 1988 to 1994 and on the Kuskokwim from 2004 to 2009. It is evident from these moratoriums that humans influenced moose distribution and abundance in the region. The hunting closures successful establishment of sustainable moose populations that now support regulated harvest within the YKD.

Management, Monitoring and Research

Management of the new moose population along the lower Kuskokwim River is important for its long-term sustainability and continued harvest opportunities by local residents. Wildlife management in Alaska is complicated in that a dual-management system occurs between both federal and state lands making it critical for managers to work together. However, dual management between the Alaska Department of Fish and Game (ADFG) and the US Fish and Wildlife Service (USFWS) is challenged by their differing legal mandates. State wildlife managers are legally required to increase or maintain ungulate densities at high levels according to the state's constitution: "Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall be utilized, developed, and maintained on the *sustained yield principle*, subject to preferences among beneficial uses" (author's italic emphasis; Article VIII, § 4, Constitution of the State of Alaska, 1956). The USFWS, specifically Yukon Delta NWR, is mandated: “to conserve fish and wildlife populations and habitats in their *natural diversity* including, but not limited to… and to provide… the opportunity for continued subsistence uses by local residents…” (author’s italic emphasis; Title III § 302 subparts (7)(B)(i-iii) ANILCA 1980). Although charged with differing mandates, both agencies were able to work together and accomplish the mutual goal of allowing the moose population to expand and establish for the benefit of the people on the lower Kuskokwim River.

Following either of the governing mandates, both agencies require basic ecological knowledge of moose on the YKD in order to make informed management decisions and to ensure that a viable population of moose on the lower Kuskokwim endures. The previous moratorium on the lower Yukon was successful, but little demographic data was collected other than a few surveys and no additional knowledge on population dynamics was obtained during or immediately after the moratorium. Thus, evaluation of the effect of the moratorium and increased knowledge of the ecology of an expanding moose population was not realized. Subsequently managers understood that it was important to monitor and study moose ecology in the lower Kuskokwim region during the moratorium in order to investigate population demographics and acquire baseline data on a colonizing moose population that was dispersing into previously unoccupied habitats.

The moose population of the lower Kuskokwim River utilizes both state and federally managed lands, so a cooperative long-term monitoring system was deemed critical. Long-term research and monitoring programs are important for understanding the ecological factors affecting a wildlife population (Peterson et al. 1984, Franklin 1989, Burt 1994, Rempel 2011) and are critical for the management of the system (Gaillard et al. 2000, Lindenmayer and Likens 2009). Monitoring can be both science and research based (Lindenmayer and Likens 2010) by providing long-term data to document baseline conditions, to compare future changes or to evaluate ecological responses to disturbance (e.g., moose colonizing a new area), and for detecting change or evaluating ecosystem structure and function (e.g., density dependence factors; Gordon et al. 2004).

Long-term support and funding to monitor population parameters are critical elements of resource management objectives (Young et al. 2006), such that managers are necessarily and actively incorporating adaptive monitoring and management practices. An adaptive monitoring framework allows the program to change as new information emerges and reveals new questions, thus changing research focus that may not have been anticipated at the beginning of the program (Burt 1994, Lindenmayer and Likens 2009). A change in focus based on previous monitoring information can lead to targeted monitoring in which monitoring design and implementation are based on a single or subset of questions (Nichols and Williams 2006). For example, if monitoring reveals that the population is declining, then adapt and change focus to targeted monitoring to better understand why or what are the causes of the decline.

Population parameters such as parturition rates, twinning rates, calf and adult survival, herd composition, age at first reproduction, body conditions, and population size can provide important focus to understanding the population dynamics and the relationship with the environment including how these processes are linked to the socioeconomic pressures (Gaillard et al. 1998, Gordon et al. 2004) of the region, specifically subsistence needs. Adaptive and targeted monitoring focuses precisely on the information needed by resource managers to make efficient and effective decisions.

Monitoring moose population dynamics on the lower Kuskokwim region will provide managers insight into herd health, as well as determining if objectives are being met (i.e., population objectives, bull:cow ratio, etc.). Several population parameters being monitored on the YKD such as parturition rates, twinning rates, age of first reproduction, mass of short-yearlings, and body condition during the course of the moratorium will help test the hypothesis that expanding moose populations are not nutritionally constrained (Boertje et al. 2007, 2009). Young moose reproducing, larger short-yearlings, high parturition and twinning rates and thick rump fat are all indicators of a healthy and productive moose population (Franzmann and Ballard 1993, Testa and Adams 1998, Boertje et al. 2007, 2009, Cook et al. 2010).

Population estimates are used to inform harvest regulations, evaluating herd objectives, and for overall trend analyses that can direct more focused research, if the trend is declining. On the YKD, moose surveys can be difficult due to unpredictable and unfavorable environmental conditions. Moose surveys in this region are typically conducted using the GeoSpatial Population Estimater (GSPE; Ver Hoef 2002, Kellie and DeLong 2006) method, which requires certain snow conditions that ensure complete ground coverage of most grasses, tundra, and low growing shrubs (on the YKD snow should be at least 8 inches deep). Unfortunately, the YKD experiences unpredictable freeze-thaw cycles from coastal weather patterns causing snow conditions to deteriorate to unsurveyable conditions within a single day. This unpredictable pattern has created the need to test an alternative survey method, Distance Sampling, for the type of habitat and snow conditions that are exhibited on the YKD.

Although population estimates and parameters are important factors in moose ecology, the interaction of moose and plants, particularly browse species, is equally important (Bowyer et al. 1997). Colonizing moose can, and most likely will, disturb the landscape affecting the structure and function of the ecosystem they inhabit (Pastor et al. 1988, Bryant et al. 1991, Kielland et al. 1997, Kielland and Bryant 1998). The browse species along the lower Kuskokwim drainage would have had only light or no browsing pressure before moose were allowed to become established in the region. Monitoring browse architecture and severity can be of significant value in describing the baseline condition of the area and will be a benchmark for future comparisons to address hypotheses derived from resource management (e.g., overabundance and/or harvest intensity).

Dissertation Framework

This dissertation focuses on the management of moose colonizing and establishing a sustainable population within the lower Kuskokwim River drainage within the Yukon-Kuskokwim Delta region. The following chapters help address current moose management issues and will improve the ecological knowledge of this recent colonizer. Long-term research and monitoring efforts are critical to the sustainable management of a large concentrate selector, the moose. In Chapter 2, I examine a historical perspective of moose and moose management on the YKD. I follow the arrival of moose to North America during the late-Pleistocene and eventually into the YKD region in recent times. I also describe the dual management system between the State of Alaska and the Federal Government for managing moose in Alaska and give specific examples of effective dual management actions injunction with Co-Management with local residents of the area. In Chapter 3, I examine a distance sampling methodology for estimating moose abundance in narrow riparian corridors in low snow condition years. I utilize standard distance sampling analyses and compare those density function models to a non-parametric kernel density function model. Finally in Chapter 4, I characterize and index moose browse within the core of the study area (Kwethluk River). Here I categorize the condition of the browse within two strata, river corridor and floodplain, and determine differences between the strata. I collected density information on preferred (e.g., willow, birch, popular) and some non-preferred (e.g., spruce, alder) browse plants within both strata. I determined a brooming index by preferred species based on browse severity. The overall characterization of the moose browse architecture will give a comparable point for future browse surveys and/or allow managers to determine if more intense biomass production and removal studies are warranted. These chapters combined will expand the knowledge of moose ecology within the YKD and gives both state and federal managers tools to better understand and mange this newly expanding moose population.

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CHAPTER 2

THE HISTORICAL PERSPECTIVE AND MANAGEMENT OF MOOSE ON THE YUKON-KUSKOKWIM DELTA: AN ARGUMENT FOR DUAL AND CO-MANAGEMENT[1]

Abstract

Moose (*Alces alces*) entered North America less than 15,000 years ago by way of the Bering land bridge during the last glacial period. They followed the changing seral communities across the land bridge to ice-free refugiums, which eventually developed into the present day boreal forest of Alaska. Moose persisted here in low numbers for thousands of years and eventually expanded and dispersed into other areas as climate and habitat permitted. More recently, their distribution and abundance has varied greatly in Alaska and in the Yukon-Kuskokwim (Y-K) region over the last 200 years. Moose were relatively scarce throughout this region during the early 1800s, even though adequate habitat was available. Russian explorers reported during the mid-1800s that moose were plentiful in the far-upper Kuskokwim and Yukon Rivers within the boreal forest. By the late 1800s, moose remained scarce in the central portions of the Y-K region. In response to extensive wildfires during the early 1900s, moose expanded throughout the upper Y-K region and by the early 1940s, moose were well established between the village of Aniak and the upper Kuskokwim and Yukon rivers. The upper region experienced more extensive wildfires coupled with predator control in

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the 1940s and 1950s leading to moose populations peaking between the late 1960s and early 1970s. Severe winters in the early 1970s dramatically reduced moose populations in many parts of the state, and moose in the central Y-K region recovered slowly thereafter. Moose have recently become an important subsistence resource on the Yukon-Kuskokwim Delta (YKD) where wildlife management is critical to ensure continued subsistence use of this resource. The passage of the Alaska National Interest Lands Conservation Act (ANILCA) and the repeal of the rural resident-clause from the state of Alaska's Subsistence Law created the now contentious dual management system used to manage Alaska's wildlife. Dual management split management jurisdictions for the purpose of managing subsistence uses and resources such that federal agencies manage subsistence resources for rural residents on federal lands, and the State of Alaska manages resources on non-federal lands for all Alaskans. Despite the split, agencies still work together with stakeholders to manage wildlife at landscape levels. This collaboration was evident when managers considered ways to establish a viable moose population along the lower Kuskokwim River. Federal and state wildlife managers partnered with local residents to embark on a dual and co-management initiative implementing a moose hunting moratorium to allow moose expansion and establishment along the lower Kuskokwim. Ultimately the people of the lower Kuskokwim made the moratorium work, and their commitment to the moratorium resulted in establishing a sustainable moose population in their backyard. The Yukon-Kuskokwim Delta is a positive example of dual and co-management between state, federal and native organizations for the management of moose within the region.

Historic Perspective

Moose (*Alces alces*) are widely studied across their circumboreal distribution, and continue to be the focus of research since they are relatively recent additions to the North American fauna and are still dispersing into suitable, but unoccupied, habitats. Fossil evidence indicates that members of the genus *Alces* are as old as 2.0 to 2.5 million years (*A. gallicus*; Lister 1996) and eventually gave rise to *A. alces* approximately 100,000 years ago in Eurasia (Telfer 1984, Lister 1993). Hundertmark et al. (2002b) supported the relatively recent date by calculating conservative genetic divergence times (~85,000 years) for *A. alces* worldwide. Although *A. alces* appear in the earlier paleoecology record, they are rare among fossils in the late Pleistocene era (approximately 25-16 ka before present [BP]; Guthrie 1995).

The evolution and expansion of *Alces* distribution is likely driven by climatic change, especially climate reversals (Guthrie 1982, 1984, 1995). During periods of glaciation (especially glacial maximums), the climate was much colder and drier, forcing *Alces* to southern extents of the glaciers due to ice sheets and/or lack of habitat and forage for moose. There were at least two climate reversals during the Pleistocene with the last interstade starting about 12 ka BP (Guthrie 1995). This brought a warmer and moister climate that advanced the boreal forest north again and began the transitional phase from the Pleistocene to the Holocene eras (~13.5-11.5 ka BP; Guthrie 2006).

The transition from late Pleistocene to the Holocene (Holocene starting ~ 11.5 ka BP) brought great landscape changes. Pleistocene climates across northern Eurasisa and North America provided an environment conducive to grazers such as mammoths (*Mammuthus* spp.) and horses (*Equus* spp.) because of the preponderance of graminoids that thrived in the cold-dry climate (Ager and Brubaker 1985). Browsers such as moose were affected by the lack of high quality forage during times of graminoid dominance, which ultimately limited their distribution. Guthrie (1968) showed this scenario clearly through recovered fossils from Pleistocene sediments near Fairbanks, AK, where nearly 90% of all remains were from wooly mammoth (*M. primigenius*), giant bison (*Bison priscus*) and horse (*E. caballus*), all of which were grazers. Lister (2004) states that moose were restricted to the wooded phases of the Quaternary period. Pollen records show a clear landscape transition from a cold, dry steppe vegetation (graminoid dominate) to a warmer and more mesic landscape, promoting dwarf *Betula* spp., *Salix* spp., *Populus* spp. and *Picea* spp. (Ager and Brubaker 1985, Elias et al. 1996, Guthrie 2006), which all are good fodder for moose (Renecker and Schwartz 2007). Pollen records show that by 14 ka BP herbaceous tundra began to transition into shrub tundra as climate warming began and by 11 ka BP, *Populus* spp. started to increase and follow the succession (Ager and Brubaker 1985). Moose benefited from the new surge of nutritious forage and expanded rapidly during the Holocene, dispersing across the Bering land bridge on the forward edge of the boreal forest hardwoods (Guthrie 1995).

Moose (*A. alces*) followed the vegetation succession and made a single entry (<15 ka BP) into North America across the Bering land bridge (Geist 1998; Guthrie 1995; Hundertmark et al. 2002a, 2002b; Hundertmark and Bowyer 2004; Bubenik 2007) at a time when sea level was about 100 to 120 m lower than present, exposing Beringia. Flooding effectively separated Asia and North America approximately 11-10 ka BP (Ager and Brubaker 1985, Elias et al. 1996, Manley 2002, Guthrie 2004). One of the oldest *A. alces* fossils recovered and dated from Alaska is 12201 ± 85 yr BP from Fairbanks Creek, AK with most other fossils from Alaska younger (i.e., 10-8 ka BP; Guthrie 1990, Hundertmark et al. 2003, Guthrie 2006 with supplement material). Although Hundertmark et al. (2003) reported a moose radio carbon date of 32,250 yr BP and Porter (1986) reported a moose bone in a sediment layer with bison remains that were dated to be approximately 30,000 yr BP, both of these instances may have been from the much older moose-form *Cervalces*. The modern moose, *Alces alces*, apparently replaced *Cervalces latifrons* about 15,000 yr BP with very little coexistence, if any (Guthrie 1990).

Genetic analyses of moose show a lack of mitochondrial diversity worldwide indicating recent divergence and expansion including a small founding group into North America (Hundertmark et al. 2002b, 2003). Hundertmark et al. (2002b) estimated the effective population size of dispersing moose at 464 to 1856 female moose, supporting the small founder population hypothesis for North America. Unexpectedly, genetic results indicate that the far East Siberian moose (*A. alces buturlini*) is not the closest relative to the Alaskan moose (*A. alces gigas*), but rather that *A. a. gigas* is more closely related to the moose from East Asia and the Yakutia region of Russia (probably *A. alces cameloides*), from which all extant moose are now thought to originate (Hundertmark et al. 2002a, 2002b, 2003). Although the two moose subspecies on either side of the Bering Strait are genetically dissimilar, they exhibit very similar karyotype, morphology, and behavioral characteristics and are now thought to be the result of convergent evolution (Hundertmark et al. 2002b).

During the late Pleistocene and early Holocene, unglaciated areas within Alaska and Canada provided ice-free refugiums (Ager 1983, Ager and Brubaker 1985, Manely and Kaufman 2002) for moose as they continued dispersing south along the eastern front of the Rocky Mountain range where an ice-free corridor was open between the massive Laurentide and smaller Cordilleran ice sheets (Figure 2.1; Guthrie 1995, West 1996). The refugiums in central Alaska and Canada eventually developed into today's boreal forest (Figure 2.2; Viereck and Little 1972). Although the climate is conducive for boreal forest development, the moderating climate effects (including the effects on permafrost) of the Bering Sea and Arctic Ocean have left the extreme north, southwestern and Seward Peninsula areas of Alaska as lowland and upland tundra (Viereck and Little 1972, Viereck et al. 1992). Additionally, moose habitat in far western Alaska may have been suppressed by the Little Ice Age, approximately 1350-1900 AD (Yesner 1989, Mann et al. 1998, Britton et al. 2013). Current climate conditions (including fire within the boreal ecosystem) may be improving and/or expanding moose habitat (Viereck 1973, Chapin et al 2006).

Recent genetic studies of moose within Alaska show some genetic structure between moose in southeast Alaska and the rest of the state (Hundertmark et al. 2006, 2003, Schmidt et al. 2009). These results suggest that moose from Canada are genetically older than moose in Alaska, indicating that the current moose in Alaska are more recent and likely dispersed from Canada (Hundertmark et al. 2002a, Schmidt et al. 2009). This contradicts an expectation that the moose in the area of original dispersal across the Bering land bridge would be older than the eastern front of the Holocene expansion. One hypothesis is that moose expanded through Alaska and did not completely establish populations (or did so, but not sustainably), thus creating a void for moose to disperse westerly back into Alaska from Canada with the expansion of the boreal forest (*Picea* pollen appears in west coastal sites about 5.5 ka BP; Ager and Brubaker 1985). Evidence of suboptimal habitat during the late Pleistocene in interior Alaska is supported by Guthrie's (1968) findings that most faunal remains were from grazers and only an average of 1.5% of the remains from several mining locations were identified as moose, a concentrate browser (Hofmann 1985).

Once established in Alaska, moose dispersed into suitable, or even fringe, habitats across the state. Genetic variation suggests that of the moose populations in Alaska (with the possible exception of southeast Alaska), the oldest are from the interior, centralized around the Tanana Flats region. These then dispersed west towards the Seward and Alaska Peninsulas in a stepping-stone fashion (Schmidt 2007, Schmidt et al. 2009). It is hypothesized that the Alaska Peninsula is a population sink receiving genetics from several different populations across the state (Schmidt 2007). Moose in the Yukon-Kuskokwim region (Figure 2.3) were not included in the genetic analyses, however, from a least-cost path analysis, the likely sources are from the Koyukuk (middle Yukon River) and the Alaska Peninsula populations (Schmidt 2007).

The Yukon-Kuskokwim Delta (YKD) region was not glaciated, however a glacial island covered the Kilbuck Mountains (i.e., Ahklun Mountains) to the south during the late Wisconsin period (Figure 2.2; Hoare and Coonrad 1959, Ager 1983, Manley and Kaufman 2002, Kaufman and Manley 2004). Small remnant, but shrinking, glaciers still exist there today (Walsh et al. 2007). Pollen records from three lakes within the Yukon Delta suggest that the vegetation there followed a similar transitional pattern as in other parts of the state during the early Holocene, but core samples indicated a range retraction of *Populus* spp. during the period of 10 ka to 7.5 ka BP (Ager and Brubaker 1985), which could indicate a range retraction for moose, as well.

Information on the presence of moose in the vicinity of the YKD since their arrival in Alaska is scarce. Evidence from archaeological sites in interior Alaska (eastern Beringia) suggest that humans hunted moose in low numbers every millennia since moose arrived during the late Pleistocene (Potter 2008). However, few archaeological sites with faunal inventories exist on or near the YKD. Ackerman (1996, 2001) surficially excavated sites on Nukluk and Spein mountains, which were not glaciated and are on the western foothills of the Kilbuck Mountains about 80 kilometers southeast of present day Bethel. He found several stone artifacts, but no datable bone material. A piece of radiometric-dated charcoal from the site showed occupancy around 10,040 yrs BP along with stone projectiles indicating that the area was used for hunting (especially along this glacial boundary, a corridor for migrating animals). Ackerman (1985) also describes his archeological expeditions into the headwaters of the Kanektok, Eek, Kwethluk and Kisaralik Rivers that were glaciated during the late Pleistocene, where he recovered many stone artifacts that indicated a continuous occupancy of this region starting 8 to 6 ka BP to present day. Although no faunal remains were recovered at these sites, it was suggested from the recovered stone projectile technology and evidence of fencing that caribou were likely the most important game animal hunted in the area (Ackerman 1985). About 275 kilometers northeast of Spein Mountain and across the Kilbuck mountains south of the Kuskokwim River, an archaeological site at the Lime Hills Cave (occupied by both humans and carnivores during different periods) produced many mammalian bone fragments where osteometrics indicated a few moose elements among many caribou bones dating to the late Pleistocene and early Holocene (~14 to 8 ka BP; Ackerman 1996, Endacott 2008). Interpretation of faunal remains (or lack of) at archaeological sites could be misleading if the hunters boned-out meat at the kill site to facilitate transport (Binford 1978, O'Connell et al. 1988); or as a result of cultural underpinnings such as throwing bones into rivers. This was reported for the residents of Crow Village along the Kuskokwim, in order to prevent dogs from chewing on them because dog chewing would offend the spirit of the animal and make it more difficult to kill that species again (Oswalt and VanStone 1967).

Archaeological sites of more recent settlements or occupied sites can give insight into the diets and local fauna during the time of occupation. The westward expansion of moose in relatively recent times is demonstrated by Hall (1973) who reported moose remains from archaeological sites in northwestern Alaska from Cape Krusenstern on the Bering Sea coast, and from the Kobuk River near the Seward Peninsula, dating from 1000 to 1400 AD. In southwest Alaska, an archaeological investigation of more recent occupation (1350 to 1630 AD) is currently ongoing near the village of Quinhagak just south of the mouth of the Kuskokwim River of the YKD. The reports of faunal remains have yet to be published, but isotopic analyses of human diets at the site (from human hair and recovered faunal remains) indicated that no moose remains have been recovered nor were moose evident in the native diet based on isotopic analyses, while caribou and possibly muskoxen were (Britton et al. 2013).

Reports and diaries recounting early expeditions into southwestern Alaska provide valuable information about what early explorers found for resources including wildlife (mainly for economic potential such as furbearers and food resources). Early Russian explorers were some of the first Caucasians to enter this region of Alaska. Petr Korsakovskiy led an expedition from Kodiak, AK to the Togiak and Nushagak Rivers (Fort Alexander: Alexandrovski Redoubt) region to explore the country north of Bristol Bay and to open new areas to the fur trade during the summer of 1818 (VanStone 1988). His travel journals indicated that they ate an abundance of caribou, seal (*Phoca* spp. and *Erignathus barbatus*), salmon (*Oncorhynchus* spp.), beaver (*Castor canadensis*) and ducks, but did not mention hunting or eating moose (as they were always hungry, they would not have passed up a moose). They did describe some of the area in the upper reaches of the Togiak and Nushagak Rivers as having willow, poplar, birch and spruce indicating that there was adequate moose habitat available then.

During the mid-1800s, another Russian explorer, Lieutenant Lavrentii Alekseevich Zagoskin, travelled to the Yukon-Kuskokwim region in 1842-1844 under orders of the governor-general of the Russian-American Company, Ferdinand Petrovich Wrangell. Wrangell sent Lieutenant Zagoskin to explore Russia's American colony in pursuit of ethnological and scientific knowledge (Zagoskin 1967). Lutz (1960) summarizes Zagoskin's journals of his expeditions (as related to accounts of moose) on the Yukon and Kuskokwim Rivers. In these interpretations, Zagoskin mentions that his party found a dead moose killed by a flood on the Yukon well above Nulato; he also noted that natives hunted moose in the middle interior along the Yukon (near present day Ruby; Figure 2.3) and on the lower Koyukuk and Innoko Rivers. Zagoskin also reported that there was good habitat and forage for moose on the middle Kuskokwim River (near present day Sleetmute) where natives killed caribou and moose (Lutz 1960). Also, from translations in Zagoskin (1967), the Lieutenant states: “The land [*Innoko River area*] is rich in beaver and otter; on the tundra the numberless herds of deer [*caribou*] and American elk [*moose*] find plentiful food;…”.

In 1869, Captain C. W. Raymond, was ordered up the Yukon River to obtain the coordinates of Fort Yukon and to determine if the Hudson Bay Company was still operating on American Territory (Alaska was purchased for 5 cents/hectare [2 cents/acre] from Russia and became an American Territory in 1867). In his report to the 42nd US Congress, Raymond (1871) mentioned that moose were abundant along the upper Yukon, but were rarely seen below Nulato; however, it was reported that a moose was killed on an island near the mouth of the Yukon in 1869 (Raymond 1871).

Eleven years later in 1880, E. W. Nelson, a Signal Service observer based in St. Michael, set out to explore the lower Yukon River and describe its people. He noted that moose were very scarce, but hunted by natives during winter on snowshoes in deep snow and in summer when moose swam across the Yukon River (VanStone 1978). Nelson also mentioned that most natives had muzzle-loading rifles and many had obtained breech-loading rifles. The increased efficiency of the rifles (especially the breech-loader) for hunting is thought to have had significant impacts on game. In the same year as Nelson’s trip Ivan Petroff, of the U.S. Census Office, made a trip to Alaska in order to conduct the first official census in Alaska and to gather information on its people, industries and resources (Petroff 1884). In his report, he made comments about moose in southwestern Alaska, specifically in the Kuskokwim River region, and stated: “Game and fur-bearing animals do not abound in this section of river valley [*near*

Kolmakovsky Redoubt, which was near the confluence of the Holokuk River up river of present day Aniak; Figure 2.3], as it is an old hunting-ground, and has been drained by constant traffic for more than half a century." He also writes about his impression of the lower Kuskokwim River: "According to our standard the people of the lower Kuskokvim [*author's spelling*] river and of the tundras are very poor indeed, their country offering nothing but seals in the sea and the river, myriads of minks, some foxes, the brown bear, and a few moose" (Petroff 1884; p 13).

In the late 1800s, Spurr (1900) reported on his reconnaissance to southwestern Alaska during 1898 for the U.S. Geological Survey. He noted that after the upper Kuskokwim River emerges from the mountains (near present day Aniak; Figure 2.3), it flows through an area that, in his opinion, apparently supported little life. However, he did note that horns [*antlers*] of moose, caribou and sheep were found at a number of native camps further up river in the mountains. Additionally, Spurr (1900) mentions that on, the Kuskokwim flats, the natives had meat from moose, but not in large quantities. Furthermore, it is mentioned that, even though there was good habitat around, the supply of game was extremely scarce and for hundreds of kilometers they only found a scattering of moose sign.

During the mid-1930s, Kwethluk village elders recalled first seeing moose in the headwaters of the Kwethluk, Kisaralik and Eek Rivers and that moose were not seen often in the lower Kuskokwim River until the 1940s (Coffing 1991), similar to the Nushagak River region (VanStone 1967) from which some moose may immigrate to the Kuskokwim River from (Coffing 1991). Local residents along the Johnson River, which runs between the Yukon and Kuskokwim rivers near Bethel, recalled first seeing moose in the upper reaches of the Johnson River around 1941, although they were rare until the late 1950s in that region (Andrews 1989). Cady et al. (1955) were conducting geologic surveys to identify potential mineral resources of the central Kuskokwim region (above Aniak) during the period of 1941 to 1945. They traversed many creeks and tributaries of the Kuskokwim from Aniak to Sleetmute and reported that moose were highly sought by the hunters in the region and were plentiful such that the small village populations in the area were able to get as much moose as was legally allowed (Cady et al. 1955). Also, in the 1950s anthropologist Wendell H. Oswalt conducted research regarding the historical perspective of ethnic groups and human migration theory along the Kuskokwim River (Oswalt 1962). In doing his research, Oswalt gained a perspective of the game in the area from his own observations, as well as from the local residents. He reported that, within the wooded [*boreal forest*] interior, moose, bear (*Ursus* spp.), marten (*Martes americana*), river otter (*Lutra canadensis*), and beaver were the most important game for the people of the region; however, he went on to say that these species were increasingly rare upon approaching coastal tundra and only occurred as strays except for the land otter (Oswalt 1962). Although somewhat contradictory, he points out an overarching change in game distributions of caribou and moose, with moose extending its range into the tundra region in recent times (i.e., 1950s; Oswalt 1962).

Bishop and Rausch (1974) described moose population fluctuations in Alaska and indicated that moose populations increased throughout most of Alaska between 1940 and the early 1960s; an increase enhanced by extensive wildfires in the 1940s and 1950s and by relatively mild winters in the 1950s (Bishop and Rausch 1974). Moose populations began to stabilize or decline in the 1960s and early 1970s in many areas of interior Alaska, mainly due to relatively severe winters in the early 1970s (Bishop and Rausch 1974).

In their description of moose distributions and habitats in Alaska, LeResche et al. (1974; p 148 & 153) stated “To the best of our knowledge the Yukon-Kuskokwim Delta has never supported more than the occasional wandering moose.” And they go on to say “Moose distribution apparently has not changed appreciably over the last 20 to 30 years in the Yukon-Kuskokwim Delta area, where occasional wanderers are the rule, …”. Furthermore, in his description of the history of moose in Alaska, Coady (1980; p 65) states that “On the delta region of the Yukon and Kuskokwim rivers a moose population has yet to become established in spite of favorable habitat and weather conditions and low number of predators. An extremely mobile human population occupies inland areas, and the killing of moose whenever they are encountered has prevented a population from becoming established and growing in this region.”.

Local oral history from the region describes moose distributions, abundance and arrival on the YKD. The ANCSA [Alaska Native Claims Settlement Act] 14(h)(1) oral history archives (housed at the BIA ANCSA Office in Anchorage, AK) of recorded interviews from the late 1970s to late 1980s of native elders across the YKD offer a wealth of historical perspectives. These recordings capture multiple aspects of the Yupik culture, way of life, and traditional oral histories. Alexandra Akaluk of Marshall [village] (recording 82RSM013) notes that moose started appearing in that area of the Yukon River around 1950. Also, recording 82RSM020 reports that the site of Kassigluq (on the Gweek River-a tributary of the Kuskokwim River near Bethel) was “still used for moose hunting” in 1982.

To summarize historical perspectives, the occurrence, distribution and abundance of moose in the Yukon-Kuskokwim (YK) region has varied over the last 200 years. In the early 1800s, moose were relatively scarce throughout the YK region including areas to the south along the Nushagak River even though adequate habitat was available. In the mid-1800s, Russian explorers reported that moose were plentiful, in particular, in the upper (central) Kuskokwim and Yukon Rivers (Nulato) of the interior boreal forest. However, in the late 1800s, moose were still very scarce on the lower reaches of the YK rivers, and were becoming less abundant in the upper-central portions of those rivers. The reduction in populations of moose, caribou and other game is thought to be partially caused by the entry of firearms into the area allowing more efficient harvesting of game without restrictions. The effectiveness of the firearms when used by the local people created such a concern that the importation and sale of breech-loading rifles and ammunition to natives was prohibited by law in 1870, specifically for the islands of St. Paul and St. George, presumably to protect the fur seal interests. In 1875, the prohibition was extended to the mainland Territory of Alaska with the law undergoing various changes throughout the 1880s, with each iteration apparently excluding natives from owning a rifle (U.S. House of Representatives 1889). However, these rifles could still be bought or traded as contraband in trading posts along the Yukon and Kuskokwim before the law was repealed in 1896 (Swineford 1888; VanStone 1978). The early and mid-1900s experienced a recovery of moose populations again in the upper-central portions of both the Yukon and Kuskokwim rivers. The recovery and expansion of moose may have been a response to extensive and severe wildfires in the eastern interior forests and upper Kuskokwim and central Yukon regions during the first two decades of the 1900s (possibly due to increased human-caused fires from the influx of miners at this time; Todd and Jewkes 2006). During the 1920s and 1930s, moose expanded throughout the upper Kuskokwim and Yukon regions (Charnley 1983). By the early 1940s, moose were well established between Aniak and the upper Kuskokwim and Yukon rivers (Oswalt and VanStone 1967, Charnley 1983, Brown et al. 2013). Moose populations peaked between the late 1960s and early 1970s following yet another series of extensive wildfires in the 1940s and 1950s, particularly in 1957, the second largest fire year recorded (2004 is the largest fire year; Todd and Jewkes 2006 Figure 2.4). However, severe winters in 1971 and 1972 dramatically reduced moose populations in many parts of the state (Bishop and Rausch 1974) and moose in the central Kuskokwim and Yukon region recovered slowly. Tuluksak village residents reported that moose along the Tuluksak River were increasingly scarce in the 1970s to early 1980s (Andrews and Peterson 1983). Wildfire with subsequent seral succession has a major positive influence on moose habitat and thus abundance within the boreal forest of Alaska, while unusually deep snow has a significant negative influence (Bishop and Rausch 1974). Moose populations will continue to respond to ecological and management changes (e.g., harvest management and fire management) and will continue to expand into new areas if given favorable habitat conditions and a reprieve from excessive harvest.

Subsistence and Resource Management

Moose have been an important subsistence resource in Alaska since the late Pleistocene (Potter 2008), and may have become more important to humans in the last 400 years based on archaeological remains (Yesner 1989). Today, moose are a highly valued resource and have substantial recreational and economical value in Alaska for both consumptive and nonconsumptive uses (Snepenger and Bowyer 1990, Ballew et al. 2006, Timmermann and Buss 2007, Titus 2007, Boertje et al. 2009, Titus et al. 2009, Paragi et al. 2010). There are an average of 7,368 (range 5,999 to 8,689) moose reported harvested annually in Alaska from 1983 to 2012 (ADFG 2014a). Although a variety of factors can influence the success of moose hunters (Schmidt et al. 2005), average harvest success over the last 30 years has been 25% (Avg. = 29,425 hunters/year; ADFG 2014a). Alaskans harvest a significant amount of wild game annually and especially in some rural communities such as Akiachak (on the Kuskokwim River) where nearly all the non-fish protein consumed is from moose and caribou (i.e., 100 kg/person/year; Titus et al. 2009). Subsistence foods make up a large proportion of total diet of Alaskan natives living in rural villages and are extremely important because not only is consuming subsistence food part of a cultural identity, it is an economic necessity for many people (Ballew et al. 2006) especially when gasoline and heating fuel costs $1.8–$3.7 / liter ($7-$14/gallon) or more in many rural communities (personal experience). Nevertheless, the majority of the State’s populace is urban and even though significant numbers of moose and other game are harvested each year in Alaska, most of the red meat consumed by Alaskans is imported into the state (Paragi et al. 2010).

On the Yukon-Kuskokwim Delta, subsistence hunting and gathering is still a way of life (Weekley et al. 2011, Naves 2012). Moose are utilized for subsistence along the Kuskokwim River from the upper-central region (Georgetown to Stoney River; Jonrowe 1980), central region (Chuathbaluk and Sleetmute; Charnley 1983), lower-central region (upper Johnson River and Portage Lakes; Andrews 1989), and the lower region of the Kuskokim River (Tuluksak , Kwethluk, Akiachak; Andrews and Peterson 1983, Coffing 1991, Coffing et al. 2001, Brown et al. 2013). On the lower Yukon region, moose have been increasingly harvested amongst the lowest nine villages along the Yukon (Weekley et al. 2011). The lower Yukon communities used to boat far up-river (into hunt Unit 21E; Figure 2.3) to hunt moose in 2000, but now can hunt close to their home (in Unit 18) because of the increased moose population that has recently exploited the area. Moose harvest in Unit 18 (the YKD region), has increased 10-fold from the period of 1983 to 2012, which indicates an increase of moose within the lower Yukon and to a lesser extent, Kuskowim River drainages (Perry 2010, ADFG 2014a).

Although moose are expanding into the YKD, the human population is also expanding. At the time of contact with Europeans (1780-1840 AD), there were about 13,000 people on the YKD (Sandberg 2013). Today, there are approximately 25,300 people in 47 villages on the YKD (Bethel and Wade Hampton Census Areas 2012 estimates; ADLWD 2013), approximately double the population at time of European contact. This region has the highest birth rates in the state (Wade Hampton Census area: 3.3 births/100 people) and is composed of over 80% Alaskan Native heritage (ADLWD 2013). The substantial increase in population on the Delta has increased subsistence use and needs. The high demand for subsistence resources, mainly fish and game, makes resource management more challenging.

Wildlife management in Alaska has its challenges that mainly arise from its labored past leading to today's dual fish and wildlife management system between the State of Alaska and the U.S. Government (Regelin and Franzmann 1998). During the State's early years leading to statehood, the people of Alaska adopted and ratified Alaska's constitution in 1956, which was adopted and put into force when the Alaska Statehood Act (Public Law 85-508, 72 Stat. 339, July 7, 1958) was ratified by Congress in 1958 (allowing the State to select 104 million acres from the Territory) and was formally admitted as a state by a proclamation of President Eisenhower in 1959. The Statehood Act adopted the State's constitution as the governing document including provisions to reserve fish and wildlife for common use by all Alaskans (Article VIII, § 3, Constitution of the State of Alaska, 1956; McBeath 1997). The Statehood Act also transferred management of the state's fish and wildlife to Alaska, except for special provisions regarding refuges or reservations set aside for wildlife protection at that time (Pub. L. 85-508, § 6 (e), Alaska Statehood Act, 1959).

Following statehood, Alaskan Natives embarked on a historically large land settlement with the U.S. Government. The Alaska Native Claims Settlement Act of 1971 (ANCSA; US Code Title 33, Chapter 43; Public Law 92-203; December 18, 1971) allowed selection of 44 million acres of land (still being conveyed today) by Alaska Natives in addition to the $962.5 million settlement for lands that the U.S. Government previously claimed when it bought the Territory from Russia. With this Act, "…any aboriginal hunting or fishing rights that may exist, are hereby extinguished" (Public Law

92–203, § 4, (b), Dec. 18, 1971, 85 Stat. 689.). This section of the law gives authority of fish and wildlife resource management and regulation on settlement-lands to the State of Alaska with no subsistence preference as per the state constitution. However, the State recognized that subsistence is an integral part of living in Alaska and subsequently adopted a subsistence law in 1978. It states that whenever it is necessary to restrict the taking of game, subsistence *use* shall be the priority use, but the law did not define subsistence *users* (Chapter 151, § 5, SLA 1978).

Two years later, Congress passed the Alaska National Interest Lands Conservation Act of 1980 (ANILCA; US Code Title 16, Chapter 51, Public Law 96-487, December 2, 1980). This Act set aside an additional 40.46 million hectares (100 million acres) of land in Alaska for the purpose of conserving land that has "…nationally significant natural, scenic, historic, archeological, geological, scientific, wilderness, cultural, recreational, and wildlife values…" (16 USC 3101 (a)), and "…to provide the opportunity for rural residents engaged in a subsistence way of life to continue to do so…" (16 USC 3101 (c)). Additionally, this law sets preference for subsistence users defined as "rural residents", who only need to have domicile in a rural community to qualify for subsistence rights on federal lands (16 USC 3114, § 804). ANILCA requires federal management of public lands in Alaska in order to ensure the subsistence priority. However, federal management may be supplanted by the state so long as the state enacts and implements subsistence laws that give preference to rural residents according to Title VIII of ANILCA. By 1986, the State of Alaska amended the 1978 Subsistence Law and now specifies subsistence users as rural residents (Chapter 52, § 10, SLA 1986) to comply with Title VIII of ANILCA. In 1983, non-rural residents filed a lawsuit to challenge the State of Alaska's 1978 subsistence law, and later amended their lawsuit to reflect the State's 1986 rural preference amendments to the subsistence law. In 1989, the Alaska Supreme Court ruled in *McDowell v. State of Alaska*, 785 P.2d 1 [Alaska 1989], that the rural preference in the 1986 subsistence law violated several state constitutional clauses including the common use and equal rights clauses. Accordingly, the Alaska Supreme Court repealed the 1986 preference clause, citing it unconstitutional, which subsequently forced the State out of compliance for managing fish and game on federal lands according to Title VIII of ANILCA.

The *McDowell v. State of Alaska* decision forced the State of Alaska to drop its rural subsistence priority and compelled the Secretaries of Interior and Agriculture to assume management authority over subsistence uses on public lands in Alaska on July 1, 1990. The Secretaries created the Federal Subsistence Board (FSB) to oversee subsistence management on federal public lands. The expedited establishment of a new management division did not allow for expedited regulation drafting and ratifying and, therefore, the FSB published the "Temporary Subsistence Management Regulations for Public Lands in Alaska" in the Federal Register (55 FR 27114) on June 29, 1990; ironically the Secretary of Interior temporarily adopted the State's existing subsistence regulations (Case and Voluck 2012). After the Board was organized and actively operational, it published the "Subsistence Management Regulations for Public Lands in Alaska; Final Rule" in the Federal Register (57 FR 22940) on May 29, 1992. This effectively and officially created a dual management system for fish and game between the State and Federal Governments in Alaska.

Evolution and Success of Dual and Co-Management

The passage of ANILCA and the repeal of the rural resident-clause from Alaska's Subsistence Law created the now contentious dual management system used to manage Alaska's fish and wildlife (Caulfield 1992). Dual management, in the context of Alaska's fish and wildlife, is defined here as the split of management jurisdictions for the purpose of managing subsistence uses and resources such that federal agencies manage subsistence resources for rural residents on federal lands, and the State of Alaska manages resources on non-federal lands for all Alaskans (Figure5). The simple phrase of "rural resident" created a complicated, contentious, expensive, inefficient, and duplicative "dual" management system to manage fish and wildlife in Alaska (Caulfield 1992, Thornton 2001, McNeeley 2012, Fleener 2013). Federal management is structured from ANILCA and through an eight- member Federal Subsistence Board (FSB) comprised of the regional directors of five federal agencies, and three public members appointed by the Secretaries of the Interior and Agriculture: two represent rural subsistence users and one is the Federal Subsistence Board chairman (36 CFR ch II § 242.10). The Secretaries have delegated the authority to the Federal Subsistence Board to manage fish and wildlife for subsistence uses on federal lands, which are managed by several federal agencies (55 FR 27114). The Office of Subsistence Management (OSM) is a separate division within the U.S. Fish and Wildlife Service that supports the Subsistence Board and is the main point-of-contact for the ten Regional Advisory Councils (RAC), each of which has 10-13 members of the public appointed by the Secretaries of Interior and Agriculture. The Advisory Councils provide advice and recommendations to the Federal Subsistence Board about subsistence hunting, fishing, and trapping issues on Federal lands that were brought forward and discussed by local users (usually in the form of proposals to change regulations). The Board discusses the issues in the proposals brought forward and determines actions through a voting process. These decisions or regulation changes are then handed back to the users (Figure 2.5). The Federal Subsistence Board meets every two years, but will convene as needed for Emergency and/or Temporary Special Action Requests (50 CFR Part 100, Subpart B, §100.19).

State management is structured through Alaska's Constitution, predating the federal system, guiding a seven-member Board of Game (BOG) that oversees and directs the Alaska Department of Fish and Game (ADFG) to manage game on state, private and corporation lands (ADFG 2014b). The state has a separate Board of Fisheries to direct management of fish. The ADFG Subsistence Division is the point-of-contact for the 82 local Advisory Committees (AC) across the state where each committee is comprised of 5-15 members appointed or confirmed by the joint Boards of Fisheries and Game (5 AAC 96.060). The Advisory Committees provide a local forum to discuss fish and game issues and to provide recommendations to the respective Boards. The BOG meets every year to set hunting, fishing and trapping regulations for the state of Alaska (Figure 2.5).

With different management boards on differing review cycles, there is a continuous effort to "align" the state and federal policies and regulations for the benefit of the user groups. It is less confusing when there are sufficient resources for everyone, in that the State hunting regulations will apply to all state, private, and federal lands, but when there is a resource shortage, the federal agencies will take over the management on federal lands for rural subsistence users. Alaska is a pioneer of the dual management system, but subsistence priority continues to be a source of conflict in Alaska between state and federal wildlife management agencies (Thornton 2001, Fleener 2013).

Co-management can help bridge the gap between resource users and management agencies. Co-management is defined here as the shared decision-making process, formal or informal, between a government authority and an indigenous user group for managing fish and wildlife (Case and Voluck 2012). Even though Alaska natives (mainly through regional corporations set up by ANILCA) only own 10% of Alaska’s land mass, there is significant opportunity and desire by Alaska natives to work cooperatively with agency wildlife managers in the form of co-management especially regarding subsistence resources (Worl 2013). In practice, different kinds of co-management exist from informal consultations to full and equal sharing of management authority. Co-management helps resolve resource conflicts and builds partnerships for conservation and management between local residents and government agencies (Spaeder 2005). For example, conflict resolution was demonstrated for the management of the Kilbuck Caribou herd on the Yukon-Kuskokwim Delta in the mid-1980s to early 1990s (Spaeder 1997, 2005).

With its extensive subsistence population and federal lands, the Yukon-Kuskokwim Delta is a prime example of positive dual and co-management between state, federal and native organization for the management of moose within the region. In the late 1980s, on the lower Yukon River, there were growing concerns among local residents that there were no moose in this area of the Yukon and the cost of traveling up river to hunt moose in Unit 21E (Figure 2.3) was becoming excessive. The Lower Yukon

Advisory Committee (a subsistence committee that advises the State Board of Game on fish and wildlife management issues) consolidated several local communities' concerns about the low density of moose along the lower Yukon, especially from Mountain Village down river to the mouth. These concerns were put forth in a proposal designed to increase moose numbers by imposing a moose hunting moratorium in this area for a period of five years. The ADFG and USFWS biologists conducted an intensive aerial moose survey (minimum count) during the winter/spring of 1988 and reported zero moose observed in the entire survey area from Mountain Village and down river to its mouth (Perry 2010). The proposal by the Advisory Committee was put forth to the Alaska Board of Game in 1988 and led to the closure of moose hunting in this area (ADFG 1988). There is about one-third federal land in this area managed by the Yukon Delta National Wildlife Refuge (YDNWR), but this closure was prior to the *McDowell* decision; therefore, no federal regulations had to be addressed.

After the fall season of 1992, the five-year moratorium would have expired; however, there was no sunset clause written into the regulations. Subsequently, proposal WP93-44 was submitted to the Federal Subsistence Board (FSB; formed in 1990 and active beginning 1992) requesting that a moose season be established again. State and federal comments recommended keeping the season closed due to the low abundance of moose as last surveyed in 1992; although low, there was an increase. There was both support for opening the season and for keeping it closed from local residents. The FSB discussed the proposal and acknowledged local opposition to opening a season, as documented in the meeting transcripts: "Rejecting the proposal [*keeping the season closed*] would respect the local consensus in favor of the moratorium…" including the recommendation to keep the season closed by the Lower Yukon Fish and Game Advisory Committee. The proposal was rejected and the season remained closed (FSB 1993).

One year after the “five-year” moratorium was supposed to expire, a proposal entitled “Unit 18 Petition” was submitted to the BOG at their March/April 1994 meeting requesting that the moose season be opened again starting on September 5, 1994 with a bag limit of one bull moose. This proposal carried and a season was opened after being effectively closed for nearly seven full years (9/21/1987-day after the last open season to 9/5/1994-the day season opened again; ADFG 1994). Since the FSB was operational at this time, it had to open a season and set regulations for federal lands as well. Proposal WP94-45 was put forth to the FSB at their April 14, 1994 meeting to establish a federal moose season on federal lands. Transcripts of the meeting detail the success of this newly formed dual management system working with all cooperating parties by acknowledging that the: “Local residents have recognized the value of temporarily suspending hunting as a means of promoting more rapid growth in the local moose population. The present moratorium… results from a local initiative of one of the communities in the lower Yukon River in 1988.” The Board continues by recognizing that: “…it is an opportunity for the Federal Subsistence Board… to endorse the conclusions of a cooperative management planning program conducted in this case by the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, and the local villages found on the lower Yukon River.” The proposal passed unanimously and a season on federal lands was opened for the lower Yukon River (FSB 1994).

The lower Kuskokwim region has a greater human population than the lower Yukon (15,563 and 4,620 people, respectively, in 2010; ADLWD 2013) and a substantively higher demand for subsistence resources (i.e., fish, caribou and moose). The lower Kuskokwim River was experiencing the same human-induced barrier to the ability of moose to establish as the lower Yukon experienced prior to the hunting moratorium there. Although the Kuskokwim area had good and unoccupied habitat available to moose (but not as extensive as on the Yukon) and low predator numbers, very few moose were estimated to be in the area between Kalskag and Bethel during the 1990s (Perry 2010).

Area biologists (state and federal) again decided to embark on another dual and co-management initiative in order to increase the moose population along the lower Kuskokwim River and its tributaries. Since only a few local villages initially supported this initiative, there had to be extensive outreach by the management agencies. This monumental effort was led by Roger Seavoy, the state area biologist at the time. Roger learned from Randall “Randy” H. Kacyon (the previous area biologist, who was killed in a plane crash conducting moose surveys on the Yukon River on November 30th, 1996) that it takes many conversations with local residents to establish trust and confidence in an idea and it is necessary to really listen to the concerns of the residents. One of the most successful outreach programs the YKD had ever initiated was Randy’s “moose circle” campaign (developed in conjunction with Bob Stephenson of ADFG). It was first utilized in the Yukon River region (during and after the moratorium there) to bring awareness of the reproductive potential of a single cow moose and the positive effects of not shooting a cow versus a bull moose on overall population growth. This campaign worked so well on the Yukon, Seavoy used it in the Kuskokwim region. The Kuskokwim moose discussions started in 1996 when local residents made requests for a strategy to improve moose numbers along the lower Kuskokwim. Local conservation efforts on the Kuskokwim were initially slow until March 2000 when local chairs of the Advisory Committees and Councils were invited to develop a strategy for the conservation of moose on the lower Kuskokwim River. By 2001 and into 2002 a strategy was drafted and approved for circulation (ADFG-Bethel office unpublished files). The local wildlife agency biologists and managers went to all the affected villages along the lower Kuskokwim River and explained the situation, the potential solutions and outcomes, and to just listen to resident’s concerns and ideas on how to grow the moose population. A resolution for conserving the lower Kuskokwim moose population was promoted and offered to villages to sign (ADFG-Bethel office unpublished files). Support was slowly established by starting with known villages that supported the resolution and continued to build momentum and critical mass over the next several years. One of the most beneficial factors that led to support was the weight of other villages’ support and the fact that the discussions were initiated in Yupik (the regional language), which showed sincerity in the planning efforts (Seavoy, personal communication). Additionally, support was gained by flying village leaders to the Yukon River area where moose were expanding to show the leaders many moose in that area, and then they flew back to the Kuskokwim River to show leaders that it was difficult to find many, if any, moose during these contrast flights. These flights were initially intended to obtain contextual population data for the Federal Subsistence Board between the two river systems (Seavoy, personal communication), and subsequently drove home the message that the

Kuskokwim was “empty” and the Yukon was “full” of moose. Nearly all the affected villages signed the resolution in support of the moose conservation strategy, which included a moratorium (ADFG-Bethel office unpublished files).

The local state Advisory Committee lobbied actively for a moratorium on the Kuskokwim as they did for the Yukon River moratorium. As described by Roger Seavoy; Robert Moore, former chairman of the Lower Yukon Advisory Committee from the village of Emmonak, stated before the moratorium on the lower Yukon that: “if we saw a track in the morning, it would be pot roast by supper time”, and then stated that after the moratorium, “now we don’t shoot moose out of season, or cows/calves, and we have a moose track on every sand bar”. This gave testament to the effectiveness of the moose hunting moratorium and the extensive outreach by Randy Kacyon on the lower Yukon River.

Although moose densities along the lower Kuskokwim were extremely low, the people on the Delta could still hunt moose along the upper Kuskokwim and Yukon Rivers, hunt caribou along the Kilbuck Mountains, and catch fish from the Kuskokwim River in order to meet subsistence needs. Seeing the success of recent hunting moratoriums for moose (lower Yukon and Togaiak NWR to the south) and even for waterfowl on the YKD (Zavaleta 1999), and having an alternate protein source, local residents were more accepting of the moratorium, especially if it meant being able to eventually hunt moose close to home.

After seven years of discussions, education, and communication among the local communities of the Kuskokwim, Proposal No. 2 was put forth by the Lower Kuskokwim Advisory Committee at the November, 2003 Alaska Board of Game meeting. It proposed to close moose hunting and enact a moratorium within the lower Kuskokwim River drainage in Unit 18 for a period of five years or if the population reached 1000 moose (Figure 2.3; ADFG 2003). The BOG recognized that the harvest was not sustainable and had prevented population growth, as well as recognized the extensive local support for the moratorium from the villages and the Lower Kuskokwim Advisory Committee; the proposal carried (ADFG 2003).

Under the dual management system, the actions by the state BOG for a hunting moratorium only applied to the non-federal lands making it necessary for similar regulations to be enacted on federal lands. Therefore, proposal WP04-51 was put forth at the Federal Subsistence Board meeting on May 19, 2004 (FSB 2004). The proposal mirrored the one previously passed by the BOG in which the proposal would create a moose hunting moratorium on federal lands within the lower Kuskokwim River drainage for a period of five years or if 1000 moose were estimated in the survey area. Discussions by the FSB led to minor boundary modifications (to match that of the State's proposal) and then the FSB passed the proposal as amended unanimously (FSB 2004).

Community outreach regarding the importance of a moratorium did not stop with the closing of the moose hunting season. Illegal harvest of moose was still a factor and more detrimental to population growth was the illegal taking of cow moose. The first year of the moratorium was effectively not a hard closure without take. However, as the local residents started to police themselves or add social pressure to the illegal taking of moose, there was a drop in illegal harvesting. This again showed significant support by the majority of the local residents for the moratorium and recognizing the possibilities of providing moose meat for future generations. The moratorium's dual and co-management efforts by the ADFG, USFWS and local residents were working based on the increased moose densities. The population estimate in 2004 (start of the moratorium) was 0.03 moose/km^2 (70 moose) in the survey area from Kalskag to Bethel (2251 km^2) and increased to 0.23 moose/km^2 (515 moose without a sightability correction factor) in the same survey area by 2008 (Perry 2010). This was a significant increase in density and many local residents were seeing moose near their homes for the first time. This was both positive and negative, however. It was positive because the moratorium was working, but negative because many people thought the work was done and hunting should resume immediately.

In 2008, discussions about ending the moratorium were increasing among local residents and the local advisory committees. The five-year clause would expire in 2009, but the moose population was still below the 1000 moose objective in the original proposals. The debates started to form around either opening the season at the five-year expiration or extending the closure for at least another year. The local land managers modeled scenarios to illustrate what the effects on the moose population if either proposal were embraced. This was co-management at its most developed; the local residents were now in complete control of either ending the moratorium after the five-year closure or extending it if they chose to do so. Discussions continued from the individual resident of the Kuskokwim all the way to the Federal Subsistence Board. The FSB meeting on May 1, 2008 brought forth discussions regarding the potential ending of the moratorium the following year. Greg Roczicka, representing the Yukon-Kuskokwim Delta Regional Advisory Council, spoke to the Board regarding the moratorium: "…

moose have been certainly present in the lower Kuskokwim... just not in very large numbers. It goes back to past practices where anything that stuck its nose out of the brush was in the stew pot before long." He goes on to acknowledge that the population is growing, and to discuss the debate among the local residents, "As far as the opening hunt next year… there's real strong disagreement on the Kuskokwim side about opening too soon and losing what we sacrificed for over the last five years… it's about 50/50 really…" (FSB 2008).

The debate continued until April 2009 when the local Advisory Committee submitted a proposal to the BOG to reopen the lower Kuskokwim moose hunt. During their April, 2009 meeting, the BOG heard testimony for and against opening the season and discussed the issues. Finally the Board voted to pass the proposal and it established the limited registration hunt RM615 in response to the five-year moratorium that expired on June 30, 2009. The 2009 State season was Sept. 1–Sept. 10 with a one antlered bull harvest limit and a total harvest quota of 75 antlered bull moose (ADFG 2009a, 2009b). Immediately after the first moose hunt in over 5 years, local residents forwarded three additional regulation proposals regarding the lower Kuskokwim. The BOG considered these at their November 2009 meeting in Nome. Proposal No. 2 was to lengthen the resident registration moose season in the lower Kuskokwim by 10 days; Proposal No. 3 proposed a resident winter moose season in the lower Kuskokwim registration area; and finally Proposal No. 4 wanted to change the boundary for the lower Kuskokwim hunt area. Proposal No. 2 and 3 did not pass because of the conservation concerns that still existed with this new moose population, and Proposal

No. 4 passed with some modifications to make the northwestern boundary more distinguishable for both moose hunters and law enforcement (ADFG 2009c).

Management actions continued into 2010 under the dual management system, which was still working, but at a different pace. The reason for not opening a moose hunt on federal lands at the same time ADFG did in 2009 was simply a timing issue. The FSB went to a two-year cycle instead of meeting annually, which put the Board out of cycle for 2009. The FSB met in May of 2010 and discussed Proposal WP10-54, which was submitted by the Yukon Delta National Wildlife Refuge requesting the Board to establish community harvest quotas for moose in the lower Kuskokwim area of Unit 18 (i.e., the moratorium area; FSB 2010). There were a large number of federally-qualified users that are eligible to hunt moose here, but the number of surplus of moose is minimal; thus, this proposal attempted to reduce the number of qualified users. An analysis of ANILCA section 804 was conducted to further limit the number of qualified users that met the rural resident criteria. Section 804 mandates that the taking on public lands of fish and wildlife for non-wasteful subsistence uses shall be accorded priority over the taking on such lands of fish and wildlife for other purposes. It further requires that “whenever it is necessary to restrict the taking of populations of fish and wildlife on such lands for subsistence uses in order to protect the continued viability of such populations, or to continue such uses, such a priority shall be implemented through appropriate limitations based on the application…” of three criteria, including “customary and direct dependence upon the populations as the mainstay of livelihood, local residency, and the availability of alternative resources” (ANILCA, Title VIII, § 804). A Section 804 analysis was developed for this proposal due to the small number of moose anticipated to be available for harvest and the large number of subsistence users (42 villages) with a customary and traditional use determination to harvest moose in the moratorium area of Unit 18. This analysis identified 14 of the 42 villages while considering the three factors outline in section 804. The Board explained that: “we believe it’s necessary to limit the pool of users to those who are most dependent on the resource as defined in Section 804 of ANILCA” (FSB 2010). However, this proposal did not actually open a hunting season; it only allocated harvest priority to the 14 villages when a season would eventually be opened on federal lands. It became apparent during agency comments and Board discussions that a season was intended, and specifically to match the State’s season. The Board continued to discuss legal ways to address setting the season and how to modify the original proposal to include opening a season and establishing a bag limit; however, it was determined that it was not possible legally, and the issues would be dealt with by a Special Action Request after the regular board meeting. A Special Action Request is an out-of-cycle change in a season, harvest limit, or method of harvest, and are taken when unusual situations arise (50 CFR Part 100, Subpart B, §100.19). The dual management pitfalls now became apparent: specifically the difficulties that lie in trying to make two simultaneous sets of hunting regulations for the same area and same population of wildlife. As Geoff Haskett (U.S. Fish and Wildlife Service representative on the FSB) put it: “So that’s fairly convoluted…” (FSB 2010). After the extensive discussions by the Board, WP10-54 passed unanimously with modification to add the 804 analysis; however, there was still no open season to hunt moose on federal lands. Shortly after the May meeting, the FSB received the Special Action Request (WSA10-02) from the Yukon-Kuskokwim

Regional Advisory Council to open and set regulations for a moose hunt on federal lands for fall 2010. This had little discussion and a season was granted; however, since this was a Special Action Request and out of the regular cycle of the FSB, these regulations were temporary and would have to be properly approved by the FSB during the regular meeting cycle two years later and reauthorized in the interim. Moose hunting within the “moratorium” area resumed September 1, 2010 on federal lands and was a joint State and Federal registration permit.

The people of the lower Kuskokwim River made the moratorium work. The people’s commitment to the moratorium resulted in an established sustainable moose population close to home. Allowing local resource users to have a voice and make co-management decisions during the regulatory process gave credence to the work by the dedicated State and Federal biologists to make the dual management system a success for the local residents of the Kuskokwim River.

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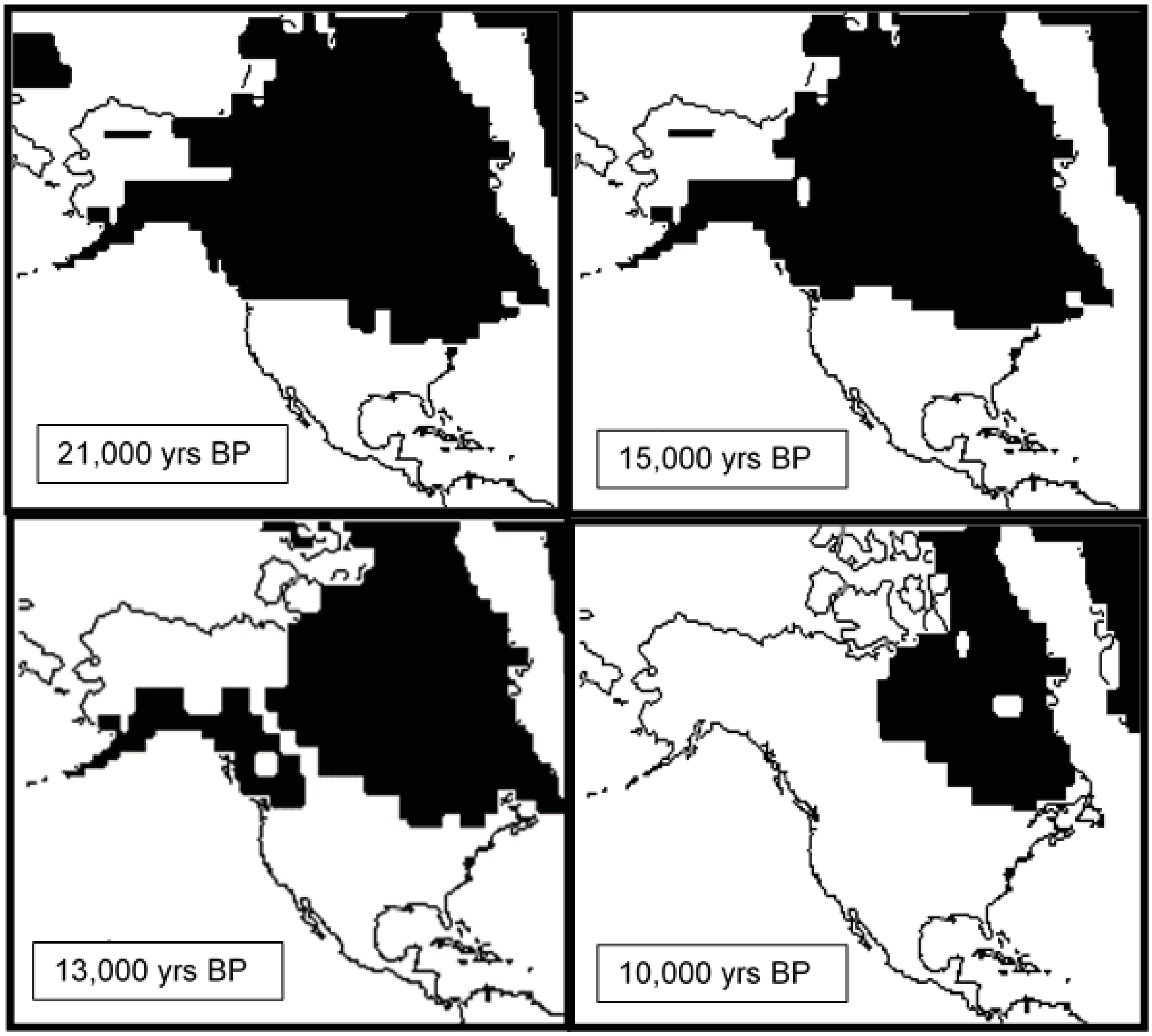

Figure 2.1. Pleistocene glacial distributions into the Holocene (21 ka-maximum, 15 ka, 13 ka, and 10 ka BP). An ice-free corridor opens along the eastern front of the Rocky Mountains about 13,000 yrs BP. Black represents glaciation extent for each time period. Resolution is 1 degree latitude/longitude grid (Peltier 1993).

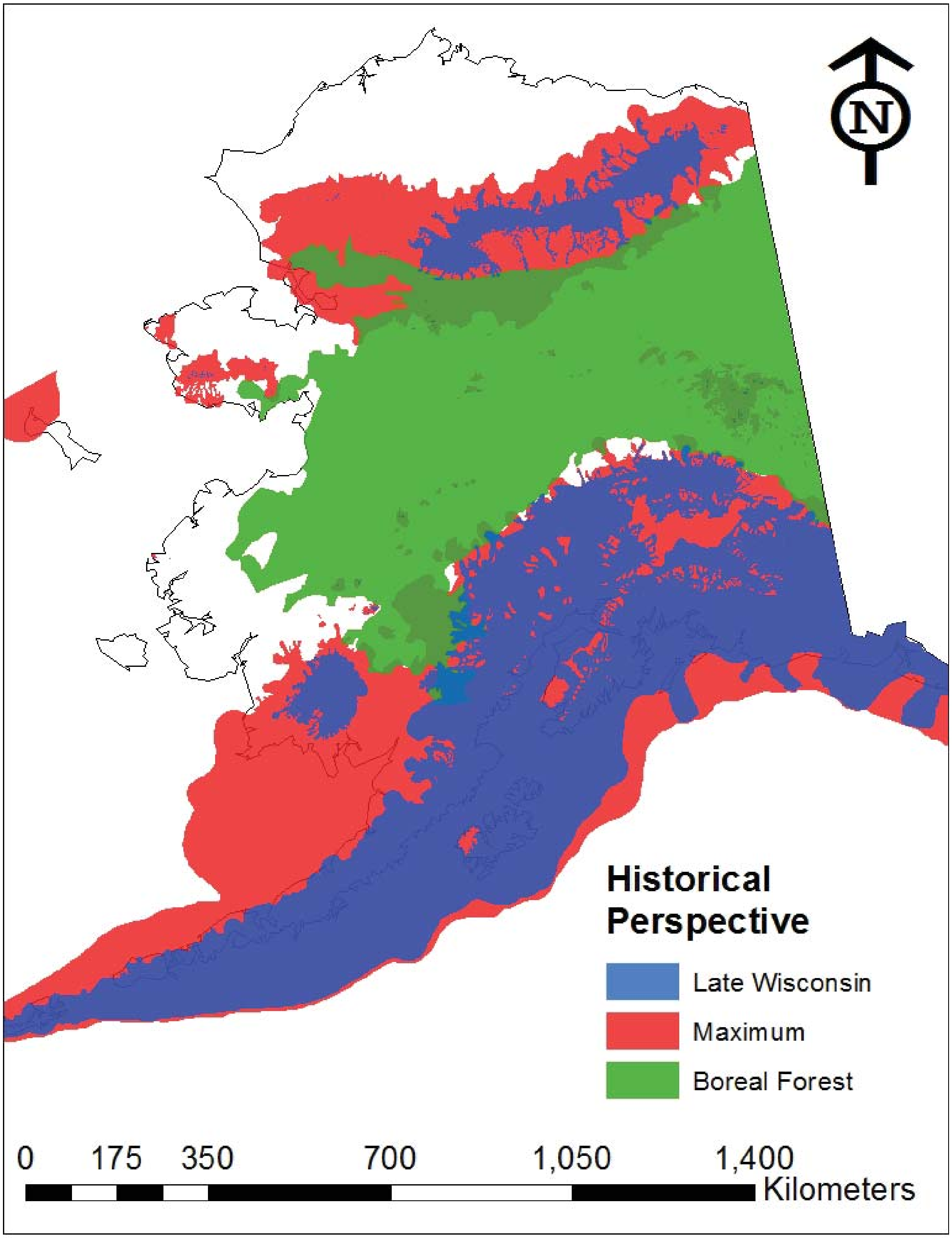

Figure 2.2. Present-day boreal forest ecoregion (Level III classification: classes 104-108; Gallant et al. 1995) and glacial extent within Alaska during the Pleistocene maximum (all-time maximum within last ~ 3 million years) and late-Wisconsin period (~24,000 to 12,000 yrs. BP; Manley and Kaufman 2002, Kaufman and Manley 2004). The historical ice-free regions within the interior of Alaska succeeded to boreal forest.

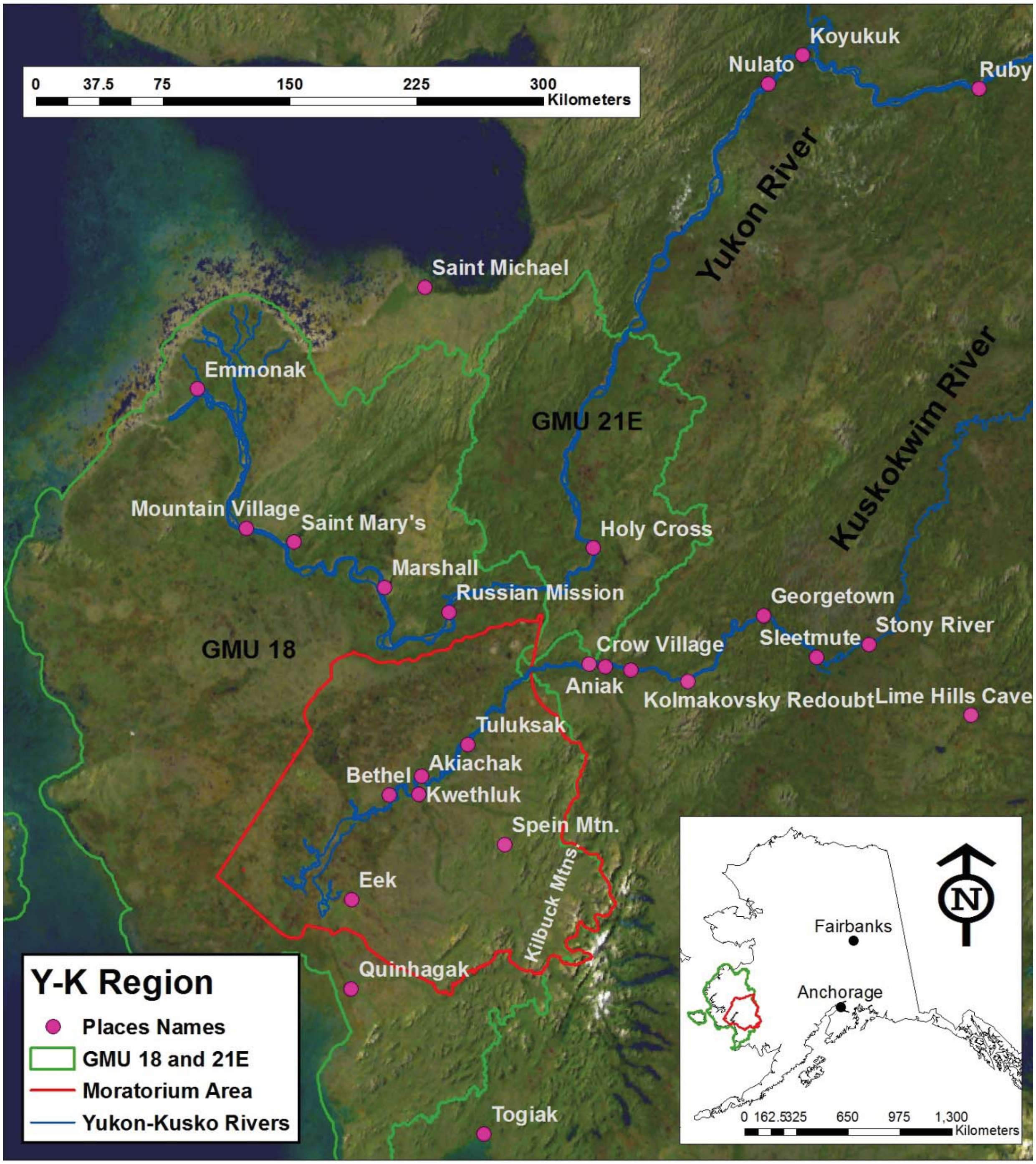

Figure 2.3. Yukon-Kuskokwim Region of Alaska. Showing game management units (GMU), moose hunting moratorium area, selected current villages, old villages and forts along the Yukon and Kuskokwim Rivers that are mentioned in the text.

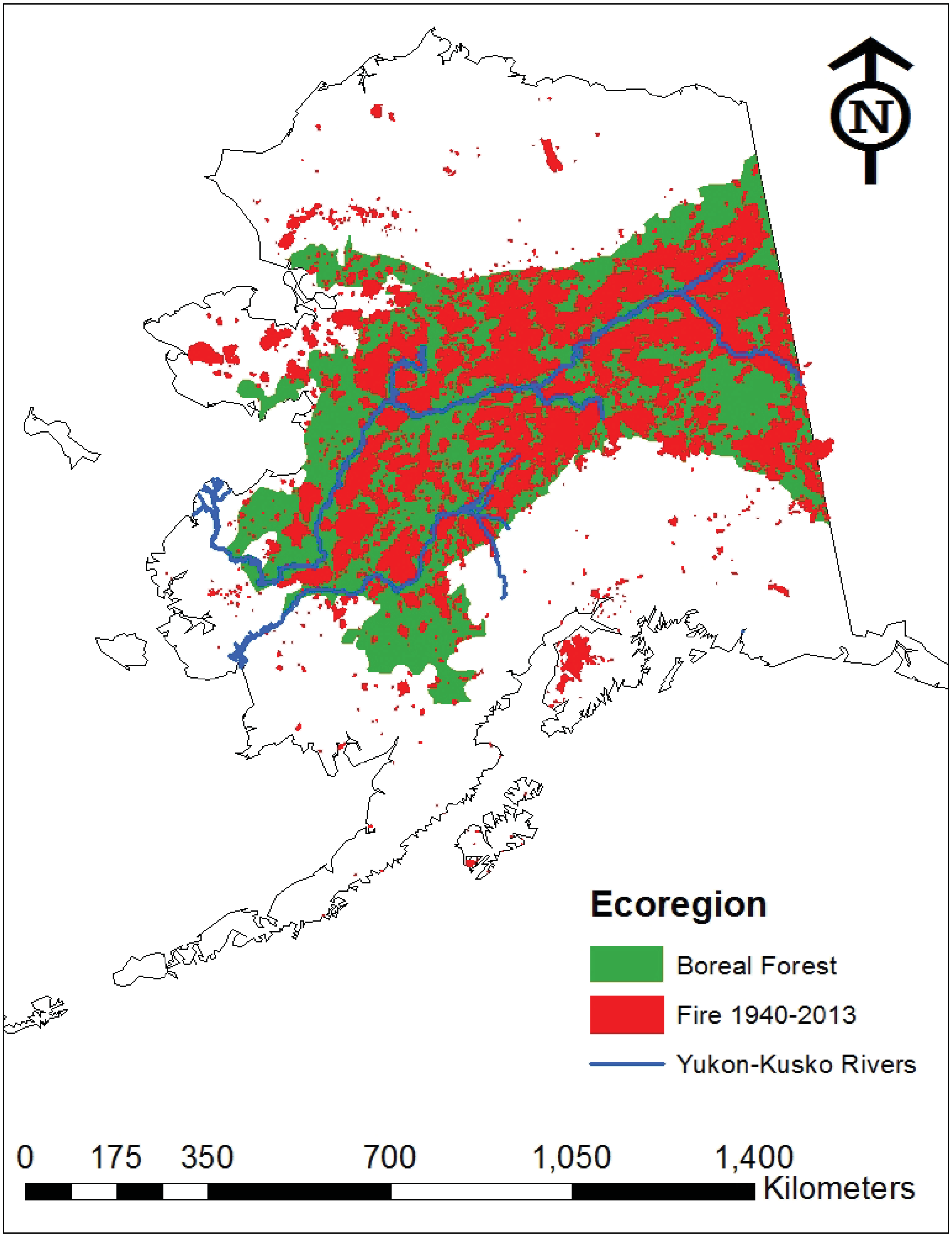

Figure 2.4. Alaskan fire perimeters combined from 1940 to 2013. There is a strong correlation of the fire pattern with the boreal forest. Fire has maintained, enhanced and expanded moose habitat within Alaska. Note the large areas burned between the Yukon and Kuskokwim Rivers leading to the Yukon-Kuskokwim Delta. (Fire data from the Alaska Fire Service: http://afsmaps.blm.gov/imf_firehistory/imf.jsp?site=firehistory accessed January, 2014).

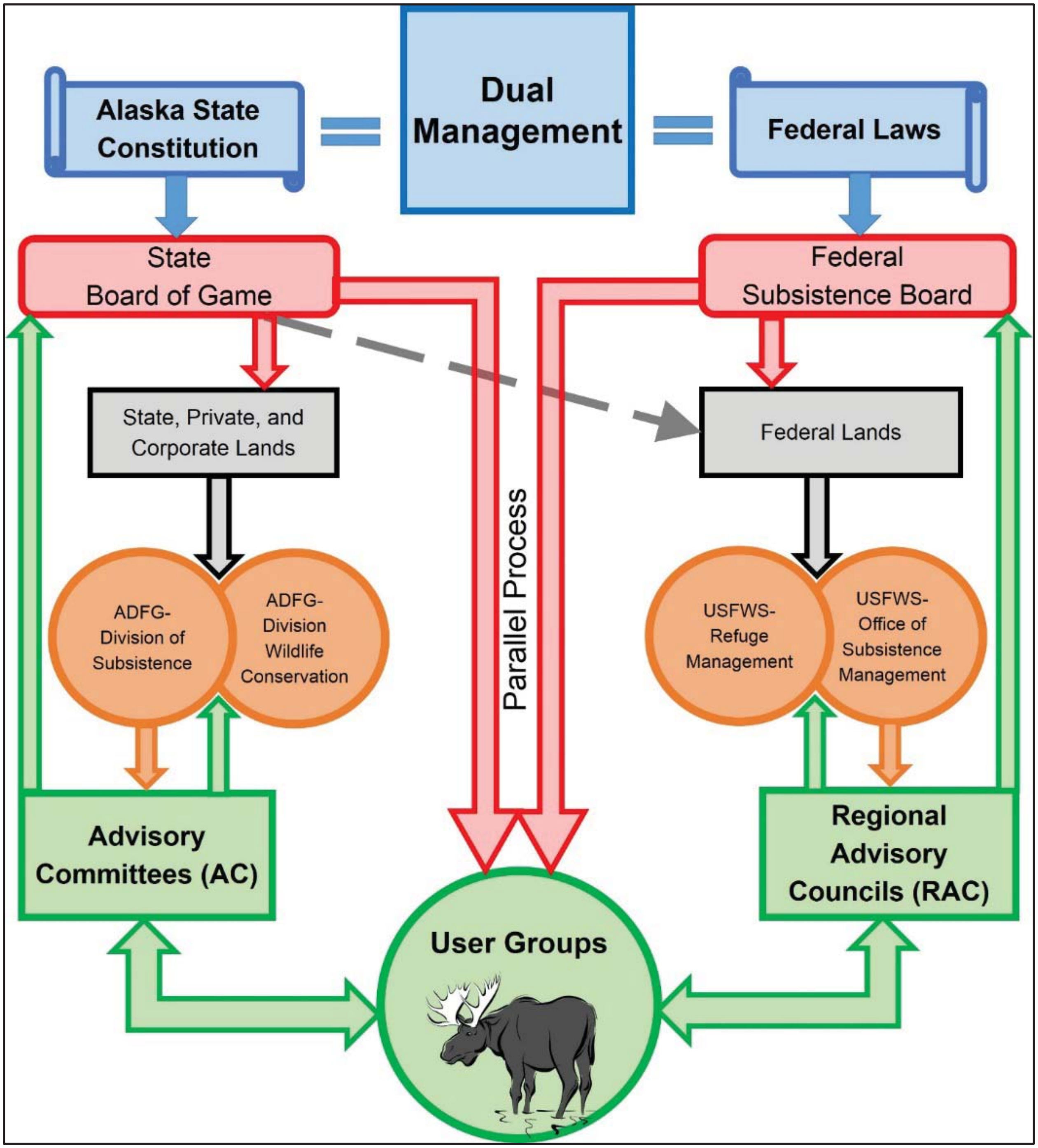

Figure 2.5. Conceptual model of the dual management system in Alaska. State and federal law set up the respective Boards that govern regulations on the respective lands (some state regulations apply to federal land also; grey broken arrow). Each agency has a subsistence and field-level divisions that interact with the Boards and the Advisory groups. The Advisory groups interact with the multiple-user groups and advises the Boards on the current issues. The Boards then make decisions and hand those back to the user groups. They are two separate bodies, but nearly identical in structure and function with a parallel process.

CHAPTER 3

ESTIMATING MOOSE ABUNDANCE IN LINEAR SUBARCTIC HABITATS IN LOW SNOW CONDITIONS WITH DISTANCE SAMPLING AND A KERNEL ESTIMATOR[2]

Abstract

Moose (*Alces alces*) are colonizing previously unoccupied habitat along the tributaries of the lower Kuskokwim River within the Yukon Delta National Wildlife Refuge (YDNWR) of western Alaska. We delineated a new survey area to encompass these narrow (0.7-4.3 km) riparian corridors that are bounded by open tundra and routinely experience winter conditions that limit snow cover and depth for traditional surveys. Moose surveys on the YDNWR are typically conducted using the GeoSpatial Population Estimator (GSPE) technique to estimate density. However, the lack of reliable snow conditions required for the GSPE technique prohibits surveying this area in most years. Furthermore, fitting the GSPE survey blocks into the narrow corridors is challenging and may not be appropriate. We tested a line-transect distance sampling approach as an alternative to estimate moose abundance in this region. Additionally, to test analysis methods, we compared standard semi-parametric detection functions available in the program Distance to a nonparametric kernel-based estimator not previously used for moose distance data. A double-observer technique was used to verify that the probability of detection at the minimum sighting distance was 1.0 (standard

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[2] Wald, E. J., and R. M. Nielson. 2014. Estimating moose abundance in linear subarctic habitats in low snow conditions with distance sampling and a kernel estimator. Alces 50:133-158.

assumption). Moose group size was 2.03 and not correlated with distance from the transect line. The top semi-parametric model in the program Distance was a hazard-rate key function with no expansion terms. This model estimated average probability of detection as 0.70 with an estimated abundance of 352 moose (95% CI = 237-540). The CV for the semi-parametric model was 20% and had an estimated bias of 1.4%. The nonparametric kernel-based model had an average probability of detection of 0.73 and an estimated abundance of 340 (95% CI = 238-472) moose. The CV for the kernel method was 18% and the estimated bias was <0.001%. Line-transect distance sampling with a helicopter worked well in our narrow riparian corridors with low snow conditions, and survey costs were similar. The kernel estimator also performed well compared to the standard semi-parametric models used in program Distance. These results validate a viable alternative to standard moose surveys, and offers more options to managers surveying moose in areas that have similar conditions.

Introduction

The Yukon Delta National Wildlife Refuge (YDNWR) is divided into four primary moose (*Alces alces*) survey units along the Yukon and Kuskokwim Rivers. Surveys in these units are typically conducted using the GeoSpatial Population Estimator (GSPE) technique (DeLong 2006; Kellie and DeLong 2006; Ver Hoef 2002, 2008), which is the preferred method adopted by the Alaska Department of Fish and Game (ADFG) and several other federal agencies including other National Wildlife Refuges in Alaska. Only one survey unit is on the lower Kuskokwim River within YDNWR, and encompasses nearly 2250 km^2 of contiguous habitat along the relatively wide riparian corridor. The GSPE technique overlays a grid of sample blocks on the study area where each block is stratified into high or low moose density based on a previous stratification flight. A random selection of survey blocks in each strata are surveyed using a fixed-wing aircraft to completely search each selected block. The analysis uses the block's spatial correlation to increase the estimate's precision based on finite population block kriging (Ver Hoef 2002). Complete and adequate snow cover is essential for this type of survey. Surveys are ideally conducted frequently (approximately every 3-5 years) to monitor trends in moose abundance. The Yukon-Kuskokwim Delta, and other coastal areas of western Alaska, experiences moderating climatic effects from the Bering Sea and has frequent thaw-refreeze events (1-9 events/winter; Wilson et al. 2013). As a result weather and snow conditions may preclude survey initiation or completion, extending the typical period between surveys.

The lower Kuskokwim has historically been an area of low moose density (0.03 moose/km^2 in 2004; Perry 2010); however, this area and the surrounding tributaries have adequate habitat to support a more sustainable moose population. Very few moose had been able to establish in this area because of extensive hunting pressure (Coady 1980). Therefore, a moose hunting moratorium was implemented on the lower Kuskokwim River watershed between 2004 and 2009. During this period, moose increased significantly (0.23 moose/km^2 in 2008; Perry 2010) and expanded into previously unoccupied, or occasionally occupied habitat. This recent expansion made it necessary for wildlife managers to create a new survey unit to include those previously unsurveyed areas

The new survey unit was developed to include the major tributaries of the lower Kuskokwim River within the YDNWR, which are narrow riparian corridors that originate from the adjacent mountains (Figure 3.1). These tributaries can support significant numbers of moose and are important landscape connections (wildlife corridors) to other parts of YDNWR and neighboring conservation units (i.e., Togiak National Wildlife Refuge; Aderman and Woolington 2006). The Kuskokwim tributary survey unit was first proposed, designed, and partially surveyed in the winters of 2009 and 2010 using the GSPE technique. Weather and lack of snow cover did not allow completion of either survey. Environmental conditions, such as snow cover, are among the most influential variables that affect survey quality (LeResche and Rausch 1974, Gasaway et al. 1986, Quayle et al. 2001, Oehlers et al. 2012). Under the GSPE, it is highly recommended that surveys be conducted when conditions include fresh or moderately fresh snow with complete ground coverage (Gasaway et al. 1986, Kellie and DeLong 2006), which typically means a minimum of 20 cm in this area. Retrospectively, we questioned the suitability of the GSPE technique for these tributaries because of the time and cost required to conduct the survey given the unreliable weather and snow conditions. In addition, we sought to evaluate whether this technique is ideal for use in the narrow linear habitats of this area given that large portions of many survey blocks (approx. 3.7 km x 4.5 km) included non-moose habitat (open tundra), and the stratified random block design of the GSPE is better suited for larger and more contiguous blocks of similar habitat (Kellie and DeLong 2006).

Alternative techniques could be utilized for this survey unit. A minimum count (termed complete count, a non-sampling approach) survey is used in adjacent areas (Aderman 2008). In this type of survey, a fixed-wing aircraft is flown throughout the entire area, counting all moose observed; the count is then the population estimate (Lancia et al. 2005). This method requires more flying time to search all areas completely and the minimum count has neither an estimate of precision (i.e., confidence intervals) nor does it typically have a sightability correction factor, for example based on collared animals (Gasaway and DuBois 1987). Simple aerial strip-transect surveys require less flying than minimum counts because of the sampling approach and it incorporates an estimate of precision (Timmermann 1974, Timmermann and Buss 2007, Jung et al. 2009); however, this method assumes equal detection of animals from the centerline out to the designated strip width (Burnham and Anderson 1984). There is typically not an estimate of sightability used in strip transect sampling (Evans et al. 1966, Timmermann 1993), although sightability could be estimated with marked animals (Anderson and Lindsey 1996), or more intensive flying at an increased cost (Gasaway et al. 1986, Gasaway and DuBois 1987).

We determined that a viable alternative was the use of line-transect distance sampling (Burnham et al. 1985, Buckland et al. 2001) using a helicopter. This technique was implemented for several reasons including: 1) this area tends to have marginal snow cover each year making it hard to complete a GSPE in any given year; 2) a helicopter can fly lower and more slowly with better visibility than a fixed-wing aircraft, helping to compensate for minimal snow cover; 3) line-transects can “fit” in the narrow riparian corridors better than GSPE blocks that typically encompass large portions of non-moose habitat; 4) distance sampling incorporates sightability corrections (e.g., weather, lighting, snow conditions, observer experience, etc.) provided that probability of detections at some distance is known or assumed, and; 5) we expected time, logistics, and costs may be similar compared to a fixed-wing GSPE survey in the same region.

Many wildlife agencies use various types of surveys to estimate ungulate populations (Rabe et al. 2002); however, distance sampling is one of the most widely used techniques to estimate abundance of wildlife (Buckland et al. 2004) without having to capture and mark individual animals (Royle et al. 2004). Although line-transect distance sampling may be better suited for open habitats (Buckland et al. 2001), it has been used widely in various habitats and conditions across the globe to estimate abundance of a variety of species, including ungulates such as pronghorn (*Antilocarpa americana*; Johnson et al. 1991, Guenzel 1997, Whittacker et al. 2003), Dall’s sheep (*Ovis dalli*; Schmidt et al. 2011), mule deer (*Odocoileus hemionus*; White et al. 1989, Koenen et al. 2002), red deer (*Cervus elaphus*; Trenkel et al. 1997), roe and fallow deer (*Capreolus capreolus*, *Dama dama*; Focardi et al. 2002), Mongolian gazelles (*Procapra* *gutturosa*; Olson et al. 2005), saiga antelope (*Saiga tatarica*; Young et al. 2010), Asian tropical forest ungulates (Khan et al. 1996, Jathanna et al. 2003), and African ungulates (Kruger et al. 2008, Shorrocks et al. 2008).

Thompson (1979) initially applied a distance sampling approach to estimate moose abundance in Ontario, Canada, where it was later improved upon by Dalton (1990). Thompson (1979) had problems fitting detection functions, and both surveys had difficulties meeting some of the sampling assumptions (e.g., exact distance measurements, movement of animals before detection, sightings not always independent) and were limited to the technological and statistical challenges of that period (Gasaway and Dubois 1987, Pollock and Kendall 1987, Dalton 1990). Significant advances in distance sampling methodology and statistical analysis have been recognized over the last 30 years (Buckland et al. 2001, 2004; Thomas et al. 2010). These improvements led to the development of distance sampling protocol for moose in interior Alaska (Nielson et al. 2006). Those techniques are also gaining popularity in British Columbia (Thiessen 2010) and Alberta (Peters 2010). Although these previous moose surveys have shown that distance sampling can be successful for estimating moose abundance in relatively large contiguous blocks of boreal forest habitat that typically receive adequate snow depth, no one has demonstrated that this technique can work in subarctic tundra along small, narrow riparian corridors.

Distance sampling analyses typically involve estimation of semi-parametric detection functions (Buckland et al. 2001, Thomas et al. 2010). During early development and analyses of line-transect distance data, Burnham et al. (1980) suggested that other nonparametric methods such as kernel estimators or splines might prove “fruitful” for estimating probability of detection. Mack and Quang (1998) further suggested that kernel methods could be a viable technique in wildlife distance sampling. The nonparametric kernel density estimator does not assume an underlying distribution for the detection function, and thus has more flexibility by allowing the data to “speak for themselves” or dictate the shape of the detection function (Silverman 1986, Wand and Jones 1995). Kernel estimators are considered a robust alternative to other density function estimators (Chen 1996a) and are computationally more efficient than polynomials (Buckland 1992). Both kernel and semi-parametric methods are robust against changing detection functions during a survey (Gerard and Schucany 2002) and are resilient to changing survey conditions such as snow depth/coverage, sun angle and overcast skies, and wind or other environmental conditions that could change during a survey over time and space (Burnham et al. 1980, Chen 1996b); as long as no correlation exists between moose densities and these changing conditions. Popular computer programs such as Distance 6.0 do not include a kernel-based detection function (Thomas et al. 2010) for use in analysis of line-transect data, although the kernel method has been used for distance data in other types of surveys (Buckland 1992, Chen 1996a, Mack and Quang 1998, Gerard and Schucany 2002, Jang and Loh 2010, Nielson et al. 2013, Nielson et al., in press), but not for moose.

The objectives of this paper are twofold: 1) evaluate use of helicopters for aerial line-transect distance surveys with a double-observer modification to obtain an estimate of moose abundance within narrow riparian corridors during a low snow year; and 2) to compare the nonparametric kernel-based detection function to the more traditional semi-parametric models in the commonly used program Distance (Thomas et al. 2010).

This paper investigates a viable alternative to the traditional moose survey methods and seeks to provide more options to wildlife managers to complete surveys in similar regions that have continuously varying survey conditions.

Study Area

The Yukon Delta NWR is located in western Alaska and encompasses the delta formed by the Yukon and Kuskokwim Rivers, which empty into the Bering Sea (Figure 3.1). The Kuskokwim tributary survey unit includes parts of four main lower Kuskokwim River tributaries originating from the mountains to the south and east. These tributaries include the Eek, Kwethluk, Kisaralik, and Tuluksak Rivers and are characterized by narrow (i.e., 0.7-4.3 km wide) riparian corridors (Figure 3.2) running through the foothills and tundra flats that drain the northwest sides of the Eek and Kilbuck Mountains.

The Eek and upper Kwethluk Rivers are represented by open riparian shrubs (*Salix* spp. and *Alnus* spp.) and scattered clumps of balsam popular (*Populus balsamifera*) trees, whereas the lower Kwethluk River transitions to open forests that include sporadic mixing of spruce (*Picea glauca*), balsam popular, and birch (*Betula papyrifera*) trees as the overstory with an understory of open willow and alder. The Tuluksak River riparian zone is primarily a narrow corridor of spruce and birch with an understory of willow and alder. The Kisaralik River riparian zone is mostly mixed coniferous open woodland which exhibits a moderate transition between the Kwethluk and Tuluksak riparian habitats. All four tributary river habitats are bounded by tundra and include variously sized open meadows, old river channels, and beaver ponds.

Weather conditions are highly variable across the survey area. Average temperatures and snow depth at Bethel, AK airport (2000-2010; NOAA 2011) during the primary survey months were -21° C [range -36° to 4° C] with 23 cm [range 0 to 56 cm] of snow in January, -10° C [-37° to 5° C] and 23 cm [0 to 64 cm] of snow in February, and -9° C [-27° to 4° C] with 20 cm [0 to 56 cm] of snow in March. In many years there are freeze-thaw events (Wilson et al. 2013) throughout the winter which ultimately limit total snow accumulation and duration. Our study period (2010) was an El Niño year, which affected the winter weather pattern on the Yukon-Kuskokwim Delta from June 2009 to March 2010 (NOAA 2013). Repeated high pressure systems over the Delta kept numerous low pressure systems south and subsequently pushed easterly, resulting in unusually clear and dry conditions with periods of colder temperatures and little snowfall over the study area during winter 2009/2010.

A portion of the survey unit experiences a “banana belt” effect, especially along the foothills from Three-Step Mountain to Elbow Mountain along the Kwethluk River and across to Spein and Nukluk Mountains near the Kisaralik River. This area is usually affected by a warming trend that typically melts snow more frequently and rapidly than other parts of the area, perhaps resulting from an inversion. This effect can have a significant role in limiting GSPE surveys because of the melting and lack of snow that usually results along the lower Kwethluk and Kisaralik Rivers in any given year.

Nearly three centimeters of new snow accumulated 4 days prior to the survey. Total snow depth was 5 cm as recorded at Bethel, AK airport, but was 8-10 cm as determined from two snow stakes in the survey area (Kwethluk River) at the time of the survey. Snow coverage ranged from 85-100% (100% is defined as complete ground coverage without regard to depth) throughout the survey area, but meadow grasses and short vegetation were protruding and snow had melted off stumps and root wads. Moose tracks were visible in most areas including areas with shallow snow.

Weather conditions during this survey were mostly clear, 9-37 kph winds, and -12° to 2° C temperatures. Day length was nearly 12 hours with sunrise at 0900 and shadows becoming long around 1500. Surveying times were typically between 0900 and 1700 each day. Flying conditions were generally favorable for the entire survey.

Methods

Field Survey

Aerial line-transect distance sampling protocol for moose followed Nielson et al. (2006). The survey area (i.e., sampling universe) was limited to the riparian corridor for the rivers of interest. Polygons were created in ArcMap 9.2 (Environmental Systems Research Institute, Redlands, California, USA) around rivers to encompass riparian vegetated areas within the floodplain and between the tundra benches on each side of the river (Figure 3.3). Satellite imagery was used to facilitate creation of survey areas which encompassed nearly 730 km^2.

Survey transects were created within river corridors and varied by length and number along each river (Figure 3.3). Multiple transects were placed in areas wide enough to allow equidistance spacing of 700 m giving a maximum 350 m search area on each side of a transect centerline. Transect length varied according to stretches of river that allowed straight transects. Sections of transects changed directions in a saw-toothed manner as the river corridor meandered (Nielson et al. 2006). Some riparian corridors were sufficiently narrow to only allow one transect, which had a random start point contingent on allowing the minimum half transect width (350 m) to be in moose habitat. Thus, the transect centerline could not be right on the edge of the habitat (i.e., one side having a hard boundary of no moose habitat or open tundra and the other side having all moose habitat) to avoid extreme asymmetry of g(*y*) around the two sides of the line, although this source of bias is minimal for most studies (Buckland et al. 2001). Areas with systematic parallel transects had a random start point for the first transect. A total of 46 transects were delineated with a combined length of 698.25 km (Figure 3.3).

We used a Robinson (R-44) helicopter with bubble windows to survey moose during 16-17 March 2010 within the Kuskokwim tributary survey unit. Helicopters provide a better platform for observing moose leading to decreased sightability correction factors, variances, and in some cases, costs compared to fixed-wing surveys (Smits et al. 1994, Gosse et al. 2002). Protocol recommends a flight altitude of 122 m above ground level (AGL), which results in good visibility and minimal disturbance of moose (Nielson et al. 2006). However, snow conditions were poor, so flight altitude was adjusted to 100 m AGL to increase visibility while remaining high enough to minimally affect moose and to prevent ground flash, the visual effect of the ground zooming by too fast when flying at a lower altitude (Becker and Quang 2009). Our target ground speed was 64 kph (40 mph) depending on terrain and wind.

Four people were onboard the helicopter during this survey. The pilot was responsible for maintaining desired altitude, speed and heading on transect centerlines using a preprogramed GPS (Garmin 695). Two observers were seated in the back (one on each side) and were the primary observers for the survey. Their responsibilities were to sight moose groups, count and classify each group, and measure the perpendicular distance from the transect centerline to each group's centerpoint. The data recorder sat in the front-left seat and was responsible for recording all data, including GPS locations, performing as a double-observer, frequently measuring helicopter AGL, and overall survey coordination.

The double-observer method was used in conjunction with the line-transect survey to test the assumption that detection was 100% on or near the transect centerline, or at the minimum available sighting distance (Buckland et al. 2001, Laake and Borchers 2004, Borchers et al. 2006). This assumption is sometimes violated (Chen 1999, 2000) and information regarding heterogeneity in observer bias should be modeled (Graham and Bell 1989), as it can result in negatively biased estimates. The data recorder in the front-left seat was paired with the rear left observer to conduct the double-observer sampling, which is essentially a mark-recapture method (Borchers et al. 2006). The data recorder focused on or near the centerline to detect moose, but recorded all moose observations at any distance. Double-observer data are used to estimate detection rate on or near the centerline by the rear seat observers. This requires that the front and rear seat observers operate independent of each other (Buckland et al. 2010). Data were recorded on the number of moose groups detected by both observers, and groups detected by the front and not the rear observer. To account for different observer bias, the two rear observers rotated sides each day to be paired with the front-left observer in order to incorporate biases from both observers into the model (Cook and Jacobson 1979). Thus, we considered the probability of detection estimated for the back-left observer based on the mark-recapture data to be relevant for both backseat observers during analyses. The recorder also worked with the pilot to keep flight speed and altitude within the range of survey protocol. A laser rangefinder (Nikon Forestry 550 Hypsometer) was frequently used to measure true vertical distance from the ground to helicopter every 2-3 minutes to check flight altitude and recommended adjustments as needed.

Distances of moose groups perpendicular to the transect centerline were measured by the rear observers using laser rangefinders (Leupold RX-1000 TBR) with built-in clinometers and had a maximum range of about 900 m. Clinometers allow for accurate horizontal measurements regardless of survey altitude. Moose groups that were hard to laser-range because of trees, helicopter movement or not ranging moose quickly enough before they passed required flying back over the groups and marking their locations with a GPS (Marques et al. 2006). Moose groups were defined as one or more moose within a 50 meter radius (Molvar and Bowyer 1994). Distances were measured to the center of the group using the laser rangefinder directed at their feet in order to not inadvertently over-estimate the distance. The distance measurement is associated with the location of the moose when first observed. If the moose moved before a distance was acquired, the observer ranged the location where the moose was when first observed. Doubling back to get GPS locations of moose worked well, but some moose moved after detection because of the aircraft hovering directly overhead, so a location where the animal was first observed was marked. Tracks in the snow were good reference points for these measurements. Distances that were obtained using the GPS method were measured in a GIS. Additional moose observed “off transect” while doubling back to obtain GPS locations, were not included in any analyses. Observers determined group size, composition (i.e., adults and calves), and classified percent habitat cover for an approximate 50 meter radius around the moose groups.

Data Analysis

Standard distance sampling theory assumes all individuals (objects) available to be detected on the centerline, or the minimal available sighting distance, are observed, and that the probability of detection is a function of perpendicular distance from the centerline. There are three essential assumptions for accurately estimating density using distance sampling; in order of importance these include: 1) objects at the minimal available sighting distance are detected with certainty, that is $g(W_1) = 1.0$, or can be estimated, 2) objects are detected prior to any movement in response to the survey, and 3) perpendicular measurements to the object are accurate (Buckland and Turnock 1992, Buckland et al. 2001). Other design/analysis assumptions exist, but they are less stringent. These include accurate measurement of group sizes, and that object density is independent of the placement of transects (i.e., uniform distance distributions; Fewster et al. 2008).

Fulfilling these assumptions allow for an accurate density estimate using:

$$\hat{D} = \frac{n\hat{E}(s)}{2(W_2 - W_1)L\hat{P}} \tag{3.1}$$

where n is the number of observed groups, $\hat{E}(s)$ is the expected (or average) group size, W_1 and W_2 are the minimum and maximum search distances from a transect, respectively, L is the total length of transects flown, and $\hat{P}$ is the estimated average probability of detection within the area searched (Buckland et al. 2001).

We tested the assumption $g(W_1) = 1.0$, where $g(W_1)$ is the minimum sighting distance, using a double-observer technique (Chen 2000, Borchers et al. 2006, Buckland et al. 2010). Observations from the left side of the helicopter were used for this analysis. Observations collected independently by individual observers on the left side were used to estimate the probability of detecting a moose group at the minimum available sighting distance. This probability was used to adjust the estimated detection curve starting at that distance (Laake and Borchers 2004).

We used logistic regression (McCullagh and Nelder 1989) in the mark-recapture analyses to estimate the probability of detecting a moose group by the back-left observer at the minimum available sighting distance, given detection by the front-left observer. We considered three models that 1) treated the probability that a moose group was detected by the back-left observer as constant across all distances from the transect line (intercept only model); 2) treated the probability of detection as a function of distance from the transect line; and 3) included both linear and quadratic terms for distance from the transect line. We used Akaike's information criterion for small sample sizes (AICc; Burnham and Anderson 2002) to identify the best model for estimating probability of detection by the backseat observers based on the mark-recapture data. The AICc was calculated as:

$$\mathrm{AICc} = -2\log(\mathit{Likelihood}) + 2kn/(n-k-1) \tag{3.2}$$

where *k* was the number of parameters in the model (including intercept term), *n* was the number of observations used to fit the model, *Likelihood* was the value of the logistic likelihood evaluated at the maximum likelihood estimates, and 'log' was the natural logarithm. The logistic regression model was fit using the program R (R Development Core Team 2010).

We designed survey transect centerlines to be a minimum of 700 m apart to ensure that moose groups were not counted more than once if they moved during the survey. In order to meet this assumption, we set the maximum search width, W_2, equal to the maximum distance a moose group was observed within 300 m of the transect centerline. Since the backseat observers had a blind spot underneath the helicopter, we used a laser rangefinder (hypsometer) to determine the minimum sighting distance for the backseat observers. While at survey altitude, the backseat observer laser-ranged through the bubble window along their line-of-sight to the ground, just clear of the helicopter skid, to determine the width of the blind spot. Using this method, the minimum available sighting distance for the backseat observers was estimated to be approximately 43 m from the transect centerline. Moose were visible to the front-left observer from 0 to 43 m through the front helicopter window, but lumping these data into a single distance of "zero", and the fact that the front-right observer (pilot) was not focused on observing moose on that side of the line, precluded using these data in the analyses. Therefore, because of lumping the data, the front-left observer observations in the 0 to 43 m range were not used. Thus, the minimum available sighting distance,

W_1, was set at the minimum distance at which a moose group was detected by a backseat observer.

Group size can influence detectability, especially at longer distances, such that larger groups may have a higher probability of detection further from the transect line compared to smaller groups (Drummer and McDonald 1987, Drummer et al. 1990). We evaluated whether correlation existed between expected group size and detection distance. We used a Pearson's correlation analysis to estimate the correlation (r) between moose group size and distance from the transect line, and calculated a 95% confidence interval (CI) for the statistic (Zar 1999). We determined no relationship existed between group size and detection distance if the 95% CI included 0.0. In this situation, we used the average of all observed group sizes for $\hat{E}(s)$ (equation 3.1). If a correlation was detected, we then used the regression method (Buckland et al. 2001) to estimate expected group size. We examined the habitat covariate, percent cover, as a potential influence on the probability of detection of moose groups (i.e., higher percent cover may have decreased probability of detection of moose groups; Anderson and Lindzey 1996, Oehlers et al. 2012).

The underpinning of distance sampling is the detection function g(y), which expresses the probability of detecting a group given that the group was observed at distance (y) from a random transect, and that the assumption g(W_1) = 1.0, or can be estimated, holds true (Buckland et al. 2001). There are many models that can be fitted to distance data in order to estimate the shape of a detection function. However, Buckland et al. (2001) focus on a suite of semi-parametric models such as half-normal, uniform, and hazard-rate key functions with cosine, simple polynomial or hermite polynomial expansions. Once a detection function is selected, it is then integrated over the search width (W_1 to W_2) to estimate the average probability of detection, $\hat{P}$, within the search area.

We used the computer program Distance 6.0 release 2 (Thomas et al. 2010) to model semi-parametric detection functions for moose groups. We considered robust key functions with expansion terms as outlined in Buckland et al. (2001) including the half-normal with hermite polynomial and cosine expansion terms, the hazard-rate with a cosine expansion, and the uniform with simple polynomial and cosine expansion terms. Additionally, the half-normal or hazard-rate key functions allow for predictor variables to help model the detection function. We used the half-normal (including hermite polynomial and cosine expansion terms) and hazard-rate (including a cosine expansion term) key functions for modeling the detection function while incorporating the percent cover variable. The number of expansion terms for each key function was allowed to vary from 0 to 5; the AICc was used to select the number of expansion terms among the various models. The model with the lowest AICc value was selected as the best model to describe the detection function (Burnham and Anderson 2002).

Use of parametric or semi-parametric detection functions may not always be the best approach to fit probability detection curves (Burnham and Anderson 1976, Buckland 1992). Instead, a nonparametric kernel density estimator without an assumed probability density function may provide a better fit to the data. We fit a nonparametric kernel estimator (Silverman 1986, Wand and Jones 1995) to our moose group observations; and used the general univariate kernel density estimator described in Wand and Jones (1995):

$$\hat{f}(x) = (nh)^{-1} \sum_{i=1}^{n} K\left(\frac{x - x_i}{h}\right) \tag{3.3}$$

where *x* is a perpendicular distance within the range of observed distances, x_i is one of the *n* observed distances, *h* is a smoothing parameter, or 'bandwidth', and *K* is a kernel function satisfying the condition $\int K(x)dx = 1$.

Since the bandwidth (*h*) governs the function smoothness (Chen 1996a, Gerard and Schucany 1999), the choice of the bandwidth is more crucial than the choice of kernel (Mack and Quang 1998, Jang and Loh 2010). We used a Gaussian kernel function (Silverman 1986, Chen 1996a) and the direct plug-in bandwidth selection method (Sheather and Jones 1991, Wand and Jones 1995, Sheather 2004) for developing the detection function for moose groups. The direct plug-in method objectively fits the bandwidth and is considered by some to be the best compromise between bias and variance among the available methods (Sheather and Jones 1991, Wand and Jones 1995, Venables and Ripley 2002, Sheather 2004).

Kernel estimators inherently do not perform well near sharp boundaries (Jang and Loh 2010). A boundary bias is created, as in our case, when distance observations are not distinguished from the right or left side of the transect line and where all values are non-negative (Buckland 1992, Jang and Loh 2010). In order to model the distances with a kernel estimator, Chen (1996a, b) and Silverman (1986) recommended reflecting the observed distances to both sides of the transect line in order for the kernel density estimator to perform properly. After shifting all observed distances by the left-truncation distance (W_1), we multiplied (reflected) the observed distances by (-1) and added them to the dataset (Buckland 1992; Chen 1996a, b). Once the kernel density function was created from the expanded dataset, the detection function to the right of the zero line (positive) was used for the density estimate. The kernel estimator was fit using the program R (R Development Core Team 2010) and the MASS package in R (Venables and Ripley 2002).

Bootstrapping is a resampling method for measuring the accuracy of derived estimates (Efron and Tibshirani 1994) without having to know the underlying distributions compared to standard parametric formulas (Manly 2007). Chen (1996b) found the bootstrap method was more accurate in estimating variance compared to non-bootstrap results for a line-transect distance sampling study. We used bootstrapping to estimate SEs and 95% CIs for final estimates of moose density and abundance within the sampled region (Efron 1981a, b; Quang 1990; DiCiccio and Efron 1996). Estimates derived from the program Distance 6.0 were bootstrapped within the program, which uses a default of 999 bootstrap re-samplings with replacement (Thomas et al. 2009). Standard errors and confidence intervals for the kernel estimates were derived from bootstrapping 999 resamples (with replacement) to be consistent with program Distance and because the bootstrapped estimates (SE, CI) usually become stable and asymptotic between 500 and 1000 resamples (Efron and Tibshirani 1994). We bootstrapped the 46 line-transects that were surveyed, in which the bootstrap would rerun the analysis for all parameter estimates including the shape of the detection function and the average probability of detection during each iteration. Additionally, we evaluated bias and precision of the density estimate using the bootstrap (Efron and

Tibshirani 1986). We used the percentile method (Efron 1981b, Efron 1982) for calculating the 95% confidence intervals using the 2.5th and 97.5th percentiles of the 1,000 estimates (999 bootstrap estimates + original estimate). The percentile method is the preferred method for calculation of CIs when bootstrapping, because using the standard formula (i.e., estimate ± 1.96[SE]) requires the additional assumption that the bootstrap estimates generally follow a normal distribution (Buckland 1984, Efron and Tibshirani 1994). We estimated relative percent bias of the density estimates as:

$$\%Bias = \left[\frac{\{D_{boot} - D_{orig}\}}{D_{orig}}\right] * 100 \tag{3.4}$$

where D_{boot} is the average density estimate from the bootstrap and D_{orig} was the original density estimate. We measured dispersion or the extent of variability in relation to the final density estimate by calculating the coefficient of variation (CV) as $CV = (SE / \hat{D}) \times 100\%$. The standard deviation (SD) of the 1,000 estimates was used as the estimated SE.

In order to estimate the total length (L) of transects needed in future surveys to achieve a certain level of precision (i.e., CV value), we used the formula from Buckland et al. (2001):

$$L = L_0\{cv(D)\}^2/\{cv_t(D)\}^2 \tag{3.5}$$

where L_0 is the total length of transects surveyed, $cv(D)$ is the coefficient of variation of the density estimate from this study and $cv_t(D)$ is the desired target coefficient of variation.

Results

A total of 162 moose in 78 groups were detected during the survey along 698.25 km from 46 transects within a series of polygons encompassing 730 km^2 of riparian moose habitat. Forty-eight moose were identified as calves, and 114 as adults. There were 37 cow moose that had calves, which included 26 singletons and 11 pairs of twins for a twinning rate of 30% in March. Group sizes ranged from 1 to 5 moose with 73% of groups comprised of 1-2 moose and only 6% of groups had 4-5 moose.

One of the moose groups detected by the front-left observer was 244 m to the right of the transect line, and was not detected by the back-right observer. Because the mark-recapture portion of this study was intended to occur only on the left side of the aircraft, this observation was not included in the analysis. Ten of the 78 moose groups were detected only by the front-left observer and were recorded as being seen directly on the transect line (i.e., perpendicular distance = 0). Since these moose groups could not be seen by the back-left observer and 'lumping' of the perpendicular distances occurred during data recording (i.e., these moose were likely somewhere ± 43 m from the transect line and not all directly on the line), these observations were not included in the analysis. Of the remaining observations, the minimum observed distance of a moose group by the backseat observers was 46 m away from a transect line, thus W_1 was set to 46 m. Buckland et al. (2001) recommend truncating the farthest 5-10% of distance observations to prevent undo influences. We truncated our data to 300 m, which corresponded to a reduction of approximately 8% of the farthest distance observations. The maximum observed distance of a moose group within 300 m of a transect line was 299 m, so W_2 was set to 299 m.

Analysis of moose observations within the defined search width (46-299 m from a transect line) indicated that moose group size was not correlated with distance from the transect line (r = 0.048, 95% CI from -0.20 to 0.29). The average moose group size for observations by the backseat observers within the search strip was 2.03 (95% CI from 1.78 to 2.32) and was used in the density estimate.

The mark-recapture trials had a total of 34 observations within the search width that were used to fit logistic regression equations to estimate the probability of detection by the back-left observer given detection by the front-left observer. Of the 34 mark-recapture trials only three moose groups were missed by the back-left observer, and were later deleted for the density estimate. The logistic equation with linear and quadratic terms for distance from the transect line had the lowest AICc value (19.8 versus 22.4 and 24 for the intercept only and linear distance function models, respectively). The final estimated logistic regression model was:

$$E[y_i] = \frac{\exp\left(51.461 - 0.583 distance_i + 0.0012 distance_i^{\,2}\right)}{1 + \exp\left(51.461 - 0.583 distance_i + 0.0012 distance_i^{\,2}\right)} \tag{3.6}$$

where $E[y_i]$ was the expected probability of detection for mark-recapture observation i.

Based on this final model, the predicted probability of detection of moose at the minimum sighting distance by the back-left observer was 1.0. Therefore, the estimated probability of detection curve was not scaled by a correction factor prior to integration and estimation of $\hat{P}$, and only observations by the rear seat observers were used to estimate moose density.

Comparison of models using AICc values requires that the competing models are all estimated using the same number of observations, and the same response (*Y*) values. Percent cover was not recorded for one observation, so this record was not initially included during estimation of the probability of detection curve, as it would have precluded comparisons between competing models with and without this predictor variable. In addition, due to the distribution of percent cover values for moose observations (10% to 70% in 10% increments) and few observations at the extremes, the original values were collapsed into 3 categories: 1) 10-30%, 2) 30-50%, and 3) 60-70%.

Comparison of the models with and without the covariate for percent cover indicated that a hazard-rate key function with no expansion terms was the best fit to the data (Table 1). Because the models containing the covariate for percent cover ranked last according to AICc values, we refit the models without the predictor variable using all the observations from the rear seat observers within 46-299 m of a transect line, including the one observation where percent cover was not recorded. The analysis results for these data were similar to the analysis minus the missing observation in that the top model was a hazard-rate key function with no expansion terms (Table 2). We used the goodness of fit (GOF) test statistic to determine if the top model fit the data well

(Buckland et al. 2001). There was no evidence of lack of fit for the top model (GOF test; $\chi^2 = 6.07$, df = 4, p = 0.194). Based on this final model using 59 moose group observations, the estimated average probability of detection was 0.70 (Figure 3.4) and the estimated moose density within the sampled polygons was 0.482 moose/km^2, which corresponds to a total of 352 moose (95% CI from 237 to 540). This model had a CV of 20%. The estimated bias in this density estimate was ~1.4%.

The detection function calculated using the kernel density estimator (without covariates) also had a good fit (GOF test; $\chi^2 = 6.42$, df = 5, p = 0.73) with an estimated average probability of detection of 0.73 (Figure 3.4). The estimated moose density was 0.465 moose/km^2, which equates to a total of 340 moose (95% CI from 238 to 472). This model had a corresponding CV of 18%. Based on bootstrapping, the estimated bias in this density estimate was < 0.001%.

Based on an encounter rate of 0.0845 moose groups/km (59 groups/698.25 km) and the coefficient of variation from the kernel estimator (18%), we calculated the total length of transects needed to achieve a targeted CV equal to 20%, 15% and 10%. Our analyses indicated that we need to survey 565.58 km, 1005.48 km, and 2262.33 km of transect lines, respectively, for the various targeted precision, given that the encounter rate remains constant.

Discussion

Distance sampling proved to be a viable technique for the Yukon Delta National Wildlife Refuge to monitor moose along the Kuskokwim tributary rivers in southwestern Alaska. Others have utilized distance sampling for moose within boreal transition forest of west-central Alaska (Nielson et al. 2006) and the central Canadian boreal forest habitats (Thompson 1979, Dalton 1990, Peters 2010, Thiessen 2010) during adequate to optimal snow conditions with varying degrees of success in model fitting and attaining adequate levels of estimate precision. However, we utilized line-transect distance sampling for moose in a subarctic tundra ecosystem along narrow riparian corridors for the first time. We evaluated this method as an alternative technique for surveying moose during minimal snow conditions on the Yukon-Kuskokwim Delta and regions with similar, variable climatic conditions; and we present an alternative technique for analyzing moose distance data using a nonparametric kernel density estimator to fit the detection function.

Assumptions

Distance sampling depends on three main assumptions that need to hold true, or nearly so, in order to produce unbiased and reliable estimates (Buckland et al. 2001). Although the assumptions can be relaxed to some degree in certain circumstances and still provide dependable estimates (Buckland et al. 2001), we designed our study in an attempt to meet all assumptions or to estimate our biases if we failed to meet one of them.

Assumption (1), that objects at the minimum available sighting distance were detected with certainty, has had much attention and research to determine if $g(W_1) = 1$ holds true (Bachler and Liechti 2007, Buckland et al. 2010), and if not, how to estimate it (Buckland and Turnock 1992, Laake and Borchers 2004, Borchers et al. 2006). Distance sampling inherently accounts for, or corrects for, visibility (perception) biases provided that all objects are detected on the transect centerline or at the minimum sighting distance (Buckland et al. 2001, Marques and Buckland 2004). As objects are farther from the transect line, they become less detectable, which can be caused by numerous factors such as observer experience and snow cover (LeResche and Rausch 1974), percent vegetative cover (Anderson and Lindzey 1996), animal behavior (lying, standing, walking; Ward et al. 2004), cloud cover (Oehlers et al. 2012), group size (Drummer and McDonald 1987), flight altitude (Graham and Bell 1989), and daily temperatures (Quayle et al. 2001).

Visibility bias for various types of aerial surveys has been typically addressed through developing a sightability correction factor (SCF) where modeling covariates against mark-recapture data of collared animals has improved density estimates (Gasaway et al. 1986, Samuel et al. 1987, Anderson and Lindzey 1996). Standard distance sampling technically accounts for these covariates through the distance density function without collecting covariate data or having marked animals, if assumption $g(W_1) = 1.0$ holds (Burnham and Anderson 1984, Pollock and Kendall 1987, Buckland et al. 2001); however, density estimates can be improved by collecting and modeling covariate data that are associated with observed distances for objects of interest (Marques and Buckland 2004).

Since assumption (1) is not always met (Burnham et al. 1980, Laake and Borchers 2004, Borchers et al. 2006), it should be tested and corrected (modeled), if it fails. Although many distance sampling studies do not address assumption (1) (Bachler and Liechti 2007), we utilized the double-observer method (Graham and Bell 1989) to test the primary assumption that detection of moose groups on the centerline or at the minimum sighting distance was certain. The mark-recapture logistic regression analysis of our data indicated that we met the assumption with 100% probability of the backseat observer detecting a moose group that was detected by the front-left observer at the minimum sighting distance (g(W_1)). Detection certainty along the transect line in our study was enhanced by several factors. The survey area was within narrow riparian habitat that included some conifer/deciduous trees mixed with riparian shrubs and had a relatively open canopy (percent cover data showed a range of 10-70% and an average of 39% cover classification). Moose will shift to dense conifer habitat as snow depth increases (Peek et al. 1976), but our study area had minimal snow accumulation (8-10 cm) and depth was not a factor in redistributing moose into denser cover. Additionally, detection on the centerline was further increased by the fact that we used a helicopter flying at 100 m AGL at a relatively slow speed of 48-88 kph. Although snow was shallow, visibility on the centerline was excellent.

Availability bias differs from visibility bias in that animals are not available to be detected at any distance (Marsh and Sinclair 1989). This is common in marine mammal surveys where whales, for example, are only on the surface of the water and available to detection for a certain amount of time during a day (Skaug et al. 2004). An example for terrestrial wildlife would be burrowing animals or an animal hiding in a cave or dugout and thus unavailable. If the animal cannot be detected while flying directly over it for various reasons (underwater, in burrow, under vegetation, etc.), it is considered unavailable and this bias needs to be considered in the model. Moose in our study area were assumed to be available for detection because of the relatively open habitat (39% canopy closure). One consideration would be tree root-wads from wind-fallen trees where the root-wad could hide a moose if it were to lay next to the wad in such a fashion as to not allow detection by the helicopter. However, if we flew directly over a root-wad we would detect the moose on the transect line ($g(W_1) = 1.0$). The moose would then be accounted for in the detection function at distances off the transect line (Laake et al. 2008). Availability bias could possibly be removed or reduced if the area was surveyed at different times (e.g., hours apart) to allow for animals to become available; this is likely dependent on species (Laake and Borchers 2004).

Additional methods can be used for testing assumption (1) such as by placing objects of interest (i.e., “models”) along a survey line and flying the transect, as if on a real survey, to determine how many of the known objects on the line were detected (Anderson et al. 2001). Radio-collared animals could also be used to test this assumption (Laake and Borchers 2004), however, the collared animals may not always be on the centerline, or too few of them, so binning the collars into distance categories is likely and does not allow a true estimate of $g(W_1)$.

Assumption (2), that objects are detected at their initial location, is sometimes difficult to assess (Fewster et al. 2008). An example would be an observer walking along a transect estimating ring-necked pheasant (*Phasianus colchicus*) abundance, where a pheasant will take evasive action at times by running through the grass away from the observer for some distance undetected before flushing. Not knowing where the pheasant originally was siting before the observer disturbed it is a violation of the assumption. Or in our case, it would mean that we disturbed moose and “pushed” them with the helicopter some distance before they were detected. Thompson (1979) reported that moose were not disturbed by circling fixed-wing aircraft during their survey and they did not move as the airplane approached them. However, Cumberland (2012) reported that moose usually initiated some movement when surveying with a larger turbine helicopter (Bell 206) and at a lower survey altitude (60 m AGL). Failure to meet assumption (2) would bias the density estimate low. Random movement is acceptable as long as it was not caused by the observer (Buckland et al. 2001).

We can investigate the validity of this assumption, in part, by reviewing the distance data histogram and looking for a bump or peak some distance away from the line. Our histogram shows a very slight bump in frequency at approximately 150 m from the transect line. Dalton (1990) presented a histogram showing a larger bump in frequency away from the centerline and indicated that this may have been due to recording biases or movement of moose before detection. Dalton (1990) used a larger and louder turbine-engine helicopter compared to our R-44, and flew faster and lower than we did. The increased noise from a turbine helicopter could partially explain more movement by moose before detection, but also the fact that flying faster and lower possibly created a situation where moose close to the line passed by too quickly to be detected compared to moose further off the line where the observer had more time and sighting angles to detect groups (Becker and Quang 2009). In our study, the front observer was focused on the centerline for the double-observer method, as well as looking forward of the helicopter to identify any pre-detection movement by moose (Fewster et al. 2008). Few moose were observed to have moved prior to the helicopter being in a position for the backseat observers to detect moose, where the movement was mainly in response to the helicopter being directly overhead. Because these few moose did not move into a zone of detection for the backseat observer, these movements were moot in our study.

Observations of moose within the effective search width (46-299 m) did not indicate movement prior to detection by the backseat observer. Another explanation for the bump in our data was that the backseat observers had a comfortable scanning level or sight picture (i.e., distance) while sitting in the helicopter. Observer fatigue increases as the survey progresses (Briggs et al. 1985, Schroeder and Murphy 1999) and possibly contributes to the desire to scan (subconsciously) at a less strained position. Jang and Loh (2010) graphed the classic wooden stake data outline in Burnham et al. (1980) and showed that the histogram had a large bump or spike of detections off the transect line. The spike in detections off transect is not from evasive movement by the wooden stakes, so other factors such as observer bias in estimating distances could have caused this. Overall, we most likely met this assumption as verified by the front observer scanning forward of the flight path and no appreciable increase in observed frequencies as distance increased from the transect line (Figure 3.4). Flying at a higher altitude (e.g., 122 m instead of 100 m AGL) as suggested by Nielson et al. (2006) should further increase the ability to meet this assumption.

Assumption (3), that perpendicular distance measurements are exact, is becoming easier to meet with available technology today. Measurement errors can affect density estimates (Chen 1998), but modern technology has significantly improved our ability to meet this assumption as compared to the estimation and binning of distance categories that were traditionally used, and which are still used to some degree today. Utilization of laser rangefinders, and in particular, rangefinders with built in clinometers, have greatly increased the accuracy and precision of measured distances to observed objects. Additionally, the use of GPS devices has greatly enhanced measurement accuracy, particularly when the US Government turned off selective availability for global positioning satellites in May 2000 (Office of Press Secretary, “Statement by the President Regarding the United States’ Decision to Stop Degrading Global Positioning System Accuracy”; 1 May 2000).

We utilized both rangefinders with built-in clinometers and GPS units to determine perpendicular distances to moose groups. Although both methods can be accurate and efficient, we did experience some difficulties using rangefinders. It was difficult to range moose at times, especially when groups were closer to the helicopter, which required a quick response by the observer before they were past, as well as when groups were in vegetative cover. Higher quality or industrial-type laser rangefinders may reduce this problem. We eventually adopted the technique used by Marques et al. (2006) and used GPS locations to measure moose distances. This method required more flying time and effort to fly off transect in order to obtain the moose group location, but we felt that obtaining GPS locations for distance measurements was the best option for this study area. The extra flying did disturb and move some moose before a location was obtained; in those few cases, we marked the location where we first saw the moose group, which was easily distinguished by the tracks in the snow. Increasing flight altitude while off transect may help alleviate or reduce disturbance to moose groups while marking their locations, as well as not banking hard to avoid excess noise levels. Fortunately, these moose did not move far and were not double counted on subsequent transects.

Other assumptions that are not generally discussed in literature such as the uniformity of the distance distribution and independence of group observations are typically addressed during the survey design process. The uniformity assumption is addressed by randomly distributing transect lines across the study area, or systematically arranging transects with a random start point, as we did in this study (Fewster et al. 2008, Jang and Loh 2010). The assumption that observations of moose groups are independent of each other is addressed in the same manner as distance uniformity (Buckland et al. 2001) provided that moose are not all clustered together in one part of the survey area. Estimates of density are robust to the independence assumption especially when bootstrapping by transects to obtain confidence intervals (Thomas et al. 2002). Additionally, we did not incorporate “dependent” moose groups observed while flying off transect when obtaining GPS locations for groups that were originally observed from the transect line. There were multiple instances where we found other moose groups during these off transect forays, but they were not included in the analyses.

Detection Functions

Survey design and protocol are paramount for meeting the three primary assumptions of distance sampling in order to model detection functions reliably (Thomas et al. 2010). Our survey transects were systematically distributed throughout the riparian corridors with random start points allowing for statistical inference (Fewster et al. 2009). Although transects were spaced 700 m apart and, thus, a maximum search width of 350 m could have been used in the analysis, there were very few observations beyond 300 m from a transect line. Restricting the analysis to observations within 300 m reduced the possibility that moose groups were counted more than once. In addition, Buckland et al.

(2001) recommend dropping the furthest observations prior to fitting a detection function as these are likely outliers and may have undue influence on the shape and scale of the detection function. We dropped nearly 8% of the farthest distance observations, which is within the recommended 5-10% (Buckland et al. 2001). Our effective search width (W_1 and W_2) was 253 m (46 to 299 m) and was narrower than the 700 m (Dalton 1990) and 800 m (Thiessen 2010) widths reported for moose surveys conducted in Canada. However, it was similar to the 250 m search width reported for moose by Thompson (1979). Our search width was narrow for several reasons: We were confined to a narrow corridor, we flew relatively low, and we had relatively poor snow conditions during the survey, which probably decreased visibility farther from the transect line. We recommend using narrow transect search widths during low or poor snow condition years to increase effectiveness of the survey.

Covariates can improve model precision by accounting for heterogeneity in the data (Buckland et al. 2004, Marques and Buckland 2004), but at an added cost of sample size (Giudice et al. 2012). We collected data on percent cover to help explain detection of moose groups. These data were incorporated into the models within the Distance software, but percent cover did not improve the detection function according to the higher AICc values for the models that included this covariate. This could be explained by the fact that we had a relatively narrow range of values (10-70%) and had to lump them into three categories during data analyses. Giudice et al. (2012) reported that visual obstruction by vegetation was a significant factor that affected detection of moose in Minnesota where their percent cover had a much wider range (0-95%) with a median of 60% cover. The spread of our cover data was narrow, and the average was only

39% (median 40%), which supports our perception that percent cover was not an issue in regards to detecting moose in this study area. However, we only had 58 moose group observations for analyses that included percent cover data and, therefore, the lack of model improvement could be affected by a small sample size. Buckland et al. (2001) recommends 60-80 observations and at least 10-20 replicate transects during a study in order to obtain reliable estimates with relatively good precision. Seddon et al. (2003) improved their survey precision (i.e., decreased CV values) with increasing observations. Thiessen (2010) analyzed several surveys and found a strong relationship between the number of observations and the CVs for those surveys, where surveys with 60 observations had a corresponding CV of approximately 20%. Our survey corroborates this relationship where our 59 observations used in the model without covariates had a CV of 20% (using the hazard-rate key function). Adding any covariates or stratifications would require considerably more observations to ensure the estimates are reliable with CVs at acceptable levels (i.e., CV = 20%). We examined the possibility of stratifying our study area by each tributary river (i.e, Eek, Kwethluk, Kisaralik, and Tuluksak) to increase management options; however moose densities were low enough to preclude having enough observations to acquire reliable estimates for each river alone, with the possible exception of the Kwethluk River (i.e., approximately 60-80 observation in each strata; Buckland et al. 2001).

Group size has been shown to affect detection of objects at distance (Drummer et al. 1990), and can be included as a covariate in the program Distance (Laake et al. 2008). We chose to investigate whether a correlation existed between group size and detection distance before we penalized ourselves with an additional covariate in the analysis

(Giudice et al. 2012). Although the literature suggests group size often affects detection, our analysis indicated that group size was not correlated with detection distance in this study. This is most likely a reflection of the population composition in our study area. Groups were relatively small with 73% of groups having 1-2 moose and only 6% of groups having 4-5 moose. Most observations were cows with calves. Since there was no correlation between distance and group size and the composition of groups had a narrow range of sizes (no major outliers), we used the average group size as equivalent to expected group size for the density estimate (Buckland et al. 2001).

We used the program Distance to develop a set of detection function models and used AICc model selection to identify the best fit model within the suite of models analyzed. Our choices of models to analyze were based on recommendations of Buckland et al. (2001) and past experience (Nielson et al. 2006) in order to prevent a “shotgun” approach to modeling. Models that included the percent cover covariate were ranked last and did not contribute to or improve the model according to AICc; we subsequently removed the covariate and analyzed the data without it. Our top model was the hazard-rate key function with no expansion terms. Several ungulate studies have found the half normal key function with various expansions terms to perform best (Trenkel et al. 1997, Jathanna et al. 2003, Peters 2010, Thiessen 2010); however, as in our study, several other ungulate studies reported the hazard rate key function with various expansions to be the top models (Focardi et al. 2002, Shorrocks et al. 2008, Young et al. 2010, Schmidt et al. 2011).

The kernel estimator used for the probability of detection curve does not use maximum likelihood methods, so one cannot calculate an AICc value for this model for comparison to modeling results of semi-parametric detection functions in the program Distance. However, the kernel-based estimated probability of detection, animal density, and CV were similar to those obtained from the hazard-rate model in Distance, although the CI was much narrower for the kernel estimator. Based on bootstrapping, all the semi-parametric models had estimated probability of detection biased low (i.e., lower than the kernel's $\hat{P}$ = 0.73), and thus estimated densities biased high. The estimated bias in the hazard-rate model estimate (1.4%) was higher than the estimated bias for the kernel-based estimate (<0.001%). An advantage of the nonparametric estimator is that it is free of parametric assumptions on the detection function. Additionally, using a kernel-based model does not require that detection is a monotonically decreasing function of distance away from the transect centerline, unlike semi-parametric models (Cassey and McArdle 1999). A limitation, however, is that it requires an adequate sample size in order to have a reasonable estimate (Chen 2000). Sample size was not a problem in our study for the level of precision we achieved because of our univariate analysis. However, we would need larger sample sizes when covariates are introduced, as would the semi-parametric analyses (Chen 2000). Buckland (1992) showed that the Hermite polynomial and the kernel estimates were very similar, with the kernel estimate less intensive to compute.

Survey Effectiveness

The study area is characterized by marginal snow conditions during any given year and has the most reliable conditions in February (Figure 3.5). The daily average snow depth as reported at Bethel, AK airport (2000-2010) clearly shows that the area does not accumulate deep snow and that there is a high variability between days. The daily variation is characterized by periods of warming and sometimes rain that melts accumulated snow rapidly, at times within a single day. On average, February has the greatest snow depth accumulation and daily retention, but this can vary significantly from year to year (Figure 3.5). For this study area, approximately 20 cm of snow accumulation is considered moderate to good conditions, and are required for the standard GSPE survey method. Dalton (1990) reported a snow depth of 20 cm and considered that “shallow” for his moose survey in Ontario, Canada.

Comparison of the helicopter line-transect method with the GSPE method is based on time, logistics, cost and potential estimate of precision. The GSPE method requires a minimum of 60 units surveyed between two moose density strata (30 low and 30 high strata), with preferably more units in high density areas because of the increased variation within that strata (Kellie and DeLong 2006). GSPE survey areas are a minimum of 777 km^2 because smaller areas have insufficient numbers of sample units to generate estimates (Kellie and DeLong 2006). These survey units are approximately 16.6 km^2 and require a minimum search intensity of 40 minutes/block with cub-like or tandem style fixed-winged aircraft (Kellie and DeLong 2006). The time required to fly the minimum intensity and number of units would be approximately 40 hours of flight time. One survey team can typically survey 5-6 blocks/day, so with two aircraft this survey would take a minimum of 5 days. In this region snow could melt or degrade during the survey period to the point that the survey could not be completed (Figure 3.5).

The helicopter line-transect survey was considerably more efficient in terms of area sampled and flight time than a fixed-wing GSPE. We flew a total of 16 hours in one helicopter, which included about 2.5 hours of training prior to the actual survey (training is highly recommended to prepare the survey team for duties and search patterns) and 13.5 hours for the actual survey, including all ferry times from the base of operation. We accomplished the survey in two days, which reduces the probability of snow deteriorating before the survey is over. The efficiency of the survey increases the ability to surmount deteriorating conditions by being able to quickly organize and execute the survey when conditions became favorable again. Cost based solely on flight hours of the survey aircraft was similar. A fixed-wing survey for the minimum sampling under the GSPE method in this area is approximately 6% less than using the helicopter line-transect technique. Six percent is a very small difference when the time (5 days vs 2 days) and the potential precision of estimates are considered. The helicopter survey had a coefficient of variation of 18%; in contrast, it is difficult to obtain this level of precision with the minimum number of GSPE units sampled because of potential stratification errors, sample sizes, and high variability of observations between units (Kellie and DeLong 2006).

Management Direction

The recent expansion and establishment of moose in the lower Kuskokwim River tributaries prompted our survey efforts. Our survey results show that the moose density in the study area is 0.465 moose/km^2 and is twice that of the adjacent lower Kuskokwim River survey unit during 2008 (0.23 moose/km^2, without SCF; Perry 2010). The difference can, in part, be attributed to presumably better habitat along the Kuskokwim tributaries compared to habitat along the main channel of the lower Kuskokwim River. The five-year moose hunting moratorium in the lower Kuskokwim drainage allowed moose to establish a viable population and expand into unoccupied habitat. The exploitation of this underutilized habitat is expressed in population production and is emphasized by the observed 30% composition of twin moose calves recorded during our March survey, which is high for this time of year. Comparative twinning rate data are collected in May during the peak calving period and can be used in conjunction with other variables to determine the nutritional status of moose in an area (Boertje et al. 2007). Density dependence was shown by Boertje et al. (2007) during high moose densities in interior Alaska when May twinning rates ranged from 4-21% indicating nutritional stress, whereas during years of low moose densities and recovery of vegetation, they found rates to increase (30-47%). May moose twinning rates in our study area have recently been recorded between approximately 47 and 67% (concurrent study; unpublished survey data, YDNWR) corroborating the relatively high nutritional status.

This moose population continues to grow and is an important subsistence resource for the people of the region. Continued monitoring is essential for sound management decisions regarding appropriate harvest levels in order to maintain a sustainable population while maintaining high nutritional status. We recommend that moose surveys be completed every 3-5 years to assess trends and inform management decisions.

Future surveys along the lower Kuskokwim tributaries should follow the same protocol used here (and potentially the same transects; Buckland et al. 2001), with the exception of how moose locations under the aircraft were recorded. Perpendicular distances from the transect line of moose under the helicopter detected by the front-left observer (i.e., moose groups approximately ± 43 m of the line-transect) should be estimated and recorded in future surveys. The precision of our density estimates would have been increased if we did not lump and remove from analyses the 10 observations that were under the helicopter during this survey.

The kernel density estimator was fairly precise (CV = 18%); however, if future surveys want to increase precision, then additional transects will need to be incorporated. Attaining a CV closer to 15% would require an additional 307 km of transects; a precision with a CV = 10% would require an additional 1564 km, given the current moose group encounter rate. The nature of the survey area is limited by narrow riparian corridors, which already have transects within these habitats. The only way to add more transects would be to make narrower search widths in order to fit more survey lines into the confined areas. This would however, greatly increase the chances of double counting moose. The only likely way that precision could be increased in this case is by an increase in encounter rate (i.e., more moose group observations). On the other hand, if precision of only CV = 20% is required, then a reduction of about 133 km of transects is possible.

Another consideration is pooling data across years to obtain more robust, and potentially more precise, estimates of detection probabilities (Burnham et al. 1980, Burnham et al. 2004, Fewster et al. 2005). Distance sampling is pooling robust and is demonstrated by the typical practice of pooling survey transects from a single study area since each transect typically would not have enough observations to create separate detection functions for each transect (Gerard and Schucany 2002). Pooling by year to increase sample size (observations) and to account for various survey conditions (e.g., snow conditions) could improve the global detection function for the area if repeated surveys are in the same area and preferably along the same transects (Nielson et al., in press).

If CVs range from 13%-19%, managers should be able to detect at least a 38% change in abundance using a 90% CI with 80% statistical power. This would mean for our density estimate of 0.465 moose/km^2 (340 moose) that we should be able to detect a change in density if the population changed by approximately 0.177 moose/km^2 (129 moose; 38%). Furthermore, if there is a 5-year period between surveys this would require a finite rate of change ($\lambda = e^{\{(\ln Nt - \ln N0) / t\}}$, where N_0 is the starting abundance estimate, N_t is the abundance estimate at time *t*, and *t* is the time period between surveys; Skalski et al. 2005: 295) equal to $\lambda = 0.909$ annually for a decreasing population or $\lambda = 1.066$ for an increasing population. This is a realistic change for moose in this area since the lower Kuskokwim survey unit showed an extreme growth rate of $\lambda = 1.647$ over a 4-year period (from 70 to 515 moose; Perry 2010).

This paper demonstrates a viable alternative to standard moose surveys conducted in Alaska. We demonstrate a technique to survey moose and analyze data in a subarctic tundra ecosystem that typically has marginal snow conditions. This technique worked well under our study conditions and could easily be applied elsewhere such as in areas with larger contiguous habitat and with various snow conditions. However, areas with dense canopy cover may require modeling vegetation covariates for sightability, which would require a much larger sample size of group observations and would reduce the estimate precision in areas with much lower moose densities. Nevertheless, as climate change increases the disruption of prevailing weather patterns and brings about more atypical and uncertain weather scenarios such as freeze-thaw or rain-on-snow events, wildlife managers now have more options for surveying moose. These uncertain, continuously changing, and often marginal conditions are not only on the YKD, but on portions of other moose ranges within subarctic Alaska, Canada, Scandinavia and Russia.

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Table 3.1. Estimated semi-parametric detection functions fit to 58 moose group observations using the program Distance (Thomas et al. 2010), including the number of expansion terms, whether the covariate for percent cover was included in the model, the number of parameters (*k*), AICc value, and estimated average probability of detection ($\hat{P}$), estimated moose density ($\hat{D}$), and coefficient of variation (CV) for each model.

Key Function	Expansion	Expansion Terms	*k*	% Cover (yes/no)	AICc	$\hat{P}$	$\hat{D}$	% CV
Hazard-rate	Cosine	0	2	N	627.85	0.71	0.480	19.1
Uniform	Cosine	2	2	N	629.26	0.67	0.505	25.3
Uniform	Simple Polynomial	1	1	N	629.47	0.70	0.485	17.3
Half-normal	Cosine/Hermite Polynomial*	0	1	N	629.48	0.62	0.547	21.0
Half-normal	Cosine	1	4	Y	631.40	0.85	0.398	18.2
Hazard-rate	Cosine	0	4	Y	631.42	0.68	0.498	18.4
Half-normal	Hermite Polynomial	1	4	Y	631.68	0.82	0.413	18.4

* No expansion terms were selected using AICc values.

Table 3.2. Estimated semi-parametric detection functions fit to 59 moose group observations using the program Distance (Thomas et al. 2010), including the number of expansion terms, whether the covariate for percent cover was included in the model, the number of parameters (*k*), AICc value, and estimated average probability of detection ($\hat{P}$), estimated moose density ($\hat{D}$), and coefficient of variation (CV) for each model.

Key Function	Expansion	Expansion Terms	*k*	AICc	$\hat{P}$	$\hat{D}$	% CV
Hazard-rate	Cosine	0	2	643.25	0.70	0.482	20.0
Uniform	Cosine	1	1	643.53	0.60	0.562	19.1
Half-normal	Cosine/Hermite Polynomial*	0	1	643.67	0.64	0.533	20.4
Uniform	Simple Polynomial	1	1	644.47	0.72	0.472	17.4

* No expansion terms were selected using AICc values.

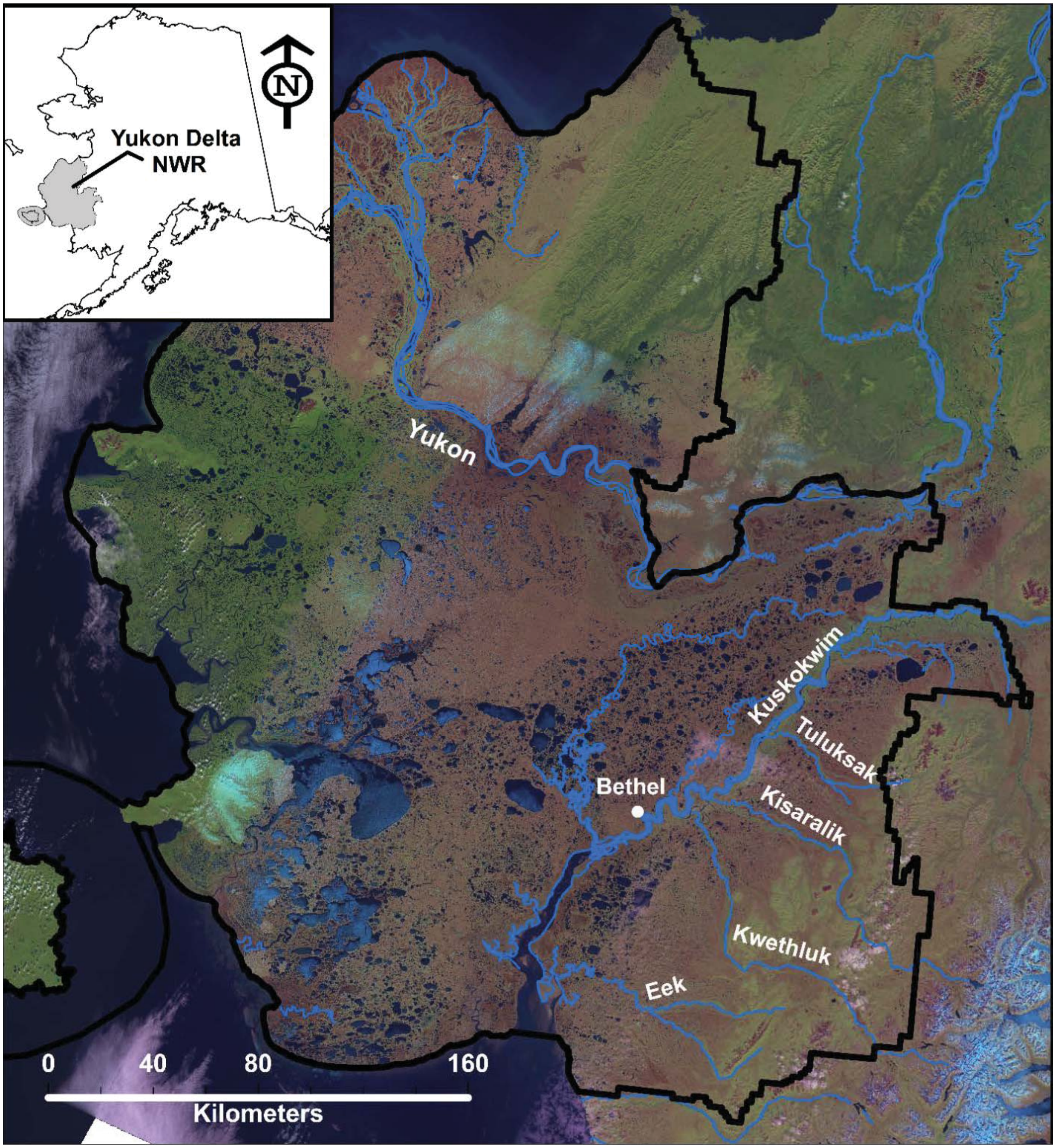

Figure 3.1. Yukon Delta National Wildlife Refuge encompasses the Yukon-Kuskokwim Delta in western Alaska. Bethel is the main community along the Kuskokwim River. The four main tributaries of the lower Kuskokwim River include the Tuluksak, Kisaralik, Kwethluk and Eek Rivers, which form the study area.

Figure 3.2. Tributary rivers within the study area are characterized by narrow riparian corridors bounded by open tundra. The relatively open forest and shrub habitat is conducive to sighting moose during a line-transect survey with a helicopter. This corridor is a part of the Kwethluk River and is approximately 800 m wide.

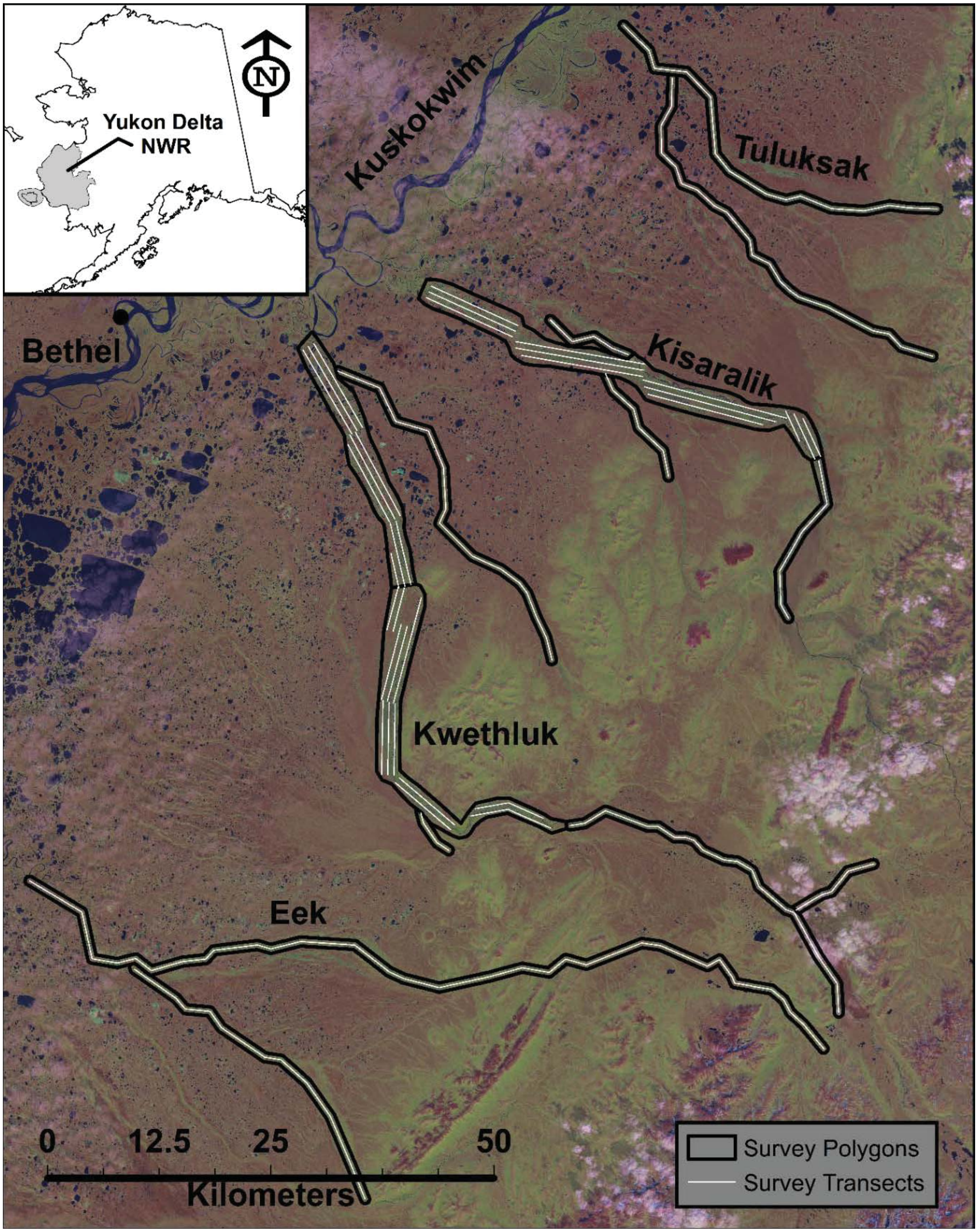

Figure 3.3. Lower Kuskokwim River tributary survey unit polygons and transects for the four main tributary rivers. These rivers are characterized by narrow riparian corridors bounded by open tundra.

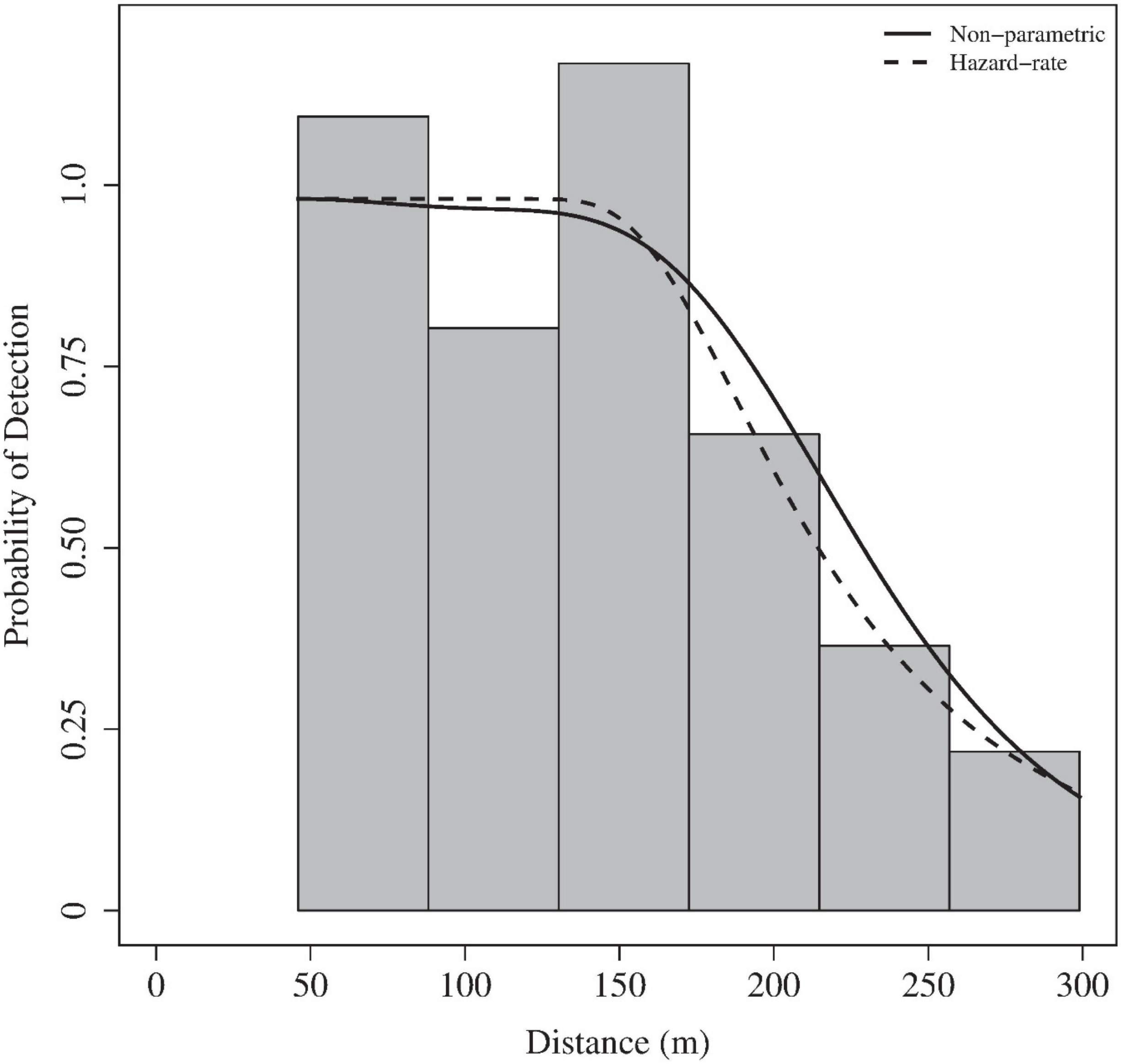

Figure 3.4. Histogram of the 59 moose group distance observations with corresponding detection functions superimposed. The final hazard-rate detection function was fit using the program Distance (Thomas et al. 2010); and the non-parametric kernel-based detection function was fit using the program R (R Development Core Team 2010). Perpendicular distances were shifted left by 46 m prior to analysis, but shifted back for graphing visual clarity.

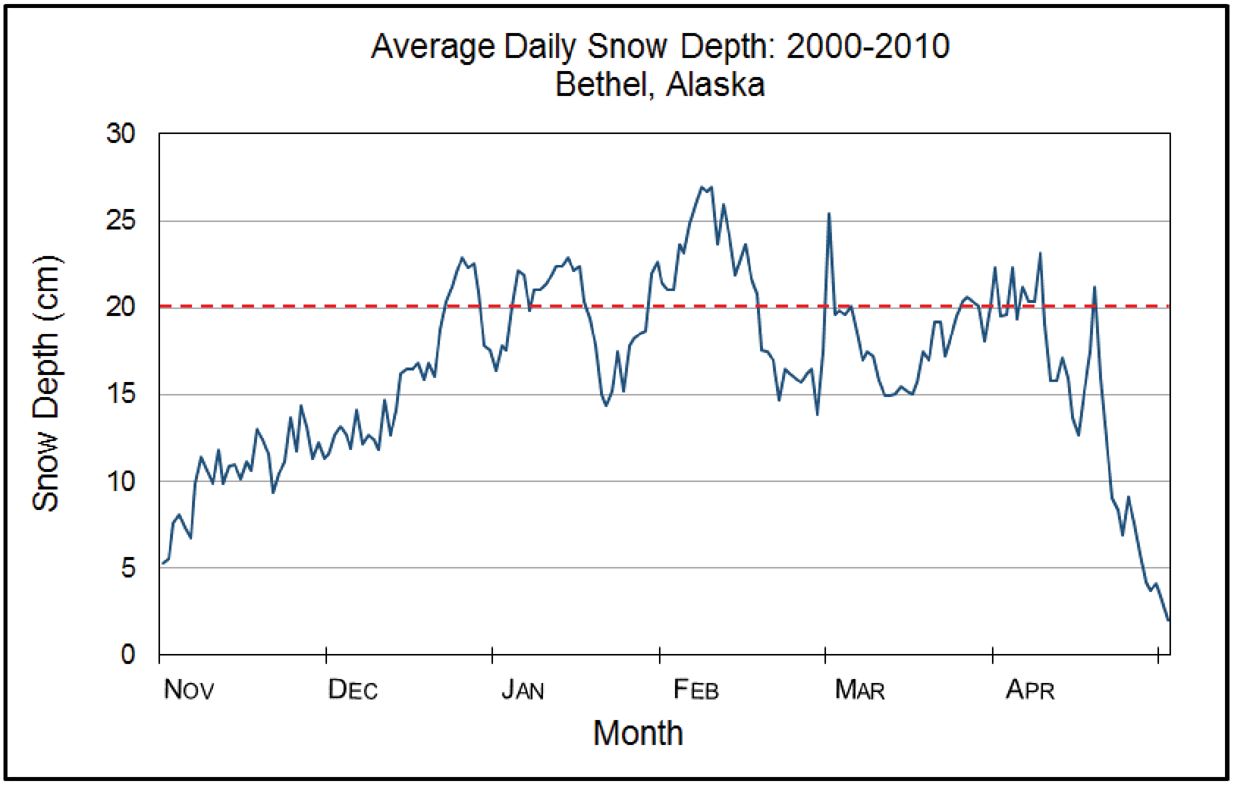

Figure 3.5. Average daily snow depth for Bethel, AK airport (2000-2010) during typical moose survey months in Alaska. Minimum snow depth for GSPE type moose surveys in this area is approximately 20 cm (dashed line). The variability in snow depth is due to periodic and rapid warming trends (NOAA 2011).

CHAPTER 4

ECOLOGICAL CHARACTERIZATION AND INDEXING OF MOOSE (*Alces alces*) WINTER RANGE IN WESTERN ALASKA[3]

Abstract

Moose recently became established and are expanding their population within the lower Kuskokwim River region of western Alaska. The habitat has previously had little browsing pressure and managers are concerned that the increasing moose population may negatively impact the structure of the habitat. Characterizing moose browse within the study area will index the current status of the habitat and establish a baseline for future management decisions. Our data clearly show that moose utilize flood plain habitat more than the active river channel habitat in this area. Greater utilization of browse species in the flood plain was evident from browse plants having more current annual growth shoots per plant, shorter willow-shrubs on average, higher probability of having dead material, and a higher probability of being broomed with a corresponding higher brooming index compared to the river channel stratum. Beaver were more probable to utilize browse plants in the river channel and selected for feltleaf willow the most. Hares utilized a broader range of browse, but highly selected against littletree willow. Moose were more probable to break branches on littletree willow and specifically in the river channel. Feltleaf willow was the most abundant and important browse species in the entire study area with sympatric hares, beavers and moose

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selecting for it. Diamondleaf willow was the second most abundant browse species in the study, and the most abundant in the flood plain. It is highly preferred by moose and is the most impacted of the browse species studied. Nearly all browse plants had some dead material, but only 11% had >50% dead material. Willows within the flood plain in general, and diamondleaf willow specifically had the highest probability of having >50% dead material. Most plants were unbrowsed, and only 11% were classified having broomed architecture. Willow-shrubs in the flood plain and diamondleaf willow specifically had the highest probability of being broomed with the highest brooming index. Brooming index values were significantly correlated to moose twinning rates and can be used to identify potential nutritional limitations in the moose-habitat system. Findings in this study support the observation that the increasing moose population has influenced its habitat. Ungulate impacts are not at a level of management intervention, however, and the browse habitat could support more utilization within this study area. It is recommended to keep monitoring the browse plants and stabilize the moose population to within the tolerances of the habitat.

Introduction

Herbivores can have a significant ecological effect on their environment and can act as agents of landscape change (McNaughton et al. 1988, Naiman 1988, Hobbs 1996, Kielland et al. 2006). Boreal forests can be considerably modified by moose (*Alces alces*; Pastor et al. 1988, McInnes et al. 1992, Persson et al. 2005), snowshoe hares (*Lepus americanus*; Bryant et al. 1983, Oldemeyer 1983, Bryant 1987) and beavers (*Castor canadensis*; Johnston and Naiman 1990, Moen et al. 1990, Donkor and Fryxell 1999, Martell et al. 2006) such that these mammals are significant ecosystem-drivers of forest succession (Risenhoover and Maass 1987, Johnston et al. 1993, Rossow et al. 1997, Butler and Kielland 2008) and nutrient cycling (Pastor et al. 1987, 1993; Kielland et al. 1997; Kielland and Bryant 1998). Because of these potential ecosystem changes, an expanding moose population, such as currently seen in western Alaska, could have subsequent effects on its habitat. The assessment of the current status of those habitats is essential for responsive wildlife management.

The heterogeneity and magnitude of effects on plant communities by moose can vary considerably (Pastor et al. 1997, Pastor and Danell 2003); however, some overarching generalizations can be made. Moose browsing on preferred forage species such as willows (*Salix* spp. L.), poplar (*Populus* spp. L.), and birch (*Betula* spp. L.) will initially elicit a compensatory growth response by the plant (Bergstrom and Danell 1987a, Danell et al. 2003, Pastor and Danell 2003) that increases the nitrogen uptake and deposition in growing tissue leading to higher quality forage (Singer and Schoenecker 2003). Higher quality litter combined with fecal and urine deposits (Persson et al. 2000) enhances decomposition, mineralization and plant uptake of nitrogen; and often times results in a positive feedback at the plant level (Pastor and Naiman 1992, Stolter 2008). Continued long-term selective browsing or an increase in browsing intensity (i.e., increased moose density) will eventually suppress or decrease plant height and vigor, leading to plant mortality and replacement by non-preferred, nutrient-poor and chemically defended plant species (Bryant and Kuropat 1980, Bryant et al. 1989). The change in plant community is typically toward a conifer-dominated stand with lower litter quality (Kielland et al. 1997, Chapin et al. 2006). Although browsing initially stimulates plant production and increased availability of preferred forage at the plant level (Peinetti et al. 2001, Danell et al. 2003), long-term browsing eventually changes the plant community structure, ultimately leading to the change from higher quality (nitrogen rich) to a lower quality litter. The nitrogen-poor litter decomposes at a slower rate with lower mineralization and uptake of nitrogen and leads to an overall decline in nutrient cycling and productivity of the site (Pastor and Danell 2003, Singer and Shoenecker 2003).

Moose are mostly recognized as a boreal forest species, but they can inhabit various ecoregions throughout their circumpolar distribution (Telfer 1984) and can exert landscape pressures across their entire range of habitats (Houston 1968, LeResche et al. 1974, Peek et al. 1976, Pastor et al. 1988, MacCracken et al. 1997). Broad-scale habitats used by moose have been classified based on a continuum of vegetation or successional stability, and their potential for supporting moose at varying densities (Telfer 1984, Peek 2007). In North America, the boreal forest is considered the least stable habitat type for moose due to succession-altering fire regimes (Rowe and Scotter 1973, Kasischke et al. 2006), whereas stream valleys dominated by willow/poplar and shrub/scrub communities (found mainly in mountainous regions), which typically support lower moose densities, are considered the most stable (Peek 2007). Large alluvial river deltas such as the Mackenzie in the Northwest Territories, and the Copper, Yukon and Kuskokwim River deltas in Alaska are considered intermediate in stability and are relatively productive (Telfer 1984, MacCracken et al. 1997). The alluvial delta habitats differ from the fire-seral communities because their main drivers of primary succession arise from erosion, flooding, and ice scouring, which provide a relatively stable and permanent habitat for moose (LeResche et al. 1974, Helm and Collins 1997). Rivers create forest corridors that extend moose habitat into arctic and subarctic tundra ecosystems (Kelsall 1972). In west-central Alaska, the Kuskokwim River flows through boreal forest habitat of interior Alaska while the lower portion of the Kuskokwim flows through subarctic tundra to the Bering Sea. The Kwethluk River, a tributary of the lower Kuskokwim River, originates in the adjacent mountains and is an example of the transition from delta flood plain to tundra-subalpine habitat, which is considerably more stable or permanent than either delta, boreal or mixed forest habitats.

Moose have been considered generalist herbivores (Belovsky 1978, 1981; Saether 1990) and have been reported to eat a wide variety of forage species (Peterson 1955, Renecker and Schwartz 2007), varying by season (Timmermann and McNicol 1988) and by plant phenology (LeResche and Davis 1973, Hjeljord et al. 1990, Dungan and Wright 2005). However, moose can become specialist herbivores selecting only a few forage species or species from one main genera during certain seasons like winter (Risenhoover 1989, Miquelle et al. 1992, McCracken et al. 1997, Shipley 2010). With habits somewhere between a generalist and a specialist (Shipley 2010) or a selective generalist (Peek 2007), moose consume a variety of woody plants (browse) in order to moderate the impact and effect of any one secondary compound from one plant species (Renecker and Schwartz 2007), in contrast to more specialized feeders (McArthur and Sanson 1991, McArthur et al. 1991) that select fewer plant species or avoid toxic plants altogether. Secondary compounds such as tannins can affect dietary selection, consumption, and protein digestibility (Bryant and Kuropat 1980, Palo 1984, Hagerman et al. 1992, Hanley et al. 1992, Stolter et al. 2005). Moose and other mammals produce tannin-binding, protein-rich saliva (Robbins et al. 1987, Austin et al. 1989, Shimada 2006) to help process specific tannins found in preferred forages such as willow, birch and poplar (Hagerman and Robbins 1993, Juntheikki 1996).

Regional forage selection by moose can significantly vary throughout their distribution (Peek 1974). For example, Scandinavian moose diets are largely comprised of rowan (*Sorbus aucaparia* L.), Scots pine (*Pinus sylvestris* L.), willow, and birch (Bergstrom and Hjeljord 1987, Vivas and Saether 1987, Histol and Hjeljord 1993, Shipley et al. 1998); whereas, in Alaska, moose generally consume willow, birch, aspen (*Populus* spp. L.) or other poplar species (Peek 1974, Van Ballenberghe et al. 1989, Seaton 2002, Renecker and Schwartz 2007). Alaskan moose utilize a high proportion of willow species for much of their diet throughout the year, and increase the use of willows during the winter (Machida 1979, Risenhoover 1989, McCracken et al. 1997). Variation in preference of willow species can vary at the regional-scale (Milke 1969, Machida 1979) and at the habitat patch-scale (Risenhoover 1987, Weixelman et al. 1998) due to forage density, morphology, nutrient quality, and secondary compound content (Oldemeyer et al. 1977, Bergstrom and Danell 1987b, Shipley and Spalinger 1995, Shipley et al. 1998, Kielland and Osborne 1998, Spaeth et al. 2002).

Studies in central-interior Alaska indicate relative preference by moose for the willow species of feltleaf (*Salix alaxensis* [Andersson] Coville), littletree (*S. arbusculoides* Andersson), diamondleaf (*Salix pulchra* Cham.), grayleaf (*S. glauca* L.), and other browse species to a lesser extent such as birch, aspen, cottonwood, poplar and highbush cranberry (*Viburnum edule* [Michx.] Raf.; Wolff and Zasada 1979, Wolff and Cowling 1981, Risenhoover 1989, Collins and Helm 1997). In south-central Alaska, Machida (1979) showed that moose preferred littletree, Scouler's (*S. scouleriana* Barratt ex Hook.), and Bebb (*S. bebbiana* Sarg.) willows, while Oldemeyer et al. (1977) indicated that birch, aspen, willow, and alder (*Alnus* spp. Mill.) represented major browse items. In the eastern-interior Alaska, Milke (1969) documented that moose highly preferred feltleaf and diamondleaf willows followed by sandbar (*S. interior* Rowlee) and littletree willows. In south-eastern Alaska, Barclay's (*S. barclayi* Andersson) and Sitka (*S. sitchensis* Sanson ex Bong.) willows were the main diets of moose (McCracken et al. 1997). In most Alaskan studies, feltleaf willow is consistently one of the most preferred species when available.

Habitat and foraging studies for moose in western Alaska are few: an expanding moose population along the lower Kuskokwim River has led resource managers to study these relationships. Moose have recently colonized the Kuskokwim Delta in western Alaska, but were held at very low densities by hunting pressure (Coady 1980) until a five-year moose hunting moratorium was successfully implemented, starting in 2004 (chapter 2-this dissertation). The hunting closure allowed moose to establish a sustainable population and to significantly increase their density along the lower Kuskokwim River (Perry 2010), and especially along the Kwethluk River (Wald and Nielson 2014), a tributary of the Kuskokwim. The relatively narrow riparian corridor of the Kwethluk River has limited habitat and forage for moose, and wildlife managers have concerns about the habitat approaching its capacity to support a higher density of moose. Monitoring these preferred habitats and key forages is prudent for proactive population and ecosystem management of herbivores such as cervids (McShea et al. 1997, Mysterud et al. 2010, Putman et al. 2011, Seaton et al. 2011). Wildlife managers have historically often utilized population density estimates alone for making management decisions (e.g., Yukon Delta NWR). Managers can expect to better develop and meet management objectives if they utilize a multi-dimensional approach that incorporates population nutrition or demographic parameters and their habitat relationships (Boertje et al. 2007, Morellet et al. 2007, Putman et al. 2011, Young and Boertje 2011). As moose alter ecosystems by extensive and long-term browsing of preferred forages, they are subsequently expected to suffer decreased nutritional status (Boertje et al. 2007, Seaton et al. 2011). These negative density-dependent factors related to forage and nutrition are likely to be manifested in the population by decreased twinning and parturition rates, an increase in age of first reproduction, and a decrease in yearling body mass (Boertje et al. 2007, Morellet et al. 2007). Because there may be a long lag period between habitat degradation and a decline in a detectable density-dependent parameter, the habitat may become significantly degraded before being detected if only density-dependent indices are used, creating a reactive instead of proactive management approach (Mysterud et al. 2010, Seaton et al. 2011). This emphasizes the need for a habitat evaluation component in management decision making.

Because density alone does not inform resource managers about the habitat-herbivore relationship, this paper addresses development of a habitat component for an adaptive ecosystem-based approach to managing moose in western Alaska. Our main objectives were to develop an understanding of current habitat conditions in relation to moose, and to establish a baseline characterization of moose browse for future comparisons under different management direction. Our specific objectives were:

1) To develop a simple, repeatable and rapid browse assessment for current moose population densities and for future reference as the moose population expands.
2) To determine plant densities, characteristics, and a browsing index for each important moose browse species in the study area.
3) To determine differences between two habitat strata (river channel and flood plain) for each measured browse characteristic and for each browse species.
4) To investigate interactions of moose, beaver and snowshoe hares as relating to browse utilization and preference of forage species within the study area.

Study Area

The study occurred along the Kwethluk River within the Yukon Delta National Wildlife Refuge in western Alaska (Figure 4.1). The region has a subarctic continental climate moderated and influenced by the Bering Sea (Alt 1977). Climate data from 2000-2010 (Bethel, AK airport; NOAA 2011) indicate average monthly temperatures range between 13˚ C in summer and -14˚ C in winter (average daily ranges: -34˚ C to 21˚ C). Average yearly precipitation is approximately 54 cm, with the majority falling between July and September. Winter months (November-March) temperatures range from -7˚ C to -14˚ C with January being the coldest. Although daily snow depth can range from 0 to 76 cm, mean monthly snow depths are minimal (10 to 20 cm) due to frequent low pressure systems depositing and melting snow throughout the winter (NOAA 2011). Areas with significant snow accumulation from drifting (i.e., tree/shrub areas) retain deeper snow longer and are less influenced by the freeze/thaw cycles that frequently occur (Wilson et al. 2013). The Kwethluk River flows north by northwest to the Kuskokwim River and is one of several tributaries that drain the Kilbuck Mountains. The study area is approximately 32 km of riparian zone along the river between Elbow Mountain (lat 60°18’32”N, long 160°57’28”W) and Three-Step Mountain (lat 60°32’39”N, long 160°05’18”W). This segment is characterized by a relatively narrow riparian zone (0.8 to 2.4 km wide) having a mixed forest overstory of white spruce (*Picea glauca* [Moench] Voss), balsam poplar (*Populus balsamifera* L.), and Alaska paper birch (*Betula neoalaskana* Sarg.) with an understory of willow and alder bounded by upland tundra on either side of the flood plain. Plant taxonomic naming conventions follow Viereck and Little (2007).

Methods

Plot Selection

Based on observed moose GPS collar data (unpublished data from a concurrent study) there were perceived differences in utilization between the active river channel habitat and the more extensive flood plain habitat. Therefore, we stratified the survey area by river channel (RC) and flood plain (FP) habitats to allow comparisons between the two habitats (Figure 4.1). Additionally, stratification would allow us to identify potential biases in browse surveys if we only sampled the river corridor, as initially proposed to save time and expense (i.e., if no differences are found, then we could potentially only sample the river corridor). Sample locations were systematic and random in the two strata. For the RC stratum, we used a random start point and overlaid the main river channel with an array of systematic points in a 400 m grid resulting in 83 points intersecting (or nearly so) the river channel. We created the FP stratum by drawing polygons around the flood plain areas (using satellite imagery) off the main river channel that exhibited high moose use (from GPS data) and generated 66 random points qualified by a 400 m minimum separation distance between the points. Stratification and sampling points were generated using QuickBird satellite imagery in ArcGIS 9.3 (ESRI, Redlands, CA) with Hawth's Tools extension (version 3.27; Beyer 2004).

At each sampling location a 30 m circular plot was used for the habitat assessment. River channel locations were originally plotted in the active channel, so we randomly selected a side of river to sample unless one side lacked riparian flora (e.g., a cut-bank into upland tundra) in which case, we sampled the other side. All river channel plot centroids were selected a minimum of 15 m (plot radius) off the active scour zone to insure that vegetation was in a successional stage with plants at least 0.5 m tall (the minimum height for moose browsing in winter; Wolff and Zasada 1979, Milke 1969). Flood plain plot centroids were moved to the nearest habitat patch if they fell within a pond.

Data Collection

Four 15 m transects were developed from the centroid of each 30 m circular plot starting with a random bearing and each subsequent transect being 90 degrees to the previous (Figure 4.2). At one meter intervals, up to 40 individual plants (only one plant per interval) considered moose browse were sampled along transects. A plant was measured if its base originated within a one meter arc forward of the sampling interval and had available moose browse between 0.5 m and 3.0 m (Figure 4.2(a)). Since we are essentially measuring winter browsing effects, this interval represents the typical "browse-zone" for moose during winter (Seaton 2002, Hjeljord et al. 2000, Seaton et al. 2011). Each plant was considered an individual if there was a minimum of one "boot" length (~12"; Winward 2000) separation between basal areas of plants. Only the closest plant to the sampling interval was sampled and if no plant was within the one meter arc, the next transect interval was sampled. If less than 30-40 plants were sampled in the first four transects, additional transects were laid out between existing transects until the desired number of plants were sampled (Figure 4.2). Extra transects were only used for sampling individual plant characteristics and not density estimates.

Browse species sampled included Alaska paper birch (PABI), balsam poplar (BAPO), littletree willow (LTWI), diamondleaf willow (DIWI), feltleaf willow (FLWI), Richardson's willow (*Salix richardsonii* Hook.; RIWI), Pacific willow (*S. lasiandra* Benth.; PAWI), Bebb willow (BEWI), grayleaf willow (GLWI) and highbush cranberry (HBCR; see Appendix 4.A for a complete list of plant acronyms used in the analyses). Since long-term or intensive browsing by moose can affect the structural characteristics of their habitat, we measured morphological parameters of the browse species to assess the habitat condition. Data recorded for each plant sampled included species, height, number of current annual growth shoots, presence of beaver or snowshoe hare use, presence of broken branches caused by moose feeding, if the plant arose from a prostrate (e.g., wind-fallen or beaver-cut) tree trunk, browse architecture, and proportion of dead material. A sampled "plant" in this case was defined as either a single stemmed individual (e.g., birch) or a cluster of stems of the same plant (< 12" apart) depending on individual species' growth form.

Plant height was measured with a telescoping pole delineated by decimeter increments. The number of current annual growth shoots was estimated within the browse-zone for each plant sampled. If plants had few shoots (<150), then all were counted within the zone. However, if the plant had many shoots (>150; e.g., littletree willow), we estimated the number by counting one third of the shoots and extrapolating to the other two-thirds of the plant.

Browse architecture was assessed within the browse-zone for each plant and categorized as broomed, browsed or unbrowsed by moose during the winter. As defined by Seaton (2002), a plant was classified as "broomed" if more than half of its current annual growth arose from lateral shoots that were a result of previous moose browsing. A plant was classified as "browsed" if less than half of its current annual growth arose from lateral shoots that were a result of previous moose browsing; and a plant was classified as "unbrowsed" if it had no sign of moose browsing. We distinguished between moose and snowshoe hare browsing by the type of cut at the point of cleavage. Hares produce a distinct clean 45° angle cut created by the top and bottom incisors, while moose leave a ragged tear cut at the point of bite created by the bottom set of incisors and the upper smooth palate (moose do not have upper incisors). The proportion of dead plant material was classified as no dead material, less dead than alive material, and more dead than alive material. These metrics give an idea of potential overuse of browse species.

Densities of browse and non-browse species (white spruce [WHSP], Siberian/green alder [*Alnus fruticosa* Rupr.; GRAL], and Sitka alder [A*lnus sinuata* (Regel ex DC.) Rydb.; SIAL]) were estimated for each plot location. The four original 15 m transects that were running 90° from each other within the sampling plot were walked and all plant species of interest that were ≥0.5 m in height and had basal areas originating within a belt of one meter on either side of the line were counted (Figure 4.2(b)). Density for each species was calculated by dividing the number of plants for each species by the area sampled within each plot (i.e., total transect area = 120 m^2).

Data Analyses

Habitat Strata Selection by Moose

To determine selection of different habitat strata (FP vs RC) by moose, we used a Design II selection ratio (Thomas and Taylor 1990, Manly et al. 2002). In a Design II analyses, use of resources are measured for each individually marked animal, and the availability of resources is measured at the population level (i.e., the same resources and amounts are available to all individuals; Manly et al. 2002). We used the flood plain and river channel strata polygons in our study area to designate the two habitat types and determine the availability of each for the selection ratio analyses (Figure 4.1). The sampled flood plain encompassed 40.29 km^2; the river channel was 20.86 km^2. Availability for each habitat type was determined as their respective proportion of the combined areas. Moose use was determined by plotting GPS collar locations (± 30 m accuracy) of 20 moose (concurrent study) within the study area. Only winter locations (December 1 through April 30) were used to represent the time period of critical browse usage by moose. Locations were recorded approximately every 90 minutes for each moose over multiple years (1-3 yrs). Not all moose had the same number of locations. In the Design II analyses, an average selection ratio was estimated for the entire population (within the study area) by calculating $\widehat{w}_{ij}$ for each individual moose using the equations (Manly et al. 2002):

$$\widehat{w}_{ij} = \frac{(u_{ij}/\, u_{+j})}{\pi_i} \quad , \tag{4.1}$$

where $\widehat{w}_{ij}$ is the selection ratio for an individual moose for a specific habitat type, u_{ij} is the observed used component of the *i*th habitat for the *j*th moose, and π_i is the available proportion of the *i*th habitat. The average selection ratio for the population is given by the expression:

$$\widehat{w}_i' = \sum_{j=1}^{n} \widehat{w}_{ij}/n \quad , \tag{4.2}$$

where $\widehat{w}_i'$ is the overall average selection ratio for moose in the *i*th habitat, and *n* is the total number of individual moose. The variance for the average selection ratio of the i^{th} category can be calculated as (Manly et al. 2002):

$$var(\hat{w}_i') = \{ \sum_{j=1}^{n} (\hat{w}_{ij} - \hat{w}_i')^2 / (n-1)n \} \quad . \tag{4.3}$$

We analyzed the selection ratio data using Package ‘adehabitatHS’ (version 0.3.9; Calenge 2006) in R. All data analyses in this study were performed using R version 3.0.2 (2013-09-25; R Core Team 2013).

Plant Densities

We analyzed plant densities by using the count data from the 120 m^2 sampling areas within plots (Figure 4.2(b)). Plant count data appeared to be zero-inflated (Appendix 4.B-1), meaning a high proportion of zeros for certain species on plots (i.e., a particular species not observed on a plot), and hence the creation of overdispersion where the count variance is larger than the count mean (Zar 1999). Akaike’s information criterion (AIC) was used for model selection (Burnham and Anderson 2002) to determine if a zero-inflated Poisson or a zero-inflated negative binomial model described the data better. Without exception, the negative binomial models performed better than the Poisson models (Appendix 4.B-2).

There are a variety of ways in which to model observed zero counts. A ‘true zero’ is a zero count at a location that has plausible habitat but, due to natural variability, the plant is not currently present. Other, ‘false/excessive’ zeros arise from design error (possibly sampling too small of an area), observer error (objects are present, but the observer failed to see or misidentified them), structural error (object not present because habitat is not adequate), or object error (object not present, but habitat is adequate). In our case for plants, ‘false/excessive’ zeroes might arise from design error (false zeros due to possible sample frame too small, or only sampling plants ≥0.5 m in height), observer error (false zeros due to possible misidentification) and structural error (true zeros due to no plants in sample frame, but adequate growing conditions).

When using the negative binomial distribution alone to model counts (denoted by NBIN in Appendix 4.B.3), it is assumed that zeroes are not overly abundant beyond what the negative binomial distribution would allow for (i.e. there are no false/excessive zeroes present). The zero-inflated negative binomial recognizes the possibility of there being both ‘false/excessive’ zeroes and ‘true’ zeroes and a two-part mixture model is used for modeling. A binomial model is used for the ‘false/excessive’ zeroes and a negative binomial model is used for the ‘true’ zeroes (Zuur et al. 2009). There are generally two approaches for the zero-inflated negative binomial modeling – 1) The use of the same covariates (regressors) for the binary and count components (denoted by ZINB.Density in Appendix 4..B.3); and 2) The use of different regressors for the binary and count components (denoted by ZINB.Density1 in Appendix 4.B.3). While the negative binomial distribution allows for naturally occurring zero counts, the Hurdle model assumes that all zeroes are false/excessive. The Hurdle model output is denoted by ZANB.Density in Appendix 4.B.3. We used model selection (AIC) and likelihood ratio testing to determine which approach to modeling zeroes was best for our data. If two models had similar AIC values, we used a likelihood ratio test to determine if there was a difference in model fit between the two. Model selection indicated that the Zero-Inflated Negative Binomial (ZINB) was best (Appendix 4.B-3).

We used Package 'pscl' (version 1.4.6; Jackman 2014) in the R program with the *zeroinfl* (Zeileis et al. 2008) model call to model our plant density count data. We calculated the mean for the ZINB model following Zuur et al. (2009):

$$E(Y_i) = \mu_i * \ (1 - \pi_i), \tag{4.4}$$

and the variance as

$$var(Y_i) = (1 - \pi_i) * \left(\mu_i + \frac{\mu_i^2}{k}\right) + \ \mu_i^2 * (\pi_i^2 + \ \pi_i)\,, \tag{4.5}$$

where (π_i) is the probability of a false or excessive zero, (μ_i) is the mean of the positive count data, and (*k*) represents the dispersion parameter or the theta statistic from the ZINB model.

Plant Heights

We used a mixed-effects framework to model plant heights and test for differences between strata. The mixed-effects model with plot, the sampling unit, as a random effects term accounts for the lack of independence (i.e., correlation) between plant samples within a plot and unequal sample sizes (i.e., unbalanced) between plots (Pinheiro and Bates 2000). We predicted the log height of plants based on strata using the Package 'nlme' (version 3.1-117; Pinheiro et al. 2014) with the *lme* model call and the restricted maximum likelihood estimator (REML; Kenward and Roger 1997) in the R program. We used the log of plant heights to transform the original height data in order to better approximate the normal distribution. The variance-covariance matrix of the model parameter estimates was used to calculate the variances and standard errors (SE) of the means for each strata. The variance for the mean of the reference strata (FP) is equal to the variance of beta0 in the variance matrix. Its subsequent SE is calculated using the general formula:

$$SE_{floodplain} = \sqrt{\sigma^2_{beta0}} \quad , \tag{4.6}$$

whereas the variance for the RC strata was calculated using the variance of each beta and the covariance between the betas, such that:

$$\sigma^2_{riverchannel} = \sigma^2_{beta0} + \sigma^2_{beta1} + 2 * cov_{beta0:beta1} \quad . \tag{4.7}$$

Furthermore, the SE for the RC strata was calculated as in equation 4.6. The 95% confidence intervals were approximated for each strata using:

$$\mu_{strata} \pm 2 * SE_{strata} \quad . \tag{4.8}$$

The mean and confidence intervals for each strata were back-transformed to the original scale for interpretation and display of results.

Plant Shoots

The plant shoot count data are quite heterogeneous (variable) and have indications of overdispersion (i.e., variance greater than the mean). We found that the typical model distribution used for count data (Poisson) was indeed affected by the overdispersion (i.e., if deviance/df-residuals equals 1, then not overdispersed; Appendix 4.C). To account for the excess variability while fitting the Poisson model, we included another model term for the individual-level random effects (i.e., plants within plots). The Poisson model with both random terms performed better than the model with only one random term, but was still affected by the excess dispersion (Appendix 4.C). Therefore, the negative binomial distribution was used to model these data and typically performed better than the Poisson when comparing AIC values (Appendix 4.C). We used a mixed-effects framework to predict the number plant shoots based on strata with plot as a random effect using the Package ‘glmmADMB’ (version 0.8.0) and the model call *glmmadmb* (Fournier et al. 2012, Skaug et al. 2014). Similar to the individual plant-level random effect in the Poisson model, we used an offset-term in the negative binomial model. The offset used was the natural logarithm of the number of plants/plot (log transformation used to put these values on the existing log scale in the negative binomial model).

The model’s offset-term is required in the modeled mean estimate for each strata; therefore, the average number of plants per plot in each strata (FP = 30 and RC = 40 plants) is incorporated into the mean estimate by adding the offset-term. The respective modeled means are adjusted by: log(meanFP) = beta0 + log(30 plants), and the log(meanRC) = beta0 + beta1 + log(40 plants). The natural logarithm of the number of plants is used to keep the values on the same scale. The variances, SE, and confidence intervals for each strata are all calculated in the same way as the plant height variable using equations 4.6-4.8. All values are back-transformed from the log-scale to the original scale (number of shoots).

Effects of Sympatric Browsers

Other browsers such as snowshoe hares and beavers have been shown to affect ecosystems shared with moose (Belovsky 1984, Moen et al. 1990). We modeled the effects that these sympatric browsers have on moose browse species within the study area. These data are binomial and the variables ‘Hare’, ‘Beaver’, ‘Log’, and ‘Broken’ were analyzed using mixed-models to model the response variables with plot as the random effect. We used Package ‘lme4’ (version 1.1-7; Bates et al. 2014) with the model call *glmer* to predict mean responses for each binomial variable based on strata and independently by species. Package ‘effects’ (version 3.0-1; Fox 2003) was used to fit 95% confidence intervals; however, when estimating the global model mean (i.e., intercept only model), the ‘effects’ package failed. Therefore, we calculated *Wald intervals* (Agresti and Coull 1998) using the ‘lme4’ package and the *confint* model call to construct intervals around the modeled global mean probability ($\hat{p}$). Although *Wald intervals* often perform poorly with small sample sizes, Vollset (1993) showed that these intervals perform similarly to several other robust methods when n >100. We compared the standard normal (e.g. equation 4.8) and a bootstrap routine to the *Wald intervals* and they were all similar, which is indicative of the large sample sizes used (n >4300) for the global models.

Architecture and Dead Class

Plant architecture and amount of dead material a plant has can be used to describe the effects that moose have on browse species (Seaton 2002), particularly intensity of use. We assume that the greater the probability of a plant being in the broomed architecture or >50% dead categories, the greater the use by moose. We used Package 'ordinal' (version 2013.9-30; Christensen 2013) to fit cumulative link mixed models to the multinomial data variables of plant architecture and plant dead class. The model call *clm* within the ordinal package was used to predict the mean probabilities of the different response levels (categories in Architecture and Dead Class) with plot as the random effect. Mean probabilities were modeled for each response level for each strata. We calculated the mean probabilities of each architecture classification (the dead classification was calculated identically) for the flood plain stratum using the equations:

$$\pi_{arch:1} = \frac{e^{(\theta_{1|2})}}{1-e^{(\theta_{1|2})}} \quad , \tag{4.9}$$

$$\pi_{arch:2} = \frac{e^{(\theta_{2|3})}}{1-e^{(\theta_{2|3})}} - \frac{e^{(\theta_{1|2})}}{1-e^{(\theta_{1|2})}} \quad , \tag{4.10}$$

$$\pi_{arch:3} = \frac{e^{\left(-\theta_{2|3}\right)}}{1-e^{\left(-\theta_{2|3}\right)}} \quad , \tag{4.11}$$

where $(\pi_{arch:i})$ is the mean probability of the i^{th} architecture level, and (θ) is the theta parameter for the cumulative threshold coefficients. For the river channel stratum, we used the equations:

$$\pi_{arch:1} = \frac{e^{(\theta_{1|2} - b_1)}}{1 - e^{(\theta_{1|2} - b_1)}} \quad , \qquad (4.12)$$

$$\pi_{arch:2} = \frac{e^{(\theta_{2|3} - b_1)}}{1 - e^{(\theta_{2|3} - b_1)}} - \frac{e^{(\theta_{1|2} - b_1)}}{1 - e^{(\theta_{1|2} - b_1)}} \quad , \qquad (4.13)$$

$$\pi_{arch:3} = \frac{e^{(-\theta_{2|3} + b_1)}}{1 - e^{(-\theta_{2|3} + b_1)}} \quad , \qquad (4.14)$$

where the additional (b_1) term is the beta coefficient for the strata predictor variable.

We used a bootstrap routine with 999 re-samples (with replacement) to estimate the confidence intervals (Efron and Tibshirani 1994) for each response level by strata. The percentile method (Efron 1981, Efron 1982) was used to estimate the 95% interval using the 2.5th and 97.5th percentiles of the 1,000 (999 simulations plus the original) bootstrap estimates.

Selection Ratios

We calculated Manly's Resource Selection Ratio (w_i) to determine preferential use of resources by wildlife given the availability of those resources (Manly et al. 2002). Data analyses of the binomial and multinomial variables determined the probability of a resource being used, but did not take into consideration how the probabilities relate to the availability of those resources. To determine selection of different browse species for the binomial and multinomial data, we used a Design III selection ratio sampling approach. In a Design III analyses, both the use and availability of resources are measured for each individually marked animal where the available resources are allowed to vary for each individual (i.e., resources are not equally available to all individuals). In our study design, an individually marked animal is replaced by an individually marked sampling plot (randomly selected) such that the available resources are those within the plot and the used resources are those within the plot that are positively associated with a particular response variable (i.e., hare browsed, beaver chewed, moose browsed, etc.). In this case, the sampling plot can be thought of as a feeding site of an individual animal with paired use and available data (McKnight and Hepp 1998). In using the Design III analysis, we account for the between plot variability in resource use and availability across the study area. Rare browse species (resources) can be highly influential on selection ratios and have wide confidence intervals due to low sample sizes (i.e., only a few plants of a particular species are available throughout the study area). In these instances, we removed those species from analyses.

The selection ratio for individual plots can be calculated using equation (4.1); however, since the availability is different for all individual plots the average selection ratio for the population in a Design III analysis is calculated by the expression

$$\widehat{w}_i = u_{i+} \,/\, \sum_{j=1}^{n} \pi_{ij} u_{+j} \quad , \tag{4.15}$$

where $\widehat{w}_i$ is the overall average selection ratio for a plot for the i^{th} habitat, and *n* is the total number of individual plots, u_{ij} is the observed 'used' component of the i^{th} habitat for the j^{th} plot, and π_{ij} is the available proportion of the i^{th} habitat and j^{th} plot (Manly et al. 2002). The variance can be calculated using equation (4.3) as was used for the Design II analysis (Manly et al. 2002). We again used the Package 'adehabitatHS' to analyze the use and available data and used the *widesIII* model call (Calenge 2006).

Brooming Index

In order to understand the intensity of browse use by moose within the study area and to have a means of comparing to other moose ranges across the state, we calculated a Brooming Index (BI) for the study area (Seaton 2002). The index is the ratio of plants classified as 'broomed' architecture and all the plants used by moose such that an index can be calculated for an individual plot and individual browse species using

$$BI_{ij} = \frac{BM_{ij}}{BM_{ij} + BR_{ij}} \quad , \tag{4.16}$$

where (BI_{ij}) is the brooming index for the i^{th} plot and the j^{th} browse species, (BM_{ij}) is the number of plants with the architecture class of broomed for the i^{th} plot and j^{th} species, and (BR_{ij}) is the number of plants classified as the browsed architecture class for the i^{th} plot and j^{th} browse species. To calculate the BI for a single plot for all browse species, we used the expression

$$BI_i = \frac{\sum_{j=1}^{n} BM_{ij}}{\sum_{j=1}^{n}(BM_{ij} + BR_{ij})} \quad , \tag{4.17}$$

where (BI_i) is the brooming index for an individual plot including all browse species of interest (*j*) through (*n*) species.

The brooming index data were not normally distributed and transformations did not improve normality. Therefore, we used non-parametric statistical analyses to model the mean BI for each browse species by strata and to model a global estimate (intercept only model) for the entire study area. We used a resampling permutation method to test if distributional means for each strata are different (Ernst 2004). We used Package 'lmPerm' (version 1.1-2; Wheeler 2010) with the model call *aovp*. The exact test permutation was too intensive to compute with (8.047926e+251) total possible combinations for the global model (145 observations). Instead, we used a sampling approach with the permutation through an iterative randomization and reassignment process. In order to stabilize the p-values, we increased the number of iterations to 1e+08.

We calculated the standard error as SE = sqrt(MSE/n), where MSE is the mean square error (residuals) and (n) is the number of observations depending on strata. Confidence intervals for the strata means were constructed at 95% using equation 4.8. We were not able to use permutations to analyze the global (intercept only) model because we only have one level with an intercept model and permutations reassign values to two or more levels. Therefore, we used a nonparametric bootstrap to resample the data (with replacement) to estimate 10000 global means. The percentile method was then used to determine the 95% confidence intervals for the global mean.

Results

We analyzed (44265) locations from 20 marked moose within the study area to determine if moose selected different habitat strata. Moose significantly selected the flood plain ($\widehat{w}'_{FP}$ = 1.2458; C.I. = 1.0650-1.4266) and avoided the river channel ($\widehat{w}'_{RC}$ = 0.5251; C.I. = 0.1759-0.8744) strata along the Kwethluk River (Figure 4.3). To characterize the study area and to determine if moose used the resources differently between the two strata, we sampled a total of 5128 individual plants from 145 plots within the river channel (81 plots) and the flood plain (64 plots) strata. The most prevalent browse species sampled was FLWI comprising 33% of all measured observations followed by DIWI (16%; Appendix 4.D-1 and 4.D-2). All statistical tests were evaluated for significance *a priori* at the alpha = 0.05 level.

Plant Densities

Density measurements did not occur on all sample plots within the river channel strata. Plant densities were estimated for 57 plots in the river channel and 64 plots in the flood plain. Feltleaf willow (0.2085 plants/m^2) was the most dominate willow species followed by DIWI (0.1214 plants/m^2), whereas, PAWI (0.0004 plants/m^2) was the least abundant in the study area (Table 4.1; Figure 4.4). The non-browse species of alder were relatively abundant (0.0904 plants/m^2), but less so than the dominate willow species. Additionally, the non-browse species of WHSP (0.0262 plants/m^2) was less dense than most browse species, but more abundant than the willows of RIWI, BEWI and PAWI. Grayleaf willow (GLWI) was rare in the study area and was found on one sampling plot where only four plants were sampled for characteristics. This particular plot was not sampled for density; therefore, GLWI does not occur in the density estimates.

There were significant differences in plant abundance between the two strata (Table 4.1; Figure 4.5). The river channel stratum had nearly twice as many plants (browse and non-browse) as the flood plain (1.1795 plants/m^2 and 0.5939 plants/m^2, respectively). Additionally, browse only plants were 1.6-times denser in the river channel versus the flood plain (0.8268 plants/m^2 and 0.5168 plants/m^2, respectively). The abundance of the primary successor FLWI along the active river channel contributed significantly to the difference in overall plant densities between the two strata. The river channel stratum was dominated by FLWI (0.4221 plants/m^2) and ALDR (0.1760 plants/m^2), and the flood plain was dominated by DIWI (0.2135 plants/m^2) and PABI (0.1005 plants/m^2). The browse species of HBCR, BAPO, and RIWI all had similar densities between strata.

Height and Shoots

Plant height naturally varies by species' growth form, so comparisons were only made between strata for a particular species or a group of species with similar growth-forms (e.g., trees or shrubs). Average browse plant heights (from global model) varied across the study area from 1.07 m for HBCR to 3.38 m for PABI (Table 4.2). Canopies of HBCR and WILLOW-SHRUBS were higher on average in the river channel stratum (t=8.096, df=63, p=0.0; and t=2.377, df=86, p=0.0197, respectively), in contrast FLWI (t=-2.502, df=101, p=0.014) and TREES (t=-4.718, df=88, p=0.0) were taller on average in the flood plain region (Appendix 4.E-1; Figure 4.6). Although there are apparent differences in canopy heights for PABI and BEWI between strata, the variability and reduced sample sizes (or reduced occurrence in a particular stratum) precluded evidence for rejecting the null.

The number of shoots on each plant varied by species across the study area from a modeled average (Global model) of 9.20 shoots on HBCR to a high average of 77.71 on BEWI shrubs (Table 4.3). Although there was high variability within all species, there were significant differences between strata based on the number of plant shoots. BAPO (z=-2.040; p=0.042), DIWI (z=-0.4606; p=0.051), FLWI (z=-5.030; p=<0.0001), and LTWI (z=-6.060; p=<0.0001) all had significantly more shoots in the flood plain region, where as HBCR (Z=2.810; p=0.005) was the only species to have significantly more shoots in the river channel stratum (Appendix 4.E-2; Figure 4.7). BEWI (z=-0.200; p=0.8437), PABI (z=1.530; p=0.130), and RIWI (z=-1.820; p=0.068) had the highest variability especially within the river channel stratum (due to low sample sizes for those species within that stratum) and were not significantly different between strata (Appendix 4.E-2; Table 4.3). All three groupings by plant growth-forms had significantly more shoots in the flood plain area (TREES, z=-8.240, p=0.0001; WILLOWS, z=-8.750, p=<0.0001; WILLOW-SHRUBS, z=-5.050, p=<0.0001).

Some species (e.g., BAPO, PABI) had a few exceptionally large plants (7 m tall) that exhibited many more shoots within the browse zone than other plants of the same species in the area. Nearly all species had these exceptional plants for both plant height and number of shoots or both, but they were not treated as outliers. Although these observations can have high influence on modeled outcomes, we wanted to include the natural range of variation in observations on the landscape.

Effects of Sympatric Browsers

Strata was a useful predictor variable for the binomial data of Beaver, Hare, Log, and Broken. The probability of observing a browse plant that had evidence of beaver browsing (z=4.751, p<0.0001), a “log” growth-form (z=3.309, p=0.0009), or had been broken by a moose (z=2.554, p=0.0107) was significantly higher in the river channel stratum (Appendix 4.F; Figure 4.8). The probability of observing a plant with hare use was not significantly higher (z=-1.813, p=0.0699) in the flood plain region. Observing a plant with signs of beaver use was 5.25-times more probable in the river channel than in the flood plain. Also, finding a browse plant that arose from a log growth-form or a branch broken by a moose was over 20 and 12-times (respectively) more probable to find in the river channel versus the flood plain region. Although not significantly different between strata for all browse species combined, it was 1.67-times more probable to find a plant used by a hare in the flood plain than it was in the river channel (Table 4.4). The modeled global average probabilities for observing a plant in the entire area that had a positive outcome for each binomial variable ranged from 0.00022 for Broken, 0.00047 for Log, 0.03042 for Beaver, and to 0.03853 for Hare (Table 4.4).

The probability of individual browse species varied within each binomial variable (Table 4.5; Figure 4.9). Not all browse species sampled within this study are represented in these analyses due to rare species and low sample sizes. We analyzed the browse species with adequate samples for modeling corresponding average probabilities. The probability of browse species used by beavers ranged from a low of 0.00681 for PABI to a high of 0.08742 for FLWI. Hares were more generalists compared to beavers and ranged from 0.01598 for LTWI to 0.05000 probability for DIWI. Also, LTWI had the highest probability (0.00251) of having a branch broken by a moose, and FLWI was the most probable (0.00239) species to exhibit a log growth-form (Table 4.5). We analyzed the three most probable browse species for the Hare and Beaver data sets to identify differences between strata. Strata was not a good predictor for any of these plant species except for HBCR. Although there was no significant difference in probability of hare use between strata for all species combined, there was a higher probability of hares using HBCR in the flood plain stratum (z=-2.08, p=0.0376).

Architecture and Dead Class

The overall modeled average probability of an observed plant being unbrowsed in the study area was relatively modest (prob=0.5329; C.I.=0.5182-0.5521), whereas the probability of a plant browsed or broomed was significantly lower prob=0.3925 (C.I.=0.3784-0.4109) and prob=0.0746 (C.I.=0.0635-0.0781; respectively) in this study (Table 4.6; Figure 4.10). Although there are more overall plants classified as unbrowsed, an increase in probability of browsing occurred at the species level, and specifically for willows. Littletree willow had the highest overall probability of being browsed (prob=0.6677; C.I.=0.6598-0.7671) and paper birch trees had the lowest probability (prob=0.1721, C.I.=0.1021-0.1867; Table 4.6; Figure 4.11).

Differences in use between strata was evident for all browse data (z=-3.67 p=0.0002; Figure 4.12). There was a significantly higher probability of plants being unbrowsed in the river channel (prob=0.6100; C.I.=0.5952-0.6320) versus the flood plain stratum (prob=0.4301; C.I.=0.4034-0.4549), whereas the flood plain had higher probabilities of observing browsed (prob=0.4613; C.I.=0.4458-0.4874) or broomed (prob=0.1086; C.I.=0.0635-0.0781) plants compared to the river channel (prob=0.3345, C.I.=0.3175-0.3526 and prob=0.0555, C.I.=0.0466-0.0578; respectively; Table 4.6, Figure 4.12). LTWI was nearly 32-times more probable to have no browsing in the river channel versus the flood plain; whereas it was over 13-times more probable to have a broomed architecture in the flood plain compared to the river channel (Table 4.6).

Categorizing browse plants into structural dead classes helps to identify potential effects of utilization by moose. The overall average probability of an observed plant in the study area with no dead material was very low (prob=0.0517; C.I.=0.0413-0.0534; Table 4.7; Figure 4.13). Most plants had some dead material (< 50% dead; prob=0.8711; C.I. = 0.8704-0.8921); however, plants had a low probability of having >50% dead material (prob=0.0772; C.I.=0.0646-0.0790; Table 4.7; Figure 4.13). Although the overall probabilities were low for the classes of no dead and >50% dead, there was variation between species. RIWI had the highest average probability of >50% dead material (prob=0.2897; C.I.=0.0149-0.3240) and PABI had the lowest (prob=0.0326; C.I.=0.0001-0.0319). HBCR and BAPO had the highest probabilities of having no dead material (prob=0.1341, C.I.=0.0968-0.1459 and prob=0.0996, C.I.=0.0483-0.1084; respectively) and DIWI had the lowest (prob=0.0028, C.I.=0.0007-0.0052; Table 4.7; Figure 4.14).

There was an overall significant difference in probabilities of dead classifications between the flood plain and river channel stratums (z=-4.301; p=0.00002; Figure 4.13). The river channel had over 2-times the probability of having plants with no dead material over the flood plain stratum for all browse species. In contrast, the flood plain had over 2-times the probability of observing browse plants that had more than 50% dead material (prob=0.1199; C.I.=0.1005-0.1274; Table 4.7; Figure 4.13). Specifically looking at the >50% dead classification, the functional group WILLOWS had the highest probability within the flood plain (prob=0.1684; C.I.=0.1315-0.1780), which was over 3-times that of the river channel (prob=0.0536; C.I.=0.0389-0.0548). However, the TREES group had relatively low probabilities for each strata with overlapping confidence intervals (Table 4.7; Figure 4.15).

Selection ratios

Hares utilized the most diverse selection of browse species of the sympatric browsers. The top three browse species used by hares were FLWI, HBCR and DIWI with compositions of total usage 29%, 23% and 21%, respectively. However, when taking into account the availability of each browse species, FLWI was selected for, while HBCR and DIWI were used in proportion to their availability (i.e., no selection; Table 4.8, Figure 4.16). Additionally, hares only selected against LTWI, even though there were three other browse species used less often by hares. Beavers utilized FLWI the most (62% of total browse used) followed by BAPO (12%) and LTWI (8%). Beavers highly selected for FLWI based on its availability with some indications of selection towards BAPO, but selected highly against HBCR, LTWI and PABI (Figure 4.16). Moose utilized willow species most often with FLWI (34%) the most used followed by DIWI (24%) and LTWI (18%). Moose also clearly selected for these three willow species, and selected against HBCR and the trees species, BAPO and PABI (Figure

4.16). All three sympatric browsers selected for FLWI indicating potential competition between beavers, hare and moose.

Brooming index

The brooming index (BI) for all browse species sampled across the entire study area was BI=0.2025 (C.I.=0.1684-0.2381; Table 4.9; Figure 4.17). DIWI had the highest intensity of use (BI=0.3537; C.I.=0.2784-0.4324) and PABI had the least (BI=0.0190; C.I.=0.0043-0.0390). WILLOW_SHRUBS was highly influenced by DIWI, which comprised most of this group. There was no difference between DIWI and LTWI indices (confidence intervals overlap; C.I=0.2784-0.4324 and C.I.=0.2366-0.3881, respectively; Table 4.9). We analyzed the “ALL_Browse” dataset without HBCR (“ALLnoHBCR”) in order to have a comparable BI value to other moose ranges that do not consider HBCR good moose browse. The two datasets had nearly identical BI values indicating no difference between the two groupings (Figure 4.17).

Intensity of browse use was significantly different between the two strata within the study area based on all browse samples (z=6.8258; p<0.0001; Appendix 4.G). All browse species that were significantly different had higher brooming indices within the flood plain stratum (Figure 4.18). However, the individual species of BAPO, HBCR, and PABI did not differ in the intensity of use between strata and had the lowest index for all species. Littletree willow within the flood plain showed the most intensive use of all browse species in either strata (BI=0.6845; C.I.=0.5709-0.7981; Table 4.9), whereas, PABI had an average BI=0.0000 (C.I.=0.0000-0.0891) in the river channel stratum.

Discussion

This study is the first to extensively characterize and provide a baseline assessment of moose browse in the lower Kuskokwim River drainage of southwestern Alaska. Characterizing and indexing the browse habitat for this recently established and expanding moose population is critical for long-term management of this species. These data will allow future comparisons of browse surveys for prudent management not only within the Yukon-Kuskokwim Delta region, but also to other moose ranges with similar habitat across Alaska. The survey technique is simple, repeatable and can be completed during the growing season. However, this method was only moderately rapid for assessing browse characteristics and could be expedited by focusing on the most important factors (e.g., browse architecture). Significant differences in browse characteristics and use between the two habitats (FP vs RC) indicate that sampling the entire study area, instead of one habitat type or another is necessary. Sampling both the FP and RC increases the survey's spatial and time requirements, but allows more accurate assessment of the habitat overall. If we would have only surveyed the river channel habitat (as initially planned because of easy access and efficiency), we would have under estimated use and misinterpreted browse characteristics, potentially leading to erroneous management decisions.

Moose clearly selected the flood plain over the river channel habitat (Figure 4.3). Habitat selection can be driven by several factors including snow depth (Telfer 1970) and browse species composition (Peek et al. 1976). Snow accumulations of 60-70 cm may start to impede moose (Kelsall 1969, Coady 1974); however, shallow snow depth during our study did not influence habitat selection by moose. Within our study region, it is in February that the most snow accumulates with a median average snow depth of 22 cm (2000-2010; Bethel, AK airport; Appendix 4.H). We recorded snow depth along the Kwethluk River within the study area using two permanent aerial snow markers (one near Elbow Mountain and one in the center of the area). Average snow depth recorded from these markers for winters 2009 and 2010 was approximately 10 and 5 cm, respectively.

The composition of browse species in our study most likely influenced selection between habitat strata by moose. Feltleaf and diamondleaf willow were the two most abundant browse species in the entire study area and are considered important browse for moose in Alaska (Wolff and Cowling 1981, Risenhoover 1989). Feltleaf willow, alder and littletree willow dominated the river channel habitat; whereas diamondleaf willow, paper birch and white spruce were more abundant in the flood plain stratum. Although feltleaf and littletree willow are selected for by moose and are more abundant in the river channel, moose still selected the flood plain habitat. Moose strongly selected against paper birch in our study, suggesting that moose presumably selected the flood plain habitat because of diamondleaf willow. Diamondleaf willows in the flood plain have nearly 3-times the number of shoots per plant on average than feltleaf willow plants in the river channel. Although we did not measure twig size or biomass in this study, the difference suggests that moose could be optimizing their foraging strategy in relation to shoot density and juxtaposition to increase forage intake while decreasing foraging time. Additionally, the feltleaf and littletree willow plants that are found within the flood plain are used more intensively than those same species in the river channel. This would suggest that the intensity of use could be related to the associational plant hypothesis in that plants occurring with other higher quality or preferred species should have an increased likelihood of being utilized (Pfister and Hay 1988, Danell et al. 1991).

Although moose can influence habitat species composition through extensive and long-term browsing (Connor et al. 2000), they can also alter the structure and function of their ecosystem and specifically, vegetative characteristics during periods of increased browsing pressure (Brandner et al. 1990, De Jager and Pastor 2010). Utilization of browse plants by herbivores can elicit plant compensatory growth responses such as increasing the number of lateral shoots following browsing (Massei et al. 2000, Karlsson and Weith 2003, Danell et al. 2003); however, continued browsing can simultaneously decrease overall plant height (Kielland and Bryant 1998, Keigley and Fager 2006, Mathisen et al. 2010). Our current study corroborates both scenarios for browse species in the flood plain region where moose use was greater and presumably more intensive than in the river channel stratum. Browse trees and willow shrubs exhibited a greater number of plant shoots and decreased heights within the flood plain influenced by the greater use by moose. There were some species specific variation to this general observation, however. Paper birch trees showed a trend for a higher average number of plant shoots and heights within the river channel stratum, although not statistically significant (this may have been a function of low samples within the river channel stratum). This trend may be due to the defenses that paper birch has against herbivores (Bryant and Kuropat 1980). Some Alaskan trees such as green alder, balsam poplar, and paper birch produce resins, especially in young adventitious shoots (Bryant 1981), that deter herbivory and facilitate their growing out of mammalian browsing zones of hare and moose (Bryant and Kuropat 1980, Bryant et al. 1989, Tahvanainen et al. 1991). Without stimulation from browsing, paper birch didn't exhibit greater compensatory lateral shoot growth in the flood plain. Feltleaf willow was taller on average in the flood plain even though there was greater browsing pressure in this stratum. A possible explanation for this observation is the fact that feltleaf willow is an early colonizer of scoured river channels, mudflats or sandbars (Walker et al. 1986). The active disturbance by the main river continually scours the river corridor keeping portions of that stratum's landscape in an earlier successional stage. Highbush cranberry had more shoots on average in the river channel. Moose did not readily utilize highbush cranberry in either strata, (in fact they selected against it) but snowshoe hares used it in proportion to its availability and were more likely to use this plant in the flood plain. Highbush cranberry's shorter overall growth form and relatively few shoots in general would allow more shoots to be removed by snowshoe hares. Although highbush cranberry produces shoots from lateral buds and can develop a broomed appearance, the hedging response is not as prominent as in a willow plant based on the physical growth form of these plants in this study area.

Snowshoe hares can impact forest structure or regeneration through browsing (Aldous and Aldous 1944, Sinclair 2003), and can induce the production of plant chemical defenses in browse species (Bryant and Kuropat 1980, Fox and Bryant 1984), especially in juvenile shoots (Bryant 1981, Bryant et al. 1983). Chemically defended plants can become detrimental to hares and possibly regulate the hare cycle (Bryant 1981). Moose may be affected by the increased chemical defense caused by hare-specific browsing or by the direct reduction of biomass caused by plant mortality from hare browsing. Considering all plants measured in this study, the probability of a plant being browsed by a snowshoe hare was prob=0.04 across the entire area and slightly higher in the flood plain. This means that only four out of a hundred browse plants are affected by hares in the study area. Although seemingly insignificant, the cumulative effect especially in localized areas or on certain selected species (such as diamondleaf willow, highbush cranberry and feltleaf willow, which can have significantly higher probabilities of use) could contribute to vegetation changes within the study area. Hare cycles are shown to be driven by food resources and predation (Krebs et al. 1995, 2001); and hares tend to peak approximately 2 years prior to peak lynx abundance (Butler 1953, Bulmer 1974). Reported lynx harvest in Game Management Unit (GMU) 18 of the Yukon-Kuskokwim Delta indicate that lynx abundance peaked in 2011 (Jones 2013) and suggests that snowshoe hares peaked approximately in 2009 within GMU18. Although these data are for a large geographic region and localized hare populations could have slightly different periodicity (i.e., hares north of the Yukon River vs. hares south of the Kuskokwim River), these data suggest that hare abundance was relatively high for this region during the study period.

Beavers can affect long-term structure and function of forests resulting in successional changes toward unpalatable forages such as coniferous species (Johnston and Naiman 1990, Moen et al. 1990, Donkor and Fryxell 1999). Moose can exert additional forces (especially at high densities) on habitat structure and succession by browsing the regenerating forest hardwoods after beavers have removed the larger hardwood parent trees (Johnston et al. 1993). Moose can in effect arrest the development of hardwoods into the canopy. Beaver use in our study was relatively low across the entire study area (i.e., prob=0.03). Although there were active beaver ponds within the flood plain region, these foci did not contribute much to the overall probability of beaver use in the area. The active river channel, however, had a significantly higher probability of use by beavers prob=0.06. Beaver activity along the river channel could have localized effects on forest vegetation up to 40 meters from the water's edge (Martell et al. 2006), and particularly on feltleaf willows stands, which beaver selected for in this study. This localized disturbance may initially reduce browse for moose, but it can also increase the quality of an area when beavers cut mature trees that are out of reach for moose and stimulate adventitious sprouting and regeneration of these browse species.

Disturbance such as wind-throw or trees felled by beaver can promote adventitious regrowth of trees and shrubs sprouting from the fallen log that is incorporated into the soil. Our analyses of plants growing from a felled log proper showed that this disturbance can have a positive outcome by producing additional forage; however, this particular positive disturbance was rare in this study. Stem breakage is also a disturbance variable that we measured, and is considered negative if the breakage kills or severely damages the browse plant (Bergqvist et al. 2001).

Moose break stems of tree saplings or willow shrubs to reach otherwise inaccessible browse at the tops of branches (Geist 1963). Moose can either break stems by using their mouth and exerting downward forces or they can straddle plants (especially tree saplings) and "ride" them down until the stem either breaks or the moose reaches the browse at the top of the plant. Oldemeyer (1983) recorded moose breaking stems of up to 5 meters in height on birch trees to reach the top twigs. The frequency of breakage increases as winter progresses (Histol and Hjeljord 1993) or in areas of high densities of browsing ungulates (Telfer and Cairns 1978). Extremely cold temperatures can also facilitate stem breakage during winter. Littletree willows have many small shoots (smaller diameter shoots are easier to digest; Spaeth et al. 2002) and were the most probable browse species to have broken branches by moose foraging in our study. An increase in frequency of broken branches caused by moose foraging could be an indicator of increased browsing pressure and/or a reduction in range quality. However, the impact of 3 plants with broken branches out of every 1000 littletree willows (i.e., prob=0.0025) is not an ecological concern in this area at this time.

Selection of browse species by herbivores is driven by many different factors of foraging ecology. In general, forage selection has been shown to be related to nutrient content and digestibility (Westoby 1974, Belovsky 1986); however, plant chemistry can affect browse palatability and subsequent selection by herbivores (Bryant and Kuropat 1980, Palo 1984). Browse utilization is also influenced by plant morphology. Shipley et al. (1998) showed that plant morphology was more correlated to selection by moose than to digestibility, nitrogen or phenols. Moose avoided plants with many, small twigs and selected forage species with fewer, but larger stems to optimize bite size and rumen fill times (Shipley et al. 1998). Whether selection is based on nutrients, chemistry or architecture, herbivores that develop learned behavior early in their life (Provenza and Balph 1987, Villalba and Provenza 2009) will have the flexibility to make profitable diet choices (Bryant et al. 1991). All factors considered, forage selectivity by herbivores typically increases when resources are plentiful (Vivas and Saether 1987) and varied, allowing for a range of ‘good’ options as opposed to one ‘optimal’ solution (Hanley 1997).

Moose utilized ten different browse species within this study based on residual winter browsing characteristics of plants. However, moose only selected for feltleaf, diamondleaf and littletree willows in relation to their availability in this study (Figure 4.16). These selections are the same for moose winter diets in the interior of Alaska (Risenhoover 1989) and in northwest Alaska (Campa et al. 2008), and are consistent with other forage studies across Alaska where in most cases, feltleaf willow, when available was the most important species used by moose (Milke 1969, Machida 1979, Wolff and Zasada 1979, Wolff and Cowling 1981). Contrary to studies on the Kenai Peninsula (Oldemeyer et al. 1977) and in Scandinavia (Lundberg et al. 1990), moose in this study highly selected against birch trees. In agreement with the findings of Collins and Helm (1997), moose in this study also selected against balsam poplar and preferred feltleaf willow. However, they and Oldemeyer et al. (1977) reported that highbush cranberry was an important forage but was often unavailable due to snow cover. Moose in our study utilized, but selected against highbush cranberry and snow cover was not an issue here.

Snowshoe hares and beavers used the same browse species as did moose, with exception of pacific and greyleaf willow. These two willow species were extremely rare in the study area, having only 5 and 4 total plants sampled for the entire area, respectively. Although hares and beaver used similar species as moose, they both only had a positive selection ratio for feltleaf willow. Hares utilized forage species more evenly across species (i.e., selection ratios near 1.0; Figure 4.8), whereas beaver mainly used feltleaf willow and balsam poplar. Although beaver readily utilized balsam poplar, moose and hares did not, which is in agreement with Sinclair et al. (1988) in that hares in their study rejected young poplar due to chemical defenses. Conversely, Butler and Kiellland (2008) reported hares in their Alaskan study readily used balsam poplar. Tahvanainen et al. (1991) suggests that mature twigs of balsam poplar are more palatable than younger, juvenile twigs, in which case felling more mature trees by beaver would allow utilization of more palatable browse parts compared to the abilities of hares or moose to use poplar in our area.

Several studies have investigated the potential interactions and potential competition between sympatric browsers such as snowshoe hares and moose (Dodds 1960, Bryant and Kuropat 1980, Belovsky 1984), and to a lesser extent moose and beavers (Pastor and Naiman 1992, Moen et al. 1990). Limited information is available for interactions or competition between all three browsers (Potvin et al. 2005). In our current study, moose diets overlapped completely with both snowshoe hares and beavers. However, in considering selection ratios, the only browse species that all three herbivores selected for simultaneously was feltleaf willow (Figure 4.16) indicating that direct competition for feltleaf exists between them. Feltleaf willow is the most abundant browse species in the study area, and arguably the most significant food source (browse) for all three herbivores along the Kwethluk River. Extent of utilization of other forage varied by herbivore and in the beaver's case, limited by proximity (e.g., beaver's high use of feltleaf willow along the river channel and little use of diamondleaf willow, which is more prominent on the flood plain away from the active river). Moose and beaver interactions are limited in this region where moose utilize the flood plain more than the river channel stratum favored by beavers. Although beavers can influence moose habitat by reverting mid-successional stage forests back to early successional stages with higher nutrient availability, they can inadvertently release non-preferred forage and expedite succession to conifer stands in these localized areas (Pastor and Naiman 1992). Moose competition with hares is more likely with significant dietary and space use overlap than moose and beavers in this study. Hares can significantly influence the production of plant chemical defenses (Bryant and Kuropat 1980), which deter not only browsing by hares, but also by moose. Direct competition for forage and indirect competition through altering plant defenses increases during peak hare cycles and especially during peak cycles coupled with severe winters (Wolff and Hall 1980). The hare cycle in this region was at or near the peak high during this study, which would suggest less competition between the two herbivores in the near-term. However, when excessive competition exists, Wood (1974) suggested that moose would “win” the competition because of their more efficient digestive system.

Herbivory affects browse plants by altering structure and can increase mortality from excessive and repetitive intense use (Edenius et al. 2002, Tremblay et al. 2007). Over 90% of all browse plants sampled exhibited some dead material, but only 11% of total plants showed signs of excessive mortality (i.e., dead class >50%). Of those plants in the >50% dead category, most were in the flood plain where there is a higher use by moose. When browse is separated into growth-form categories (Figure 4.15) for this level of dead class, there is more than a threefold increase in probability of this level of mortality within the flood plain region. As browsing intensity or severity increases, preferred species become severely malformed and mortality of those trees and shrubs increases (Bergstrom and Hjeljord 1987, Bergstrom and Danell 1995). Diamondleaf and Bebb willows in this study had the highest probability of the browse species within the >50% dead class (aside from RIWI, which had excessive variation due to sample size) indicating negative species specific utilization. Butler and Kielland (2008) identified an age shift in preferred forage species and documented an increase in dead browse plants induced by herbivory. Although our study showed some plants had excessive dead material, most plants did not have significant mortality. Our three-level classification of dead material was not at a fine enough resolution to determine where plants were on the continuum of dead classes that were less than the 50% cut point (i.e., most plants fell into this group), or to identify mortality not associated with herbivory.

In addition to increasing plant mortality, browsing can often alter plant structural form or architecture (Bergstrom and Danell 1987*a*, Danell et al. 1994, Butler and Kielland 2008). Browsing meristematic tissue on plant shoot tips induces the plant to respond by shifting to lateral bud dominance and creating clusters of shoots with increased browsing pressure (Mopper et al. 1991). Architectural responses can in effect protect the plant from more extensive browsing by creating shoot clusters which have been shown to decrease the probability of any one shoot being browsed (Shipley et al. 1998). Architecture records the browsing history of a particular plant and can be used to determine the amount or degree of intensive use (Seaton 2002, Keigley et al. 2003). In our study area, most plants sampled were unbrowsed (54%), whereas only 11% of all plants sampled had a broomed architecture. Plants sampled in the river channel and in particular, trees, had the highest probability of being unbrowsed. There is a significant increase in probability of being browsed on the flood plain, and especially if the plant is a willow. Browsing intensity also increases in the flood plain where the number and probability of broomed forage plants increases, especially in the willow shrub-like grouping, and specifically if the plant was diamondleaf willow. Diamondleaf willow had the highest probability of having broomed architecture, or hedging, indicating that some shrubs of this species are heavily used by moose. Littletree willows also had broomed architecture probabilities higher than most other browse species, and had the highest probability of having a broken branch by a moose. A browse reconnaissance survey conducted along the lower Yukon River and a portion of the Kuskokwim River in 2002 (Seavoy 2004), found that the most abundant browse species was feltleaf willow and 50% of that species was unbrowsed. Additionally, that survey showed that diamondleaf and littletree willows were also utilized more than others, with diamondleaf willow having the highest intensity of use (although sample sizes were relatively low). The same reconnaissance surveyed a portion of the Kuskokwim River with eight transects to determine that approximately 78% of the browse species were unbrowsed and no plants had broomed architecture in 2002 when the moose population was not yet fully established (Seavoy 2004); however, this survey had low sample sizes spread across a large geographic area, thus was only a reconnaissance.

Utilizing browse architecture, we created an index of browse intensity for the study area and for each browse species. It is useful to use a single index to relate overall browse utilization and intensity of an area to the condition of the browser(s), in this case, moose. Creating an index of browsing or browse severity has been proposed by others to identify effects of ungulate density on habitat constraints or vice versa. Milke (1969) utilized a browsing intensity index to identify the relative degree of browsing for each forage species by moose. More recently, Morellet et al. (2001) developed a browsing index to track species-specific forage use by roe deer. In Alaska, Seaton (2002) first proposed using the browse architecture classification used in this study as an index to monitor condition of moose or moose ranges.

Our study showed a relatively low brooming index value (BI=0.20) for all browse species sampled collectively, and showed significant variation between specific browse species (Figure 4.17). These differences are corroborated with other habitat analyses within this study (e.g., plant architecture, plant dead material classification, and selection ratios by moose). Additionally, there are significant differences between habitat strata (Figure 4.18); most of the more intensive browsing (in this study) occurred in the flood plain region. Diamondleaf and littletree willows, and willow-shrubs in general, were the most intensively used browse plants in the study area, and specifically in the flood plain stratum. The more intensive use of willows in the flood plain, represented by the brooming index, coincides with greater use of this area by moose. Increases in moose densities or increases in intensity of use by moose in specific areas during certain times of year can adversely affect the area's resources (Seaton et al. 2011). The reconnaissance survey conducted near our study area within the Kuskokwim River proper during 2002 estimated a brooming index of zero when moose densities were very low (0.042 moose/km^2; Seavoy 2004). As moose increased in this region (chapters 2 and 3-this dissertation), the brooming index for our study site increased to BI=0.20 with a coinciding moose density of 0.466 moose/km^2. Similarly, as moose densities in other parts of Alaska increase, so does the brooming index (data inferred from Boertje et al. 2007: table 1; and Paragi et al. 2008: figure 7).

Density-dependent effects on habitat resources can have nutritional consequences on reproductive success in moose (Keech et al. 2000). Further expansion and interpretation of our data can be used to relate the brooming index score to condition of moose in the study area. There are several indices proposed for estimating nutritional condition of moose such as the population demographic parameters of parturition rates, yearling mass, and twinning rates (Boertje et al. 2007). Twinning rates have been proposed as a nutritional index by others (Franzmann and Schwartz 1985) and are shown to be a reliable surrogate for condition of moose in Alaska (Boertje et al. 2007). However, the knowledge gained from population demographic data is typically reactive in nature meaning that negative impacts on the habitat has already occurred, and often for multiple years, before the effects manifest in the measured population parameter(s). Utilizing browse characteristics and indices is stepping back, in a sense, and allowing a proactive approach to managing resources (Mysterud et al. 2010). We hypothesized that if the brooming index increases there would be a subsequent decrease in nutritional condition of moose manifested in a reduction of their twinning rate. We investigated a correlation between moose twinning rates and the brooming index based on plant architecture. We found a significant correlation (Pearson's r=-0.8567, t=-4.9824, p-value < 0.001) between twinning rates and brooming indices for several sites across Alaska (Figure 4.19). Our study fits this correlation well with a corroborating twinning rate of 55% (four year average from a concurrent study in the same region).

The brooming index correlation follows a similar analysis by Seaton et al. (2011) who used a browse production: consumption ratio (i.e., proportion of biomass removed) to correlate to moose twinning rates and nutritional condition of moose in their studies.

They found similarly high correlation and were able to identify changes in moose population density with their ratio index. Paragi et al. (in prep)[4] discuss that the brooming index used here may not be as sensitive in identifying population change as is the production: consumption index especially when there has been a long history of intensive browsing. Once a population has been reduced, the vegetation can take many years to recover and allow for measurable improvement of the browse architecture. However, brooming index appears to correlate well with twinning rates from various sites across Alaska with varying moose densities. In particular the brooming index is especially efficient at tracking habitat conditions in the initial establishment of a population or when a population is allowed to increase after a long period of repression, or when the habitat is "reset" by a disturbance such as fire. This index is useful in our study to understand the condition of moose habitat at this expansion point of this newly established population, and allows us to better understand the capacity or tolerance (of the habitat) for continued use by moose.

Management Implications

This study was initiated because moose recently became established and are expanding their population in the lower Kuskokwim River of western Alaska. The habitat has previously had little browsing pressure and the increasing moose population could have significant effects on the habitat. Indexing moose browse within the study

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[4] Paragi et al. (in prep). Browse removal, plant condition, and twinning rate as metrics of density-dependent response by moose. *in* T.F. Paragi and K.A. Kellie. Winter habitat evaluation for moose management in interior Alaska. Final Wildlife Research Report, ADF&G/DWC/WRR ###, Project 5.20. Juneau, Alaska.

area will allow characterization of the current status of the habitat, allow a baseline for comparisons in the future, and inform managers on harvest regulations.

Our data clearly show that moose preferentially utilize the flood plain stratum compared to the river channel habitat. Greater utilization of browse species in the flood plain was evident from browse plants having more current annual growth shoots per plant, shorter willow-shrubs on average, higher probability of having dead material, and a higher probability of being broomed with a corresponding higher brooming index compared to the river channel stratum. Feltleaf willow was the most abundant species in the entire study area with all three sympatric browsers selecting for it, but feltleaf willow was not detrimentally impacted (i.e., % dead material or brooming) at this time. Given its abundance and selection for by the suite of browsers, feltleaf willow is the most important browse species ecologically for the Kwethluk River. Diamondleaf willow was the second most abundant browse species in the study area, and the most abundant in the flood plain. Diamondleaf willow is highly preferred by moose and is the most impacted of the browse species in the study area. It had the highest probability of having >50% dead material and the highest probability of being broomed with the highest brooming index.

Findings in this study indicate that the increasing moose population is influencing its habitat. Ungulate impacts are not at a level of management intervention, however, and the browse habitat could support more utilization within this study area. It is recommended to keep monitoring the browse plants and stabilize the moose population to within the tolerances of the habitat. Since we identified significant differences in the way that the habitat is used and affected by moose, future sampling and analysis should take that into consideration. More efficient analysis using global models built from sampling the entire study area randomly (not partitioning by strata) would allow for increased spatial coverage while reducing sampling variation. We sampled 145 plots between the two strata and suggest future efforts to be similar (100-150 plots) with random allocations throughout the entire study area (see Seaton et al. [2011] for variation in number of plots sampled). Surveys should take place approximately every 5 years to allow for sufficient time between moose density and habitat changes in order to identify trends in habitat use. Additional browse surveys should be considered if moose population densities change significantly in a shorter time interval or if there is a major habitat disturbance such as fire that 'resets' succession. Browse surveys should not totally replace other demographic surveys (i.e., density estimates, twinning rates, yearling weights, age of first reproduction; Boretje et al. 2007), but rather augment them in order to give a more complete analyses (and to put data into perspective) for management decisions in an adaptive management approach (Morellet et al. 2007, Putman et al. 2011). This is especially true since acquiring demographic data can be unpredictable (chapter 3-this dissertation) and expensive in this study area.

The brooming index is an efficient and rapid initial assessment tool for browse utilization trends. Once the overall browsing index approaches a value of 0.40 to 0.50 (mid-point of figure 4.19), consideration should be given toward management changes or additional habitat monitoring. Managers should consider a "trigger" point at which time they start to monitor the habitat more vigorously. This could include the more intensive biomass removal (consumption: production) ratio described in Seaton et al.

(2011) as it may be more sensitive to population change at the extreme high end of browse utilization.

Additionally, indicator species or a group of browse species can be used as a tool or trigger to enact management change (Mysterud et al. 2010). Browse species that are highly preferred are typically less abundant within the habitat (Mansson et al. 2007). Rare, preferred plants can decrease in density due to extensive herbivory (Mysterud 2006), and indeed Seaton (2002) showed that willow species declined in moose diets as those browse species became depleted towards the end of winter and the use of less preferred plants increased in moose diets. It is expected that preferred forage species will have relatively higher browsing pressure even at lower ungulate densities, whereas intermediately preferred species or forage of low quality is expected to be browsed less at low ungulate densities and become increasingly utilized as the ungulate population approaches the habitat's capacity to support it (Choqnenot 1991). Monitoring rare species may be difficult to make statistical inferences due to generally small sample sizes and large variations (e.g., Pacific or Bebb willow in this study); but, changes in use of the intermediate browse species can indicate changes in browsing pressure influenced by ungulate densities (Mysterud et al. 2010). In our study, candidate indicator species could be feltleaf willow, highbush cranberry, or paper birch. Feltleaf willow is the most abundant browse species and moose selected for this species slightly more than its availability, but it is not intensively impacted at this time. Highbush cranberry is intermediately abundant, but moose select against this species; and although paper birch is not as abundant as other browse species, it is highly selected against. All three of these species have relatively low (or the lowest) brooming index within the study area. As moose densities increase, it is expected that there will be an increase in use of those three browse species. Monitoring paper birch would be of particular interest since moose in other parts of Alaska have shown to switch to the less preferred species when willow forage becomes limited (Oldemeyer et al. 1977, Seaton 2002).

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Table 4.1. Plant density (count) data modeled using a zero-inflated negative binomial model. Data are average plant counts per plot with approximate 95% confidence intervals (CI) for each strata and species. The Global 'strata' is the intercept only model without regard to strata.

Species[1]	Strata	CI-lower	Average (count)	CI-upper	Density[3]
BAPO	RC	5.3428	10.7719	16.2011	0.0898
	FP	1.3631	5.0000	8.6369	0.0417
	Global	4.4146	7.7191	11.0236	0.0643
BEWI[2]	RC	-	-	-	-
	FP	-	-	-	-
	Global	0.0000	0.6612	1.7500	0.0055
DIWI	RC	0.0000	2.1403	5.4347	0.0178
	FP	17.6856	25.6252	33.5647	0.2135
	Global	9.2564	14.5620	19.8676	0.1214
FLWI	RC	33.7150	50.6491	67.5833	0.4221
	FP	1.0150	2.2031	3.3912	0.0184
	Global	15.6608	25.0249	34.3891	0.2085
HBCR	RC	6.4459	15.2105	23.9751	0.1268
	FP	2.9727	12.9375	22.9023	0.1078
	Global	7.4347	14.0084	20.5820	0.1167
LTWI	RC	10.5853	18.1404	25.6954	0.1512
	FP	1.2720	2.5938	3.9156	0.0216
	Global	6.3175	9.9174	13.5172	0.0826
PABI	RC	0.0000	0.5614	2.8626	0.0047
	FP	7.5552	12.0625	16.5698	0.1005
	Global	3.4727	6.6446	9.8166	0.0554
RIWI	RC	0.6692	1.7368	2.8045	0.0145
	FP	0.0000	0.2500	0.6604	0.0021
	Global	0.3716	0.9504	1.5293	0.0079
PAWI[2]	RC	-	-	-	-
	FP	-	-	-	-
	Global	0.0000	0.0496	1.5795	0.0004
WHSP	RC	0.0064	0.0877	0.1691	0.0007
	FP	4.1805	5.8750	7.5695	0.0490
	Global	1.9310	3.1488	4.3665	0.0262
ALDR	RC	15.8660	21.1228	26.3796	0.1760
	FP	0.2643	1.6876	3.1109	0.0141
	Global	7.6285	10.8430	14.0576	0.0904

[1] See APPENDIX 4.A for plant species naming codes.

[2] BEWI and PAWI did not have enough samples to analyze independently by strata.

[3] Density (average) was calculated by (average count/120 m^2). Confidence intervals for average density can be calculated similarly.

Table 4.2. Back transformed estimates for mean plant height (m) and 95% confidence intervals (CI) for each strata and the Global (intercept only) model by browse category. Browse with an asterisk (*) were significantly different[1] between strata.

Browse[2]	Strata	CI-lower	Mean Height (m)	CI-upper
BAPO	RC	1.26	1.47	1.72
	FP	1.22	1.49	1.83
	Global	1.31	1.48	1.67
BEWI	RC	0.24	0.86	3.04
	FP	1.77	2.70	4.10
	Global	1.58	2.43	3.74
DIWI	RC	1.37	1.73	2.18
	FP	1.57	1.71	1.86
	Global	1.58	1.71	1.85
*FLWI	RC	2.13	2.40	2.72
	FP	2.65	3.34	4.22
	Global	2.32	2.59	2.89
*HBCR	RC	1.16	1.22	1.28
	FP	0.80	0.86	0.92
	Global	1.01	1.07	1.13
LTWI	RC	1.99	2.27	2.60
	FP	2.23	2.79	3.48
	Global	2.14	2.40	2.69
PABI	RC	2.03	4.84	11.53
	FP	2.79	3.33	3.97
	Global	2.85	3.38	4.01
RIWI	RC	1.92	2.42	3.03
	FP	1.53	2.50	4.07
	Global	1.98	2.43	2.98
*TREES	RC	1.26	1.53	1.85
	FP	2.34	2.74	3.20
	Global	1.90	2.17	2.48
WILLOWS	RC	2.13	2.38	2.66
	FP	1.81	2.05	2.33
	Global	2.05	2.23	2.42
*WILLOW-SHRUBS	RC	1.89	2.22	2.62
	FP	1.58	1.76	1.96
	Global	1.72	1.89	2.07

[1] See APPENDIX 4.E-1 for plant height model testing by strata.
[2] See APPENDIX 4.A for browse species naming codes.
[3] PAWI did not have enough samples to analyze independently, but is incorporated into the other willow groups.

Table 4.3. Back transformed estimates for mean plant shoots (no.) and 95% confidence intervals (CI) for each strata and the Global (intercept only) model by browse category. Browse with an asterisk (*) were significantly different[1] between strata.

Browse[2]	Strata	CI-lower	Mean Shoots (no.)	CI-upper
*BAPO	RC	4.77	9.06	17.22
	FP	7.57	10.96	15.89
	Global	7.69	9.76	12.39
BEWI	RC	13.60	76.49	430.09
	FP	40.14	65.86	108.08
	Global	48.88	77.71	123.54
*DIWI	RC	29.93	48.49	78.56
	FP	49.66	57.64	66.90
	Global	57.12	66.07	76.44
*FLWI	RC	12.77	22.89	41.04
	FP	31.87	44.48	62.06
	Global	21.67	25.87	30.89
*HBCR	RC	8.88	11.06	13.78
	FP	5.73	6.56	7.52
	Global	8.47	9.20	10.00
*LTWI	RC	20.59	37.21	67.24
	FP	69.64	99.08	140.98
	Global	38.92	48.76	61.09
PABI	RC	57.50	135.21	317.92
	FP	45.18	52.76	61.62
	Global	55.22	64.64	75.67
RIWI	RC	7.65	25.72	86.50
	FP	19.41	42.11	91.37
	Global	18.68	26.72	38.22
*TREES	RC	6.71	10.35	15.98
	FP	29.44	37.19	46.97
	Global	18.94	24.30	31.17
*WILLOWS	RC	20.46	28.53	39.79
	FP	51.84	61.97	74.07
	Global	36.31	42.26	49.18
*WILLOW-SHRUBS	RC	24.90	34.75	48.48
	FP	49.77	58.06	67.75
	Global	49.06	57.19	66.65

[1] See APPENDIX 4.E-2 for plant shoot model testing by strata.

[2] See APPENDIX 4.A for browse species naming codes.

[3] PAWI did not have enough samples to analyze independently, but is incorporated into the other willow groups.

Table 4.4. Average probability and 95% confidence intervals for the binomial data of Beaver, Hare, Log growth form, and Broken branches by strata. Difference in strata probabilities gives an idea of the magnitude of change between the flood plain and the river channel regions.

Binomial Variable	Strata	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
Beaver	FP	0.00594	0.01112	0.02071	-5.25 times
	RC	0.03950	0.05835	0.08540	
	Global[1]	0.02078	0.03042	0.04434	
Hare	FP	0.03373	0.05165	0.07833	1.67 times
	RC	0.02056	0.03097	0.04639	
	Global	0.02810	0.03853	0.05261	
Log[2]	FP	0.00003	0.00025	0.00171	-20.48 times
	RC	0.00180	0.00512	0.01447	
	Global	0.00005	0.00047	0.00398	
Broken[2]	FP	0.00001	0.00012	0.00124	-12.42 times
	RC	0.00024	0.00149	0.00899	
	Global	0.00022	0.00022	0.00022	

[1] Global models are the intercept only models (y = b0 + 1) and their confidence intervals were approximated using the *Wald* method (Agresti and Coull 1998). All other intervals were derived using Package 'effects' in R (Fox 2003).

[2] Analyses include all browse species for the Hare and Beaver variables; however, HBCR was excluded from the Log and Broken variables. HBCR does not have the ability to take on a "log" growth form or be broken by a moose due to its stature in this area.

Table 4.5. Average probability and 95% confidence intervals for the binomial data of Beaver, Hare, Log growth form, and Broken branches by browse species for the entire study area. Browse species reported are for those with sufficient sample sizes based on each binomial variable independently. BEWI and PAWI did not occur frequent enough for independent analyses by any binomial variable.

Binomial Variable	Browse Species	Lower C.I.	Average Probability	Upper C.I.
Beaver	BAPO	0.02536	0.04257	0.07059
	DIWI	0.00702	0.01294	0.02372
	FLWI	0.06035	0.08742	0.12504
	HBCR	0.00346	0.00659	0.01250
	LTWI	0.01142	0.01930	0.03243
	PABI	0.00292	0.00681	0.01578
	RIWI	0.02550	0.05277	0.10601
Hare	BAPO	0.01806	0.02993	0.04921
	DIWI	0.03184	0.05000	0.07766
	FLWI	0.02778	0.04070	0.05925
	HBCR	0.02799	0.04320	0.06611
	LTWI	0.00894	0.01598	0.02841
	PABI	0.01730	0.03120	0.05563
Log	BAPO	0.00000	0.00004	0.00118
	DIWI	0.00004	0.00033	0.00290
	FLWI	0.00028	0.00239	0.01972
	LTWI	0.00005	0.00049	0.00513
	RIWI	0.00002	0.00031	0.00482
Broken	BAPO	0.00003	0.00027	0.00252
	DIWI	0.00000	0.00004	0.00081
	FLWI	0.00008	0.00059	0.00441
	LTWI	0.00034	0.00251	0.01813
	PABI	0.00010	0.00070	0.00503
	RIWI	0.00020	0.00181	0.01581

Table 4.6. Average probability and bootstrapped 95% confidence intervals for browse Architecture classifications (ARCH) by browse species (or groupings) and strata. Difference in strata probabilities depict the magnitude of change between the flood plain and the river channel regions. See table's footnotes.

Browse Species[1, 3]	ARCH Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
ALL_Browse	Unbrowsed	FP	0.4034	0.4301	0.4549	-1.42X
		RC	0.5952	0.6100	0.6320	
		Global	0.5182	0.5329	0.5521	
	Browsed	FP	0.4458	0.4613	0.4874	1.38X
		RC	0.3175	0.3345	0.3526	
		Global	0.3784	0.3925	0.4109	
	Broomed	FP	0.0918	0.1086	0.1170	1.96X
		RC	0.0466	0.0555	0.0578	
		Global	0.0635	0.0746	0.0781	
WILLOWS	Unbrowsed	FP	0.1339	0.1660	0.1821	-3.16X
		RC	0.4984	0.5242	0.5510	
		Global	0.3174	0.3460	0.3659	
	Browsed	FP	0.5928	0.5996	0.6376	1.42X
		RC	0.4035	0.4234	0.4522	
		Global	0.5374	0.5502	0.5857	
	Broomed	FP	0.1991	0.2344	0.2598	4.47X
		RC	0.0406	0.0524	0.0539	
		Global	0.0858	0.1038	0.1083	
WILLOW-SHRUBS	Unbrowsed	FP	0.1913	0.2382	0.2625	-1.97X
		RC	0.3861	0.4702	0.5655	
		Global	0.2458	0.2948	0.3230	
	Browsed	FP	0.4816	0.4971	0.5560	1.19X
		RC	0.3613	0.4172	0.4850	
		Global	0.4770	0.4922	0.5584	
	Broomed	FP	0.2158	0.2647	0.2939	2.35X
		RC	0.0709	0.1126	0.1372	
		Global	0.1715	0.2130	0.2307	
TREES	Unbrowsed	FP	0.7874	0.7978	0.8679	1.07X
		RC	0.7080	0.7481	0.8399	
		Global	0.7745	0.7798	0.8466	
	Browsed	FP	0.1171	0.1757	0.1894	-1.24X
		RC	0.1416	0.2170	0.2581	
		Global	0.1371	0.1907	0.2019	
	Unbrowsed	FP	0.0110	0.0265	0.0259	-1.32X
		RC	0.0147	0.0349	0.0390	
		Global	0.0133	0.0295	0.0296	

Table 4.6. (Continued) Architecture classification analyses...

Browse Species[1, 3]	ARCH Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
BAPO	Unbrowsed	FP	0.6307	0.6934	0.8370	-1.08X
		RC	0.7195	0.7506	0.8441	
		Global	0.7060	0.7317	0.8279	
	Browsed	FP	0.1349	0.2430	0.3075	1.21X
		RC	0.1296	0.2008	0.2420	
		Global	0.1450	0.2152	0.2496	
	Broomed	FP	0.0205	0.0636	0.0739	1.31X
		RC	0.0184	0.0486	0.0509	
		Global	0.0215	0.0531	0.0547	
DIWI	Unbrowsed	FP	0.1955	0.2443	0.2682	-1.95X
		RC	0.3437	0.4770	0.6282	
		Global	0.2142	0.2664	0.2929	
	Browsed	FP	0.4638	0.4817	0.5427	1.19X
		RC	0.3132	0.4050	0.4940	
		Global	0.4615	0.4814	0.5481	
	Broomed	FP	0.2253	0.2739	0.3034	2.32X
		RC	0.0580	0.1180	0.1712	
		Global	0.2033	0.2522	0.2798	
FLWI	Unbrowsed	FP	0.0834	0.1395	0.1912	-3.76X
		RC	0.4928	0.5240	0.5531	
		Global	0.4042	0.4458	0.4817	
	Browsed	FP	0.6884	0.7082	0.7603	1.57X
		RC	0.4255	0.4503	0.4851	
		Global	0.4888	0.5178	0.5655	
	Broomed	FP	0.0909	0.1524	0.2120	5.91X
		RC	0.0163	0.0258	0.0281	
		Global	0.0235	0.0364	0.0388	
HBCR	Unbrowsed	FP	0.7497	0.7927	0.8777	1.14X
		RC	0.6559	0.6929	0.7653	
		Global	0.7120	0.7303	0.7954	
	Browsed	FP	0.1122	0.1839	0.2256	-1.46X
		RC	0.2069	0.2681	0.3082	
		Global	0.1841	0.2370	0.2637	
	Broomed	FP	0.0088	0.0234	0.0271	-1.67X
		RC	0.0195	0.0390	0.0425	
		Global	0.0155	0.0327	0.0348	

Table 4.6. (Continued) Architecture classification analyses...

Browse Species[1, 3]	ARCH Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
LTWI	Unbrowsed	FP	0.0028	0.0123	0.0133	-31.53X
		RC	0.3103	0.3868	0.4448	
		Global	0.1221	0.1869	0.2211	
	Browsed	FP	0.1140	0.2316	0.2955	-2.40X
		RC	0.5145	0.5557	0.6512	
		Global	0.6598	0.6677	0.7671	
	Broomed	FP	0.6929	0.7561	0.8825	13.14X
		RC	0.0264	0.0575	0.0603	
		Global	0.0805	0.1454	0.1527	
PABI	Unbrowsed	FP	0.8010	0.8160	0.8873	-1.12X
		RC	0.6960	0.9168	1.0000	
		Global	0.8062	0.8184	0.8927	
	Browsed	FP	0.1084	0.1746	0.1922	2.20X
		RC	0.0000	0.0794	0.2850	
		Global	0.1021	0.1721	0.1867	
	Broomed	FP	0.0019	0.0094	0.0124	2.47X
		RC	0.0000	0.0038	0.0173	
		Global	0.0019	0.0095	0.0124	
BEWI[2]	Unbrowsed	Global	0.2232	0.6115	0.8456	
	Browsed	Global	0.1492	0.3635	0.7975	
	Broomed	Global	0.0009	0.0250	0.0427	
RIWI[2]	Unbrowsed	Global	0.0995	0.2608	0.3470	
	Browsed	Global	0.5175	0.5785	0.8082	
	Broomed	Global	0.0420	0.1607	0.2209	

[1] See APPENDIX 4.A for browse species naming codes.

[2] Not enough samples to analyze by strata. Only the global model was used for these species.

[3] PAWI did not have enough samples to analyze independently, but was incorporated into the other willow groups.

[4] Global models are the intercept only models (y = b0 + 1)

Table 4.7. Average probability and bootstrapped 95% confidence intervals for browse Dead classifications (DEAD) by browse species (or groupings) and strata. Difference in strata probabilities depict the magnitude of change between the flood plain and the river channel regions. See table's footnotes.

Browse Species[1, 3]	DEAD Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
ALL_Browse	No Dead	FP	0.0245	0.0323	0.0344	-2.27X
		RC	0.0596	0.0732	0.0766	
		Global	0.0413	0.0517	0.0534	
	<50% Dead	FP	0.8439	0.8478	0.8698	-1.03X
		RC	0.8714	0.8724	0.8926	
		Global	0.8704	0.8711	0.8921	
	>50% Dead	FP	0.1005	0.1199	0.1274	2.20X
		RC	0.0435	0.0545	0.0572	
		Global	0.0646	0.0772	0.0790	
WILLOWS	No Dead	FP	0.0061	0.0104	0.0114	-3.47X
		RC	0.0244	0.0361	0.0381	
		Global	0.0139	0.0216	0.0229	
	<50% Dead	FP	0.8134	0.8212	0.8603	-1.11X
		RC	0.9103	0.9103	0.9346	
		Global	0.8887	0.8895	0.9155	
	>50% Dead	FP	0.1315	0.1684	0.1780	3.14X
		RC	0.0389	0.0536	0.0548	
		Global	0.0684	0.0889	0.0904	
WILLOW-SHRUBS	No Dead	FP	0.0026	0.0087	0.0096	-1.63X
		RC	0.0041	0.0142	0.0215	
		Global	0.0035	0.0100	0.0121	
	<50% Dead	FP	0.8213	0.8276	0.8860	-1.06X
		RC	0.8525	0.8794	0.9436	
		Global	0.8365	0.8409	0.9009	
	>50% Dead	FP	0.1101	0.1637	0.1723	1.54X
		RC	0.0428	0.1064	0.1393	
		Global	0.0932	0.1491	0.1549	
TREES	No Dead	FP	0.0178	0.0451	0.0470	-1.31X
		RC	0.0217	0.0591	0.0683	
		Global	0.0196	0.0500	0.0500	
	<50% Dead	FP	0.9100	0.9124	0.9633	1.00X
		RC	0.9086	0.9086	0.9607	
		Global	0.9100	0.9118	0.9652	
	>50% Dead	FP	0.0157	0.0425	0.0438	1.32X
		RC	0.0097	0.0323	0.0393	
		Global	0.0135	0.0382	0.0382	

Table 4.7. (Continued) Dead classification analyses...

Browse Species[1, 3]	DEAD Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
BAPO	No Dead	FP	0.0533	0.1119	0.1297	1.20X
		RC	0.0429	0.0934	0.1093	
		Global	0.0483	0.0996	0.1084	
	<50% Dead	FP	0.8290	0.8393	0.9183	-1.01X
		RC	0.8406	0.8475	0.9229	
		Global	0.8374	0.8451	0.9241	
	>50% Dead	FP	0.0182	0.0488	0.0575	-1.21X
		RC	0.0224	0.0591	0.0723	
		Global	0.0211	0.0553	0.0650	
DIWI	No Dead	FP	0.0006	0.0028	0.0052	-1.32X
		RC	0.0008	0.0037	0.0086	
		Global	0.0007	0.0028	0.0052	
	<50% Dead	FP	0.8412	0.8494	0.9031	-1.04X
		RC	0.8413	0.8804	0.9496	
		Global	0.8464	0.8521	0.9028	
	>50% Dead	FP	0.0958	0.1478	0.1563	1.27X
		RC	0.0449	0.1160	0.1567	
		Global	0.0954	0.1450	0.1514	
FLWI	No Dead	FP	0.0047	0.0116	0.0166	-3.46X
		RC	0.0232	0.0401	0.0434	
		Global	0.0173	0.0320	0.0342	
	<50% Dead	FP	0.7873	0.8353	0.9061	-1.09X
		RC	0.9093	0.9117	0.9433	
		Global	0.9072	0.9074	0.9426	
	>50% Dead	FP	0.0822	0.1532	0.2058	3.18X
		RC	0.0299	0.0482	0.0508	
		Global	0.0373	0.0606	0.0620	
HBCR	No Dead	FP	0.0654	0.1042	0.1208	-1.47X
		RC	0.1046	0.1531	0.1680	
		Global	0.0968	0.1341	0.1459	
	<50% Dead	FP	0.8326	0.8450	0.8968	1.04X
		RC	0.8036	0.8136	0.8711	
		Global	0.8162	0.8274	0.8791	
	>50% Dead	FP	0.0284	0.0508	0.0609	1.53X
		RC	0.0169	0.0333	0.0414	
		Global	0.0207	0.0385	0.0451	

Table 4.7. (Continued) Dead classification analyses...

Browse Species[1, 3]	DEAD Class	Strata[4]	Lower C.I.	Average Probability	Upper C.I.	Difference FP vs. RC
LTWI	No	FP	0.0014	0.0090	0.0097	-5.66X
		RC	0.0148	0.0509	0.0510	
		Global	0.0086	0.0334	0.0340	
	<50%	FP	0.6749	0.7495	0.8958	-1.20X
		RC	0.8900	0.8978	0.9659	
		Global	0.8900	0.8903	0.9627	
	>50%	FP	0.0987	0.2414	0.3220	4.71X
		RC	0.0165	0.0512	0.0520	
		Global	0.0266	0.0763	0.0770	
PABI	No	FP	0.0000	0.0153	0.0153	-1.47X
		RC	0.0000	0.0225	0.0230	
		Global	0.0000	0.0155	0.0156	
	<50%	FP	0.9500	0.9517	0.9998	-1.00X
		RC	0.9500	0.9549	0.9998	
		Global	0.9500	0.9519	0.9998	
	>50%	FP	0.0001	0.0330	0.0330	1.47X
		RC	0.0000	0.0225	0.0230	
		Global	0.0001	0.0326	0.0330	
BEWI[2]	No	Global	0.0012	0.0272	0.0590	
	<50%	Global	0.7398	0.8262	0.9654	
	>50%	Global	0.0279	0.1466	0.2327	
RIWI[2]	No	Global	0.0005	0.0467	0.0642	
	<50%	Global	0.6396	0.6636	0.9923	
	>50%	Global	0.0149	0.2897	0.3240	

[1] See APPENDIX 4.A for browse species naming codes.

[2] Not enough samples to analyze by strata. Only the global model was used for these species.

[3] PAWI did not have enough samples to analyze independently, but was incorporated into the other willow groups.

[4] Global models are the intercept only models (y = b0 + 1)

Table 4.8. Selection ratios (Wi) and 95% confidence intervals for sympatric browsers by browse species. Browse 'used' by moose included all plants classified as browsed or broomed in the architecture classification. Intervals that encompass the value of 1.0 indicate no selection by the browser. Values above 1.0 indicate selection for a species and values below 1.0 indicate avoidance or selection against those browse species. These data are analyzed using the Design III approach (Manly et al. 2002).

Sympatric Browser	Browse Species[1]	Wi	SE	CI lower	CI upper
Beaver	BAPO	1.2887	0.2400	0.6431	1.9343
	DIWI	1.0006	0.1698	0.5440	1.4573
	FLWI	1.3263	0.0871	1.0920	1.5607
	HBCR	0.3409	0.1127	0.0376	0.6441
	LTWI	0.5157	0.0675	0.3340	0.6973
	PABI	0.6024	0.1813	0.1146	0.9832
	RIWI	1.0957	0.2372	0.4575	1.7339
Hare	BAPO	0.8103	0.1537	0.3901	1.2305
	BEWI	1.1586	0.2430	0.4942	1.8231
	DIWI	1.0511	0.0690	0.8624	1.2398
	FLWI	1.1628	0.0656	1.0054	1.3422
	HBCR	1.0234	0.0878	0.7833	1.2636
	LTWI	0.5880	0.1402	0.2046	0.9714
	PABI	0.8864	0.1446	0.4909	1.2819
	RIWI	1.0852	0.2097	0.5118	1.6585
Moose	BAPO	0.7665	0.0567	0.6114	0.9216
	BEWI	1.0647	0.1941	0.5338	1.5955
	DIWI	1.1967	0.0369	1.0958	1.2975
	FLWI	1.0630	0.0207	1.0063	1.1197
	HBCR	0.7338	0.0467	0.6062	0.8614
	LTWI	1.1856	0.0399	1.0766	1.2945
	PABI	0.5106	0.0491	0.3764	0.6449
	RIWI	1.0447	0.0728	0.8455	1.2438

[1] BEWI did not have sufficient samples in the river channel used by beavers to include in the beaver analysis. Whereas PAWI was more rare and not included in any selection analyses.

Table 4.9. Brooming Index (BI) and 95% confidence intervals for moose browse species. BI is calculated from the architecture classification data for each browse species or grouping by strata.

Browse Species[1, 2]	Strata	CI-lower	Average (BI)	CI-upper
BAPO	RC	0.0552	0.1563	0.2575
	FP	0.0043	0.1337	0.2631
	Global[3]	0.0771	0.1478	0.2283
DIWI	RC	0.0000	0.1095	0.2996
	FP	0.3170	0.3974	0.4777
	Global	0.2784	0.3537	0.4324
FLWI	RC	0.0068	0.0507	0.0946
	FP	0.1690	0.2426	0.3163
	Global	0.0641	0.1010	0.1433
HBCR	RC	0.0329	0.1084	0.1838
	FP	0.0302	0.1226	0.2150
	Global	0.0623	0.1141	0.1740
LTWI	RC	0.0850	0.1576	0.2302
	FP	0.5709	0.6845	0.7981
	Global	0.2366	0.3104	0.3881
PABI	RC	0.0000	0.0000	0.0891
	FP	0.0008	0.0198	0.0388
	Global	0.0043	0.0190	0.0390
ALL_Browse	RC	0.0529	0.0928	0.1327
	FP	0.2964	0.3413	0.3863
	Global	0.1684	0.2025	0.2381
ALLnoHBCR[4]	RC	0.0463	0.0868	0.1272
	FP	0.2979	0.3433	0.3888
	Global	0.1653	0.2000	0.2369
WILLOWS	RC	0.0370	0.0819	0.1268
	FP	0.3502	0.4004	0.4506
	Global	0.1831	0.2234	0.2656
WILLOW-SHRUBS	RC	0.0301	0.1383	0.2465
	FP	0.3366	0.4164	0.4962
	Global	0.2523	0.3184	0.3886
TREES	RC	0.0720	0.1521	0.2322
	FP	0.0000	0.0669	0.1338
	Global	0.0548	0.1019	0.1527

[1] See APPENDIX 4.A for browse species naming codes.

[2] BEWI, PAWI, RIWI and GLWI were all rare enough to not all analyses individually, but were incorporated into the willow subset groups.

[3] Global models = intercept only models (i.e., overall estimate for the entire study area).

[4] The ALLnoHBCR data subset removed HBCR from the entire analyses to have an overall index for comparison to other moose ranges that don't consider HBCR browse.

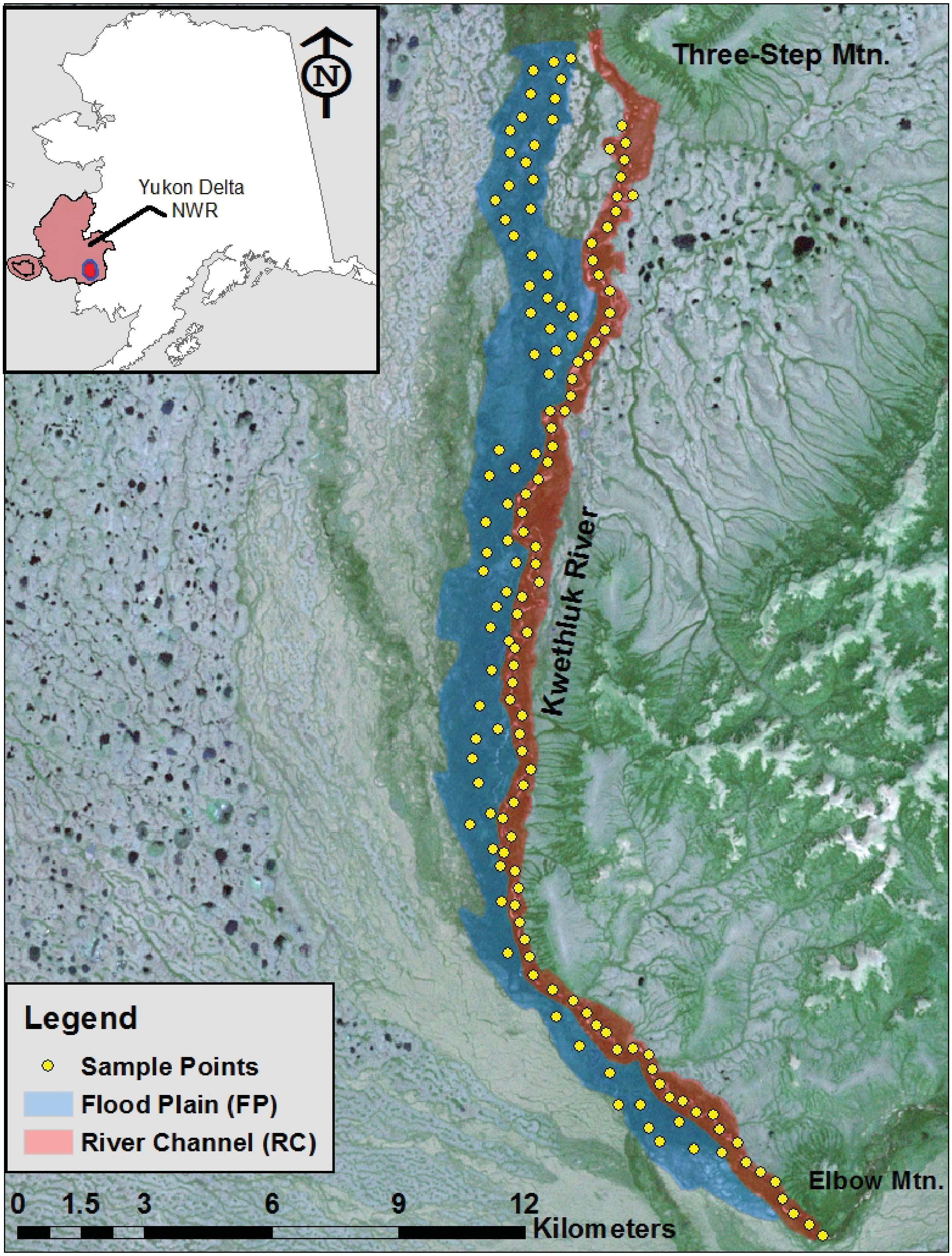


Figure 4.1. Study area along the Kwethluk River within the Yukon Delta National Wildlife Refuge in western Alaska. Map delineates sample plot locations within the two strata, river channel (RC) and flood plain (FP).

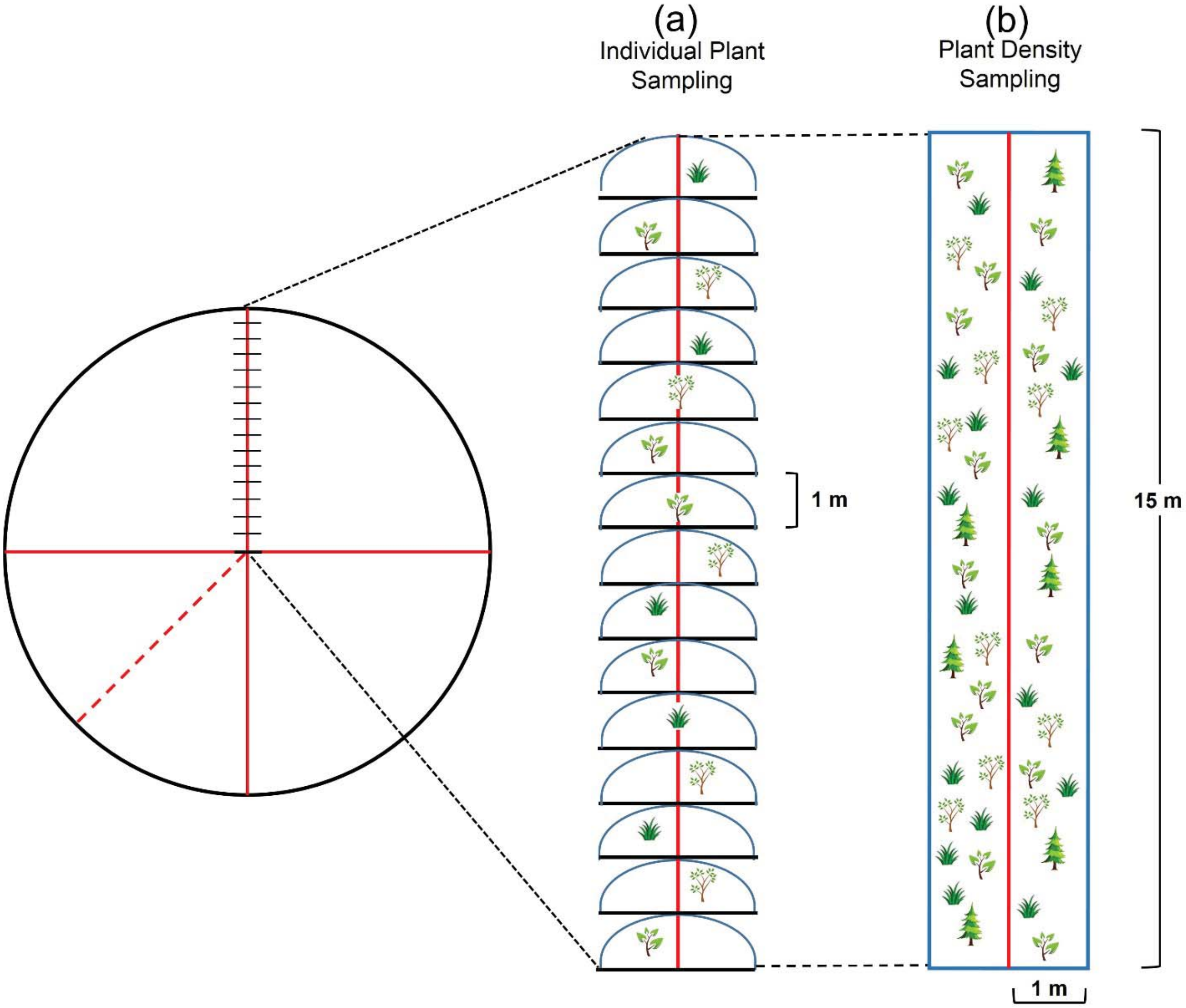


Figure 4.2. Plot schematic for individual plant characteristic sampling and for plant density estimations. Four 15 m transects were laid out with the first having a random bearing and subsequent transects being 90 degrees from each other. The dashed transect line indicates an additional transect used to increase the number of samples within the plot to the desired level of 30-40 individual plants (those transects were not used in density estimates). Individual plants were sampled at 1 m intervals along transects (a). Only one plant closest to the interval within a 1 m forward arc was sampled (a). Plant density estimates only used the four primary transects and counted all plants of interest within a 2 m wide belt transect (b).

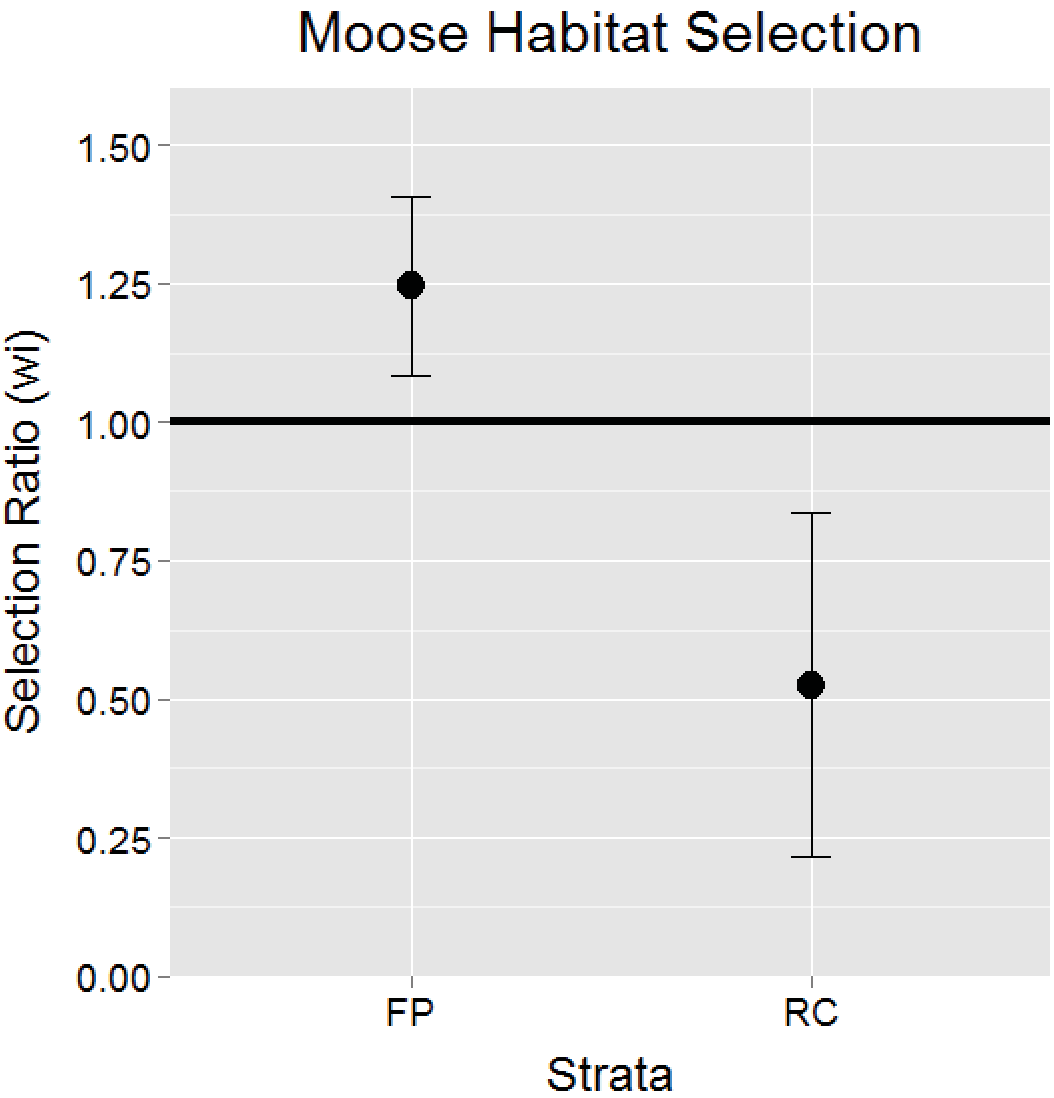


Figure 4.3. Moose habitat selection ratios for the flood plain (FP) and river channel (RC) stratums. A selection ratio of 1.0 (or its confidence intervals including 1.0) indicates that resources are used in proportion to availability and no selection (or avoidance) is occurring. Ratios below 1.0 indicate avoidance and ratios above 1.0 indicate selection.

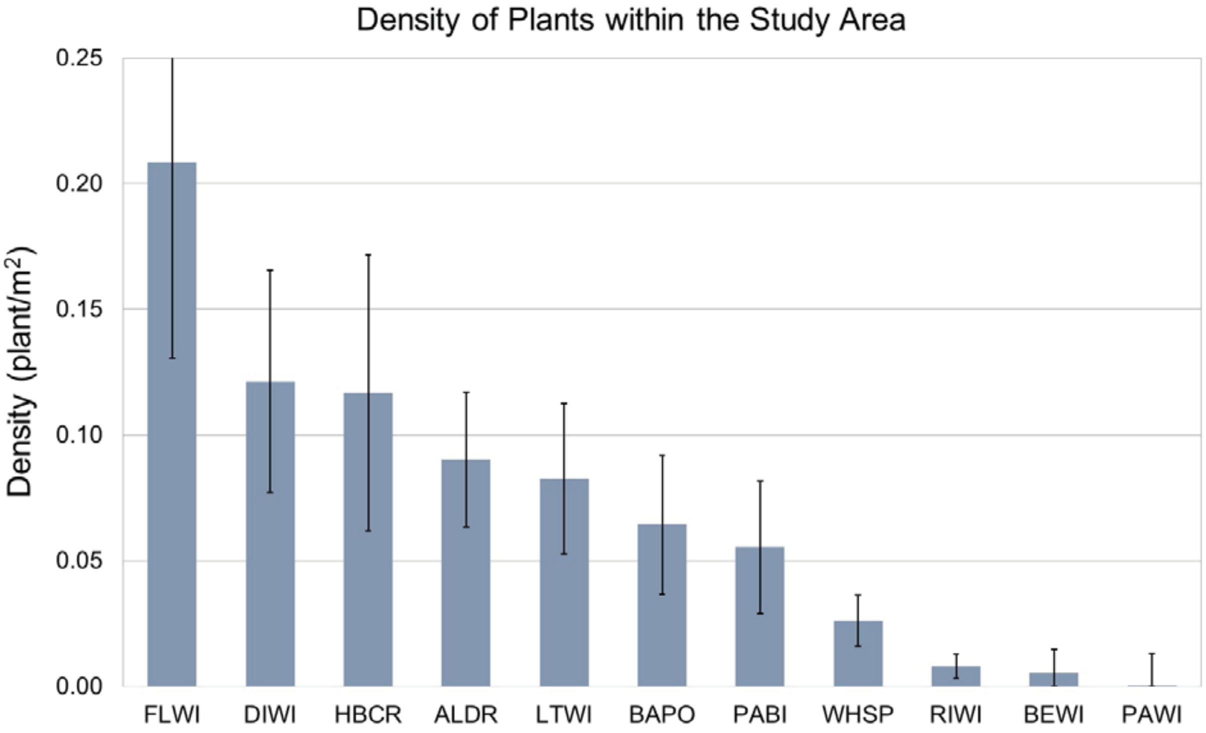


Figure 4.4. Average plant densities and 95% confidence intervals within sampled plots of the study area. Density estimates are based on the global means without regard to strata. Grayleaf willow was excessively rare and only recorded on one plot with four total plants (and some were not within the sampled belt transect). See Appendix 4.A for plant naming codes. See Table 4.1 for data.

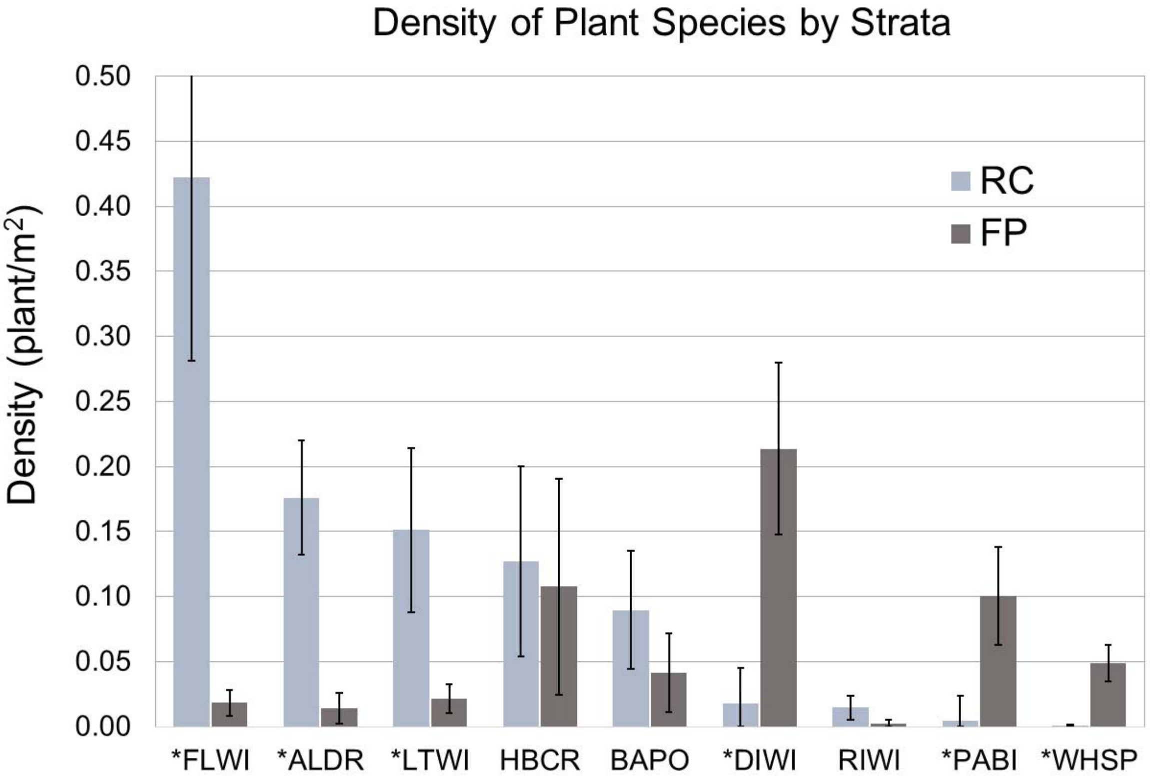


Figure 4.5. Average plant densities and 95% confidence intervals within sampled plots of the study area. Density estimates are based on the river channel and flood plain strata. BEWI and PAWI were rare enough to not allow individual analyses by strata. Grayleaf willow was excessively rare and only recorded on one plot with four total plants. Plant species with an asterisk (*) indicates a significant difference between strata. See Appendix 4.A for plant naming codes. See Table 4.1 for data.

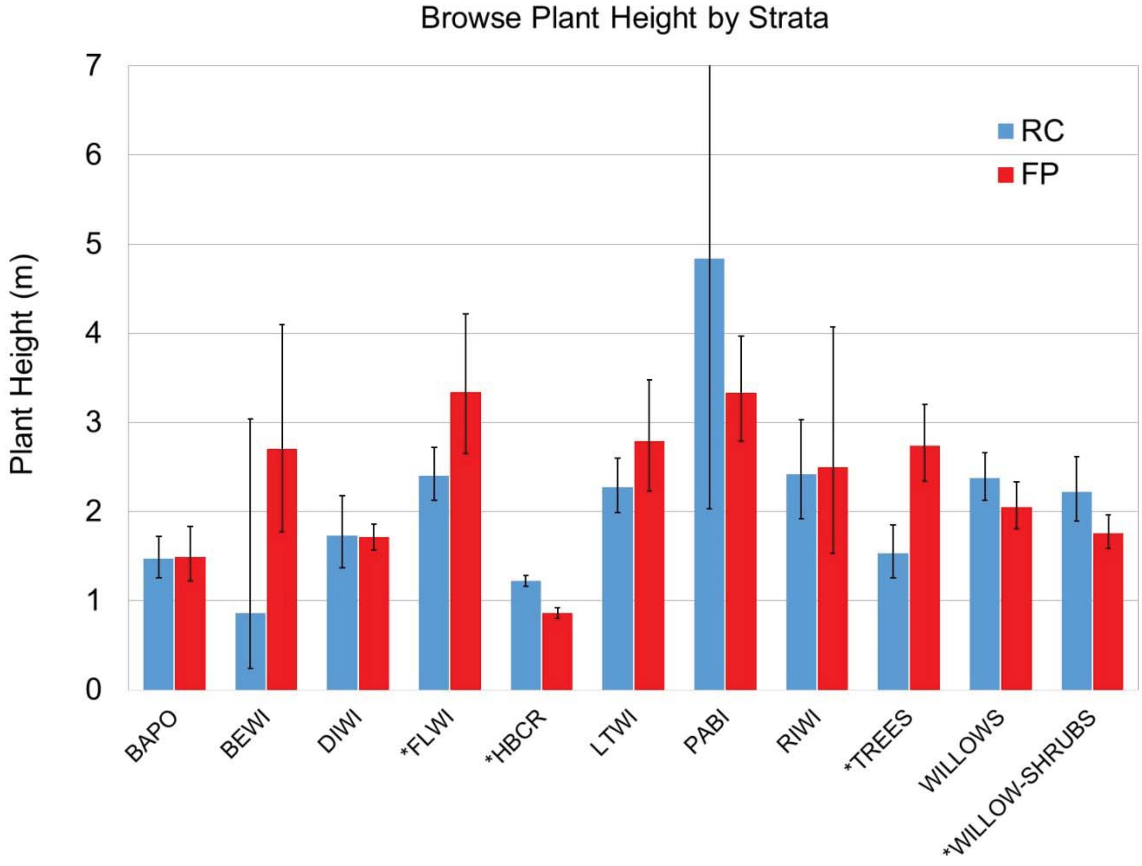


Figure 4.6. Average browse plant heights based on river channel and flood plain strata. Values are the back-transformed mean estimates of height (m) with approximate 95% confidence intervals. The browse species PAWI did not have enough samples to analyze alone, but was included in the subsets of combined willow groups. The excessively wide confidence intervals for BEWI and PABI are attributed to having very few measurements within the river channel stratum. Browse plants preceded with an asterisk (*) are significantly different between strata. See Appendix 4.A for plant naming codes. See Table 4.2 for data and Appendix 4.E-1 for models.

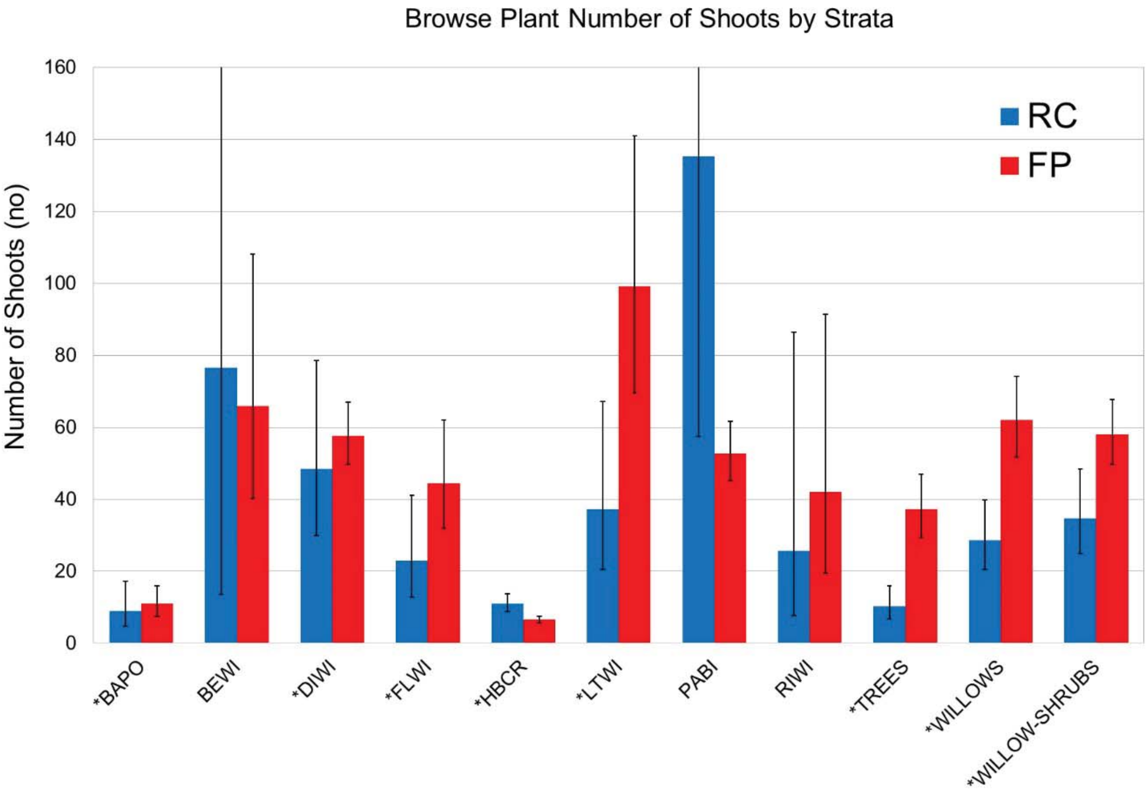


Figure 4.7. Average number of browse plant shoots based on river channel and flood plain strata. Values are the back-transformed mean estimates of plant shoots (no.) with approximate 95% confidence intervals. The browse species PAWI did not have enough samples to analyze alone, but was included in the subsets of combined willow groups. The excessively wide confidence intervals for BEWI and PABI are attributed to having very few measurements within the river channel stratum. Additionally not all plots had the number of shoots recorded reducing the total samples in this analyses. Browse plants preceded with an asterisk (*) are significantly different between strata. See Appendix 4.A for plant naming codes. See Table 4.3 for data and Appendix 4.E-2 for models.

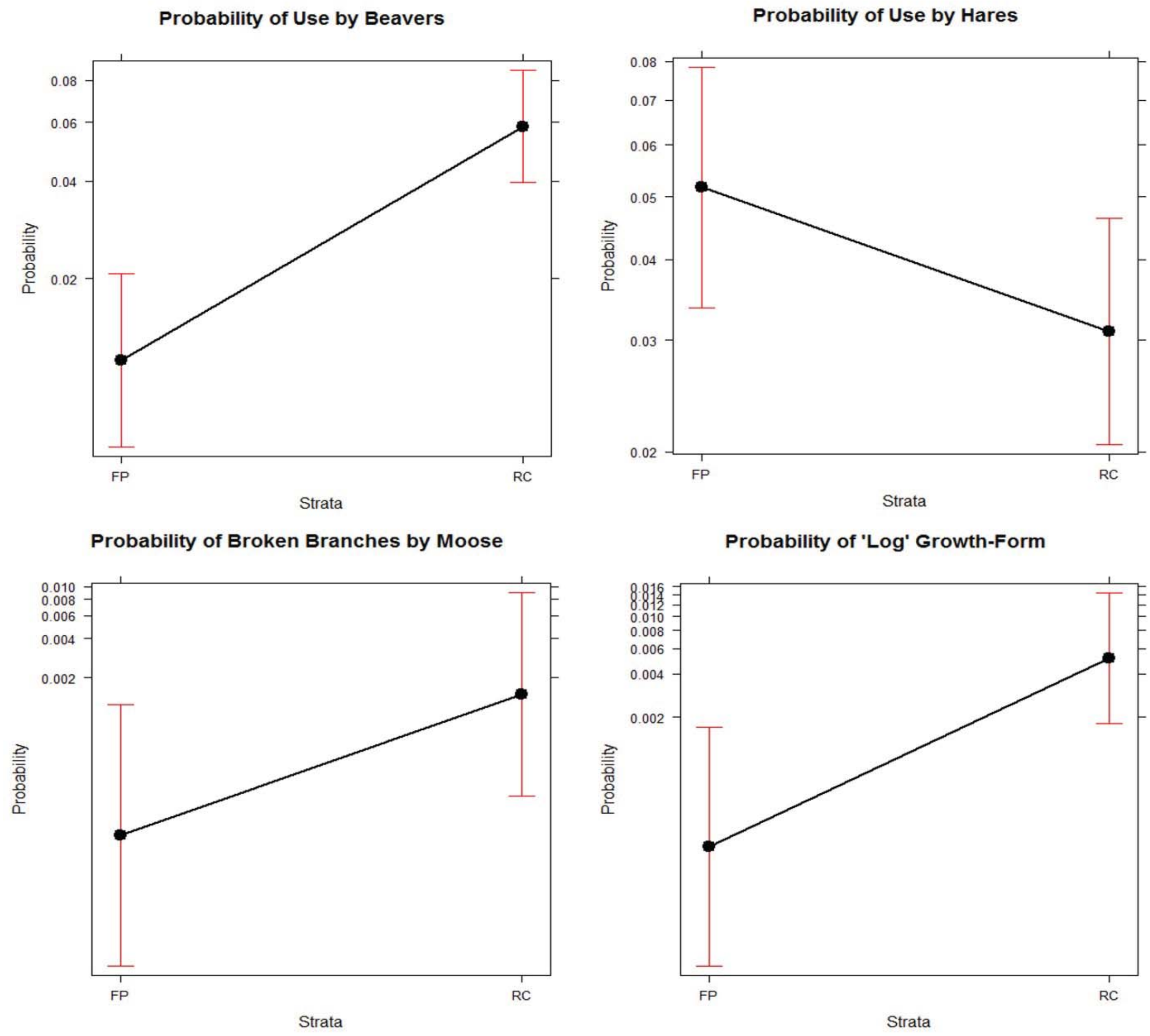


Figure 4.8. Average probability plots and 95% confidence intervals for binomial data by strata. All binomial variables were significantly different between strata except for Hare, which was minimally insignificant (p = 0.0699). Analyses include all browse species for the Hare and Beaver variable; however, HBCR was excluded from the Log and Broken variables. HBCR does not have the ability to take on a "log" growth form or be broken by a moose due to its stature in this area. See Table 4.4 for data.

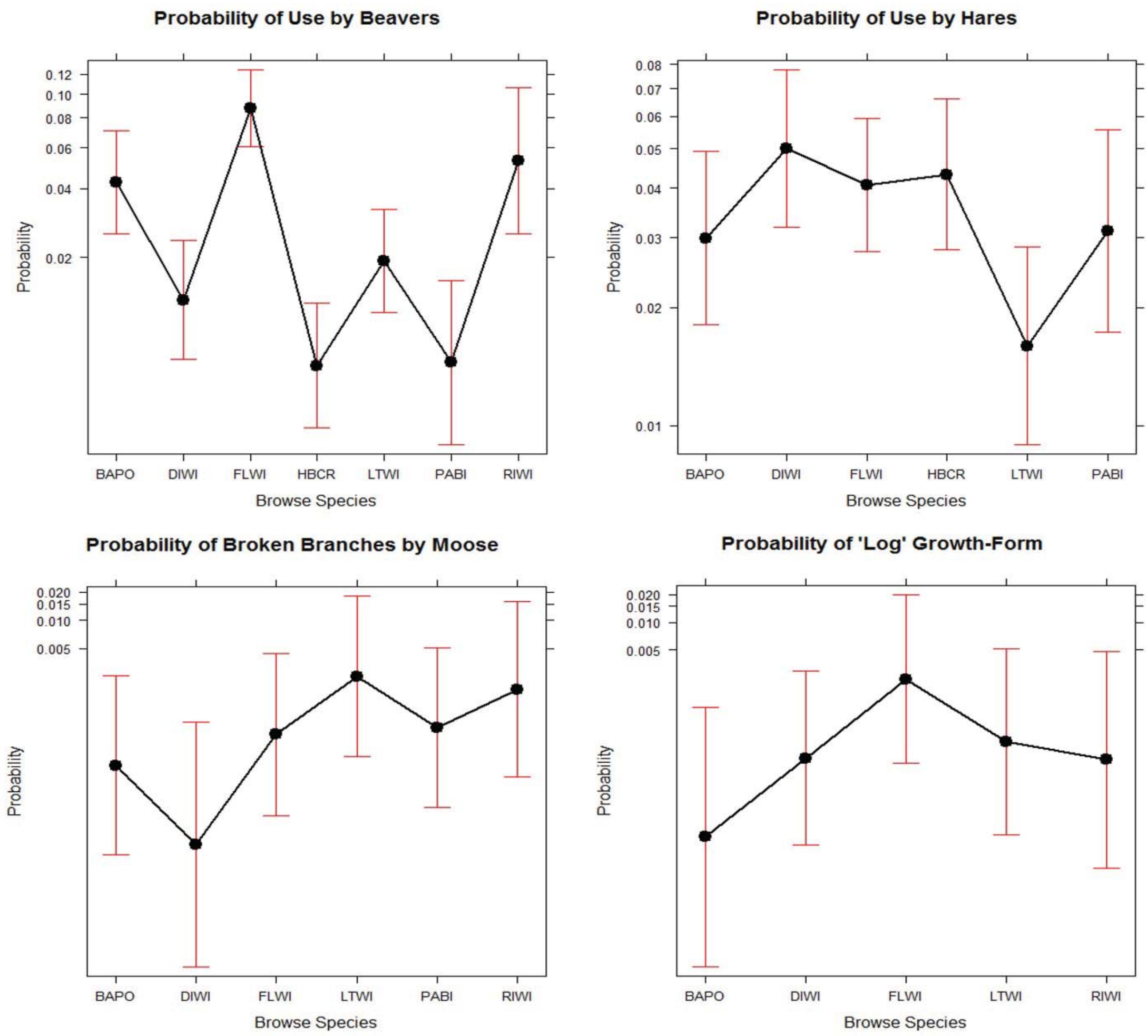


Figure 4.9. Average probability plots and 95% confidence intervals for binomial data by browse species within the entire study area (global models by species). Browse species included in models are for those with sufficient sample sizes based on each binomial variable independently. BEWI and PAWI did not occur frequent enough for individual comparisons for any binomial variable. HBCR was excluded from the broken branch and log growth form due to its inability to take on those forms. See Appendix 4.A for plant naming codes. See Table 4.5 for data.

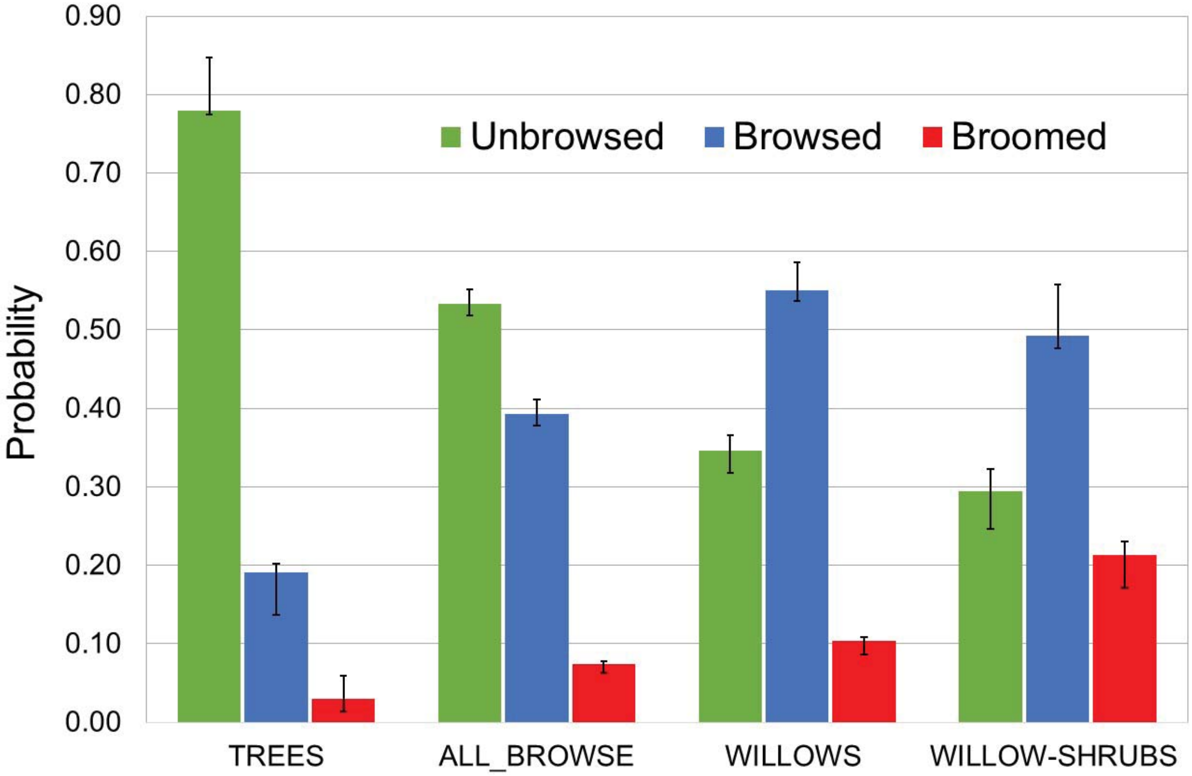


Figure 4.10. Average probabilities and bootstrapped 95% confidence intervals for the three levels of browse architecture classifications by browse groupings. Probabilities are for the entire study area (global models). See Appendix 4.A for plant naming codes. See Table 4.6 for data.

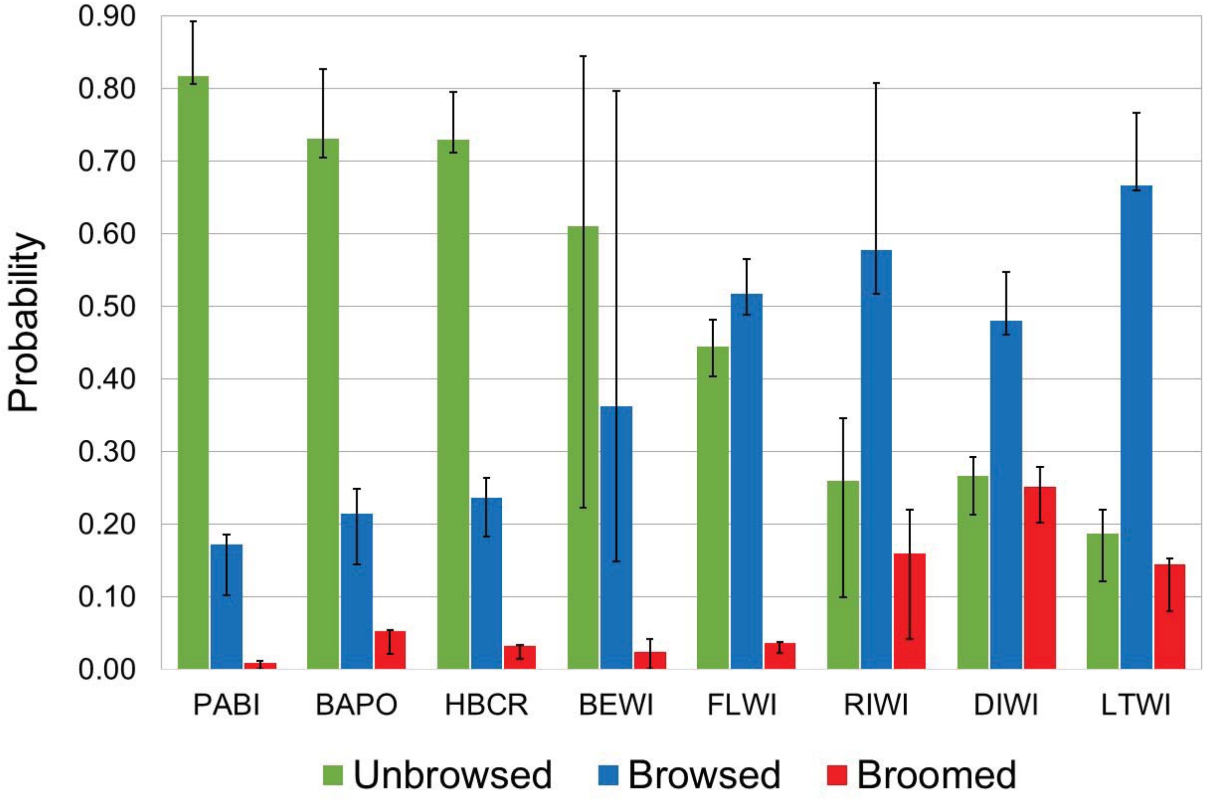


Figure 4.11. Average probabilities and bootstrapped 95% confidence intervals for the three levels of browse architecture classifications by individual browse species. Probabilities are for the entire study area (global models). PAWI was excluded from individual analyses because of insufficient observations to model the probabilities; however, it was incorporated into the willow subset groupings. See Appendix 4.A for plant naming codes. See Table 4.6 for data.

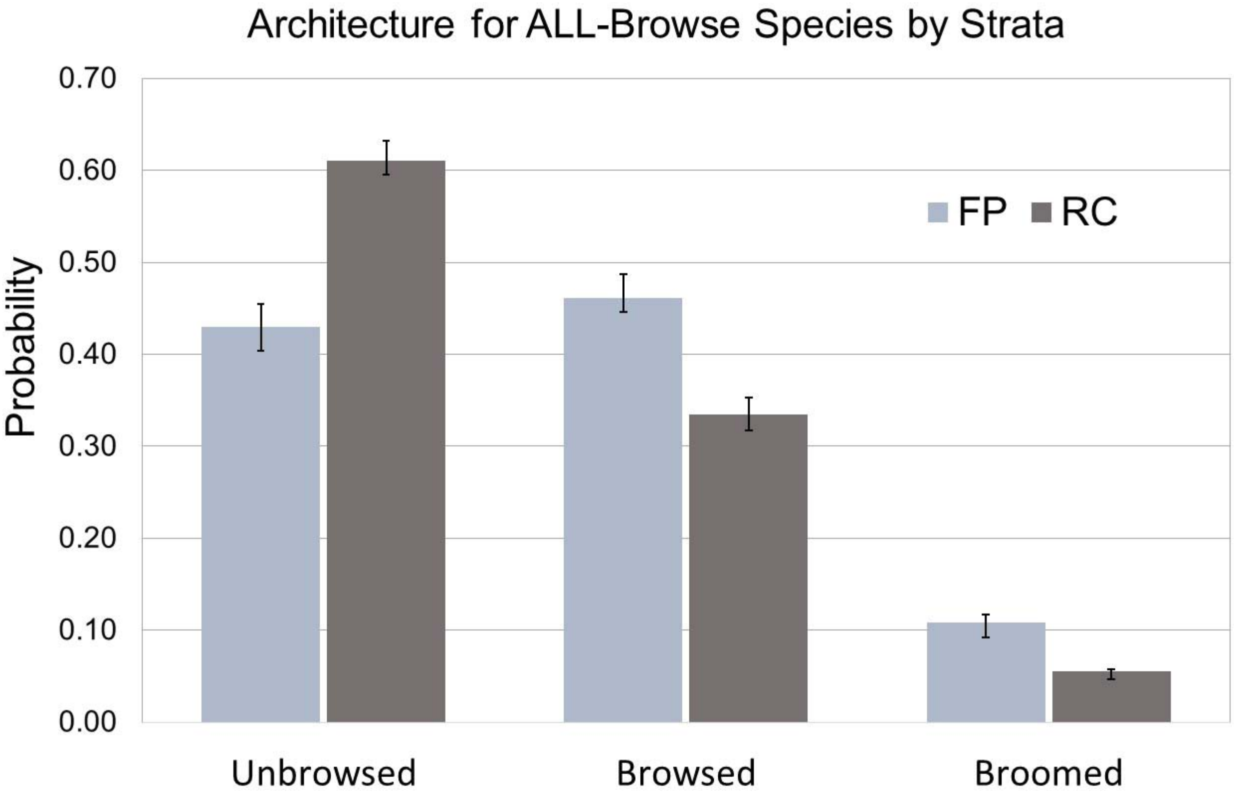


Figure 4.12. Average probabilities and bootstrapped 95% confidence intervals for the three levels of browse architecture by habitat strata. There were significant differences between strata for all classes. Probabilities are for all browse species combined. See Table 4.6 for data.

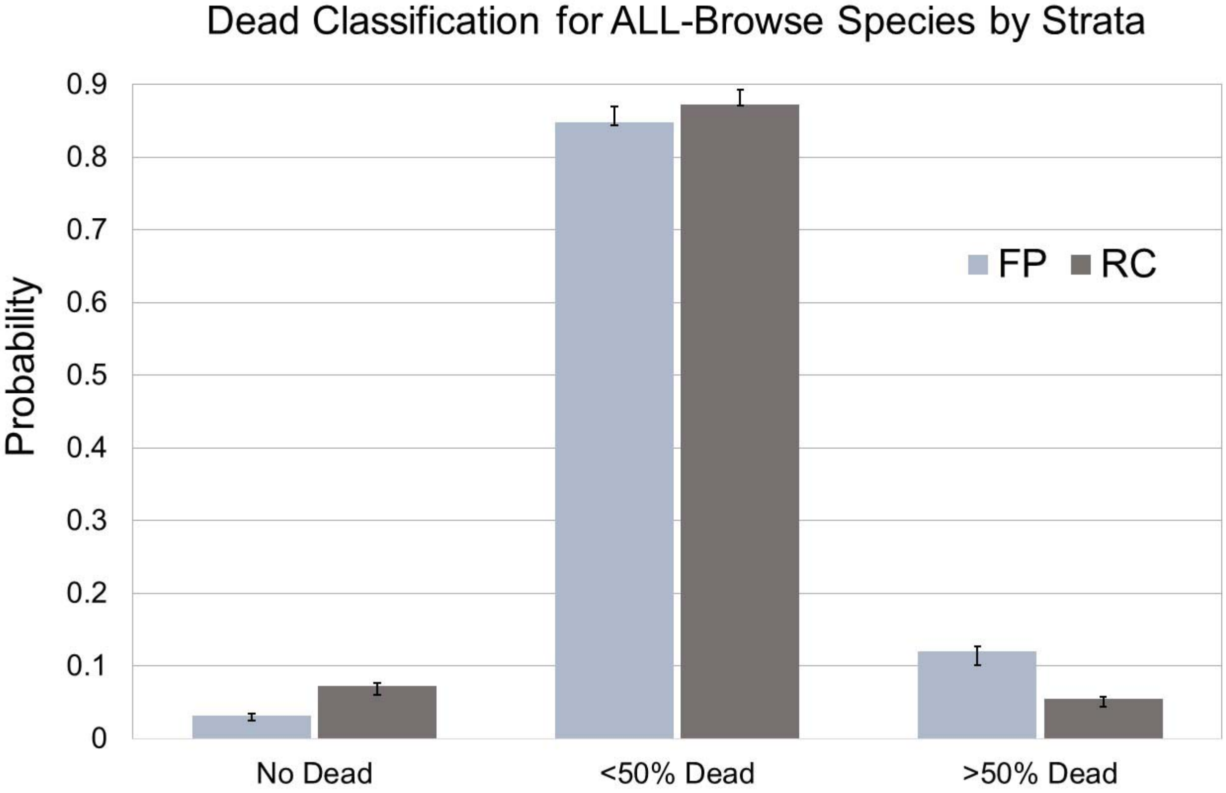


Figure 4.13. Average probabilities and bootstrapped 95% confidence intervals for the three levels of browse dead material classifications by habitat strata. There were significant differences between strata for all three classes. Probabilities are for all browse species combined. See Table 4.7 for data.

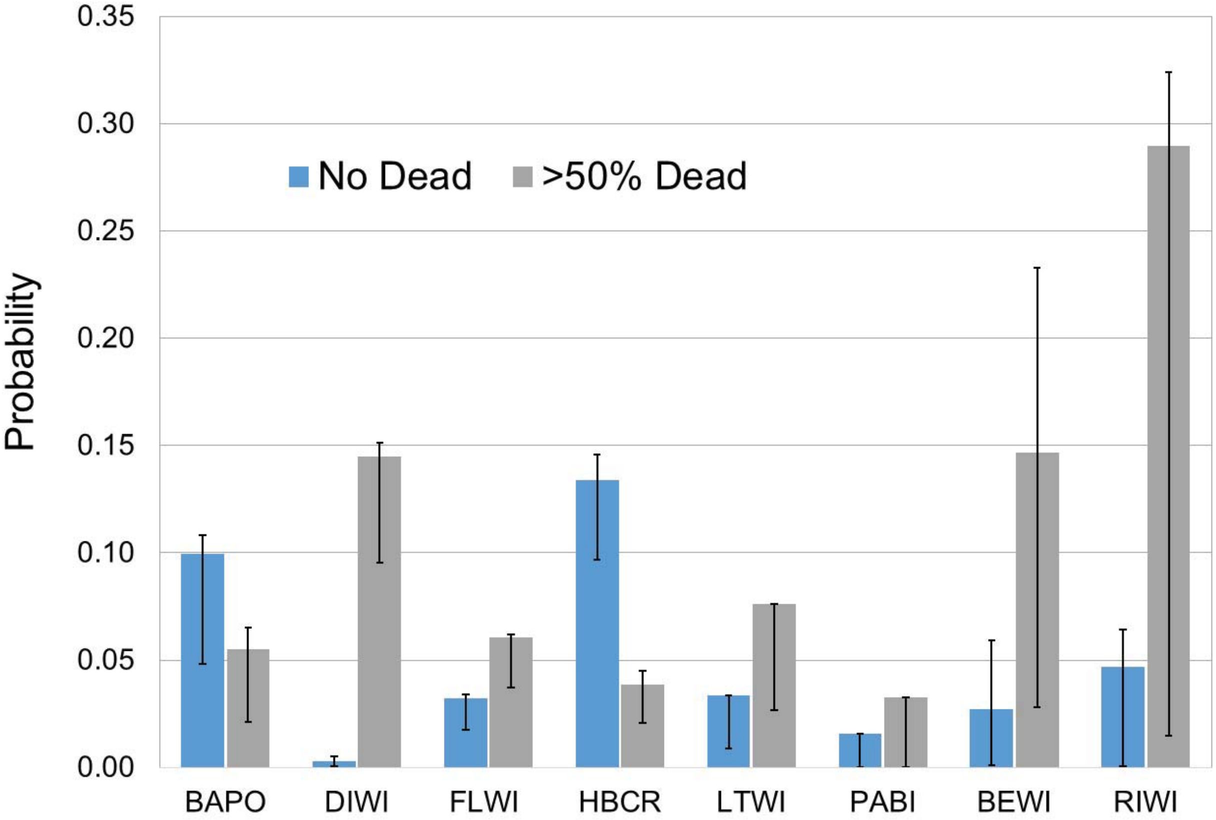


Figure 4.14. Average probabilities and bootstrapped 95% confidence intervals for only two levels of browse dead material classifications by individual browse species. The classification of “<50% Dead” was excluded from this figure because most plants had high probabilities (see Figure 4.13) in this category; therefore altering the y-axis scale. Probabilities are for the entire study area (global models). PAWI was excluded from individual analyses because of insufficient observations to model the probabilities; however, it was incorporated into the willow subset groupings. See Appendix 4.A for plant naming codes. See Table 4.7 for data.

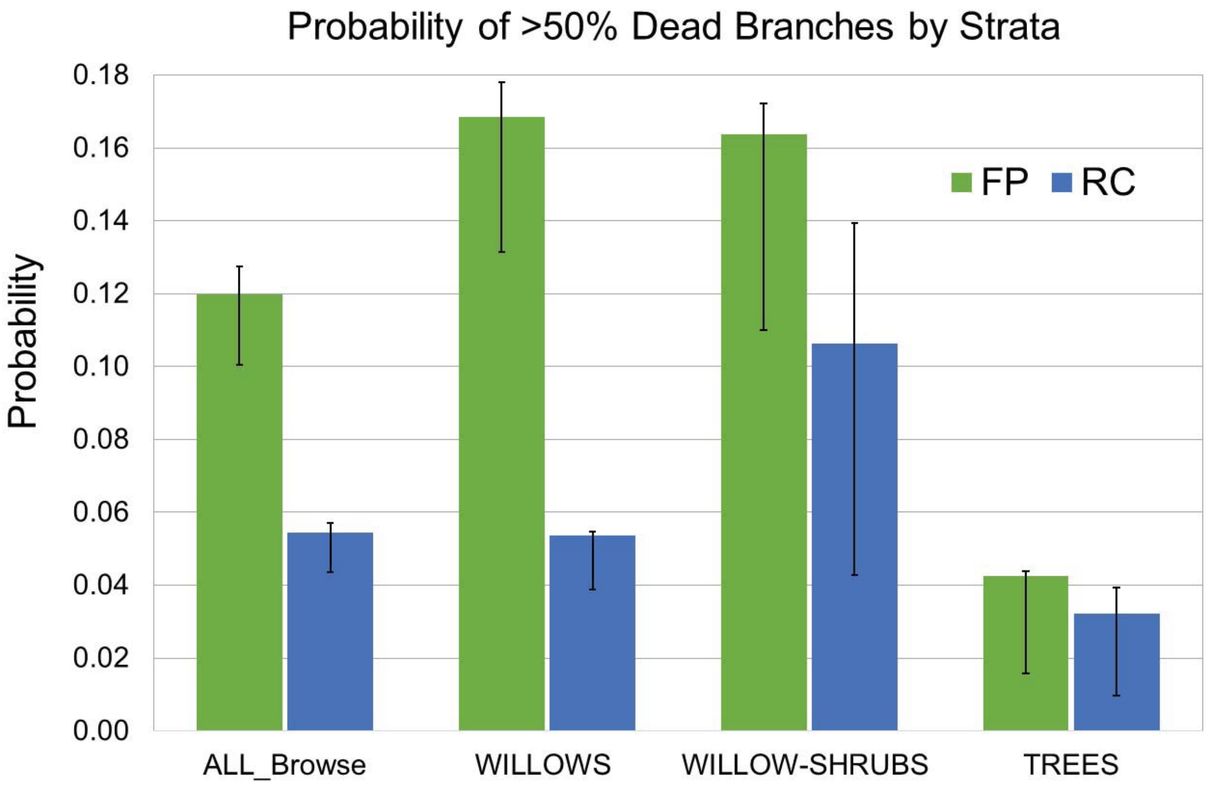


Figure 4.15. Average probabilities and bootstrapped 95% confidence intervals for only the >50% dead material classification by browse groupings. Significant differences are observed between the flood plain and river channel strata except for the trees grouping. See Appendix 4.A for plant naming codes. See Table 4.7 for data.

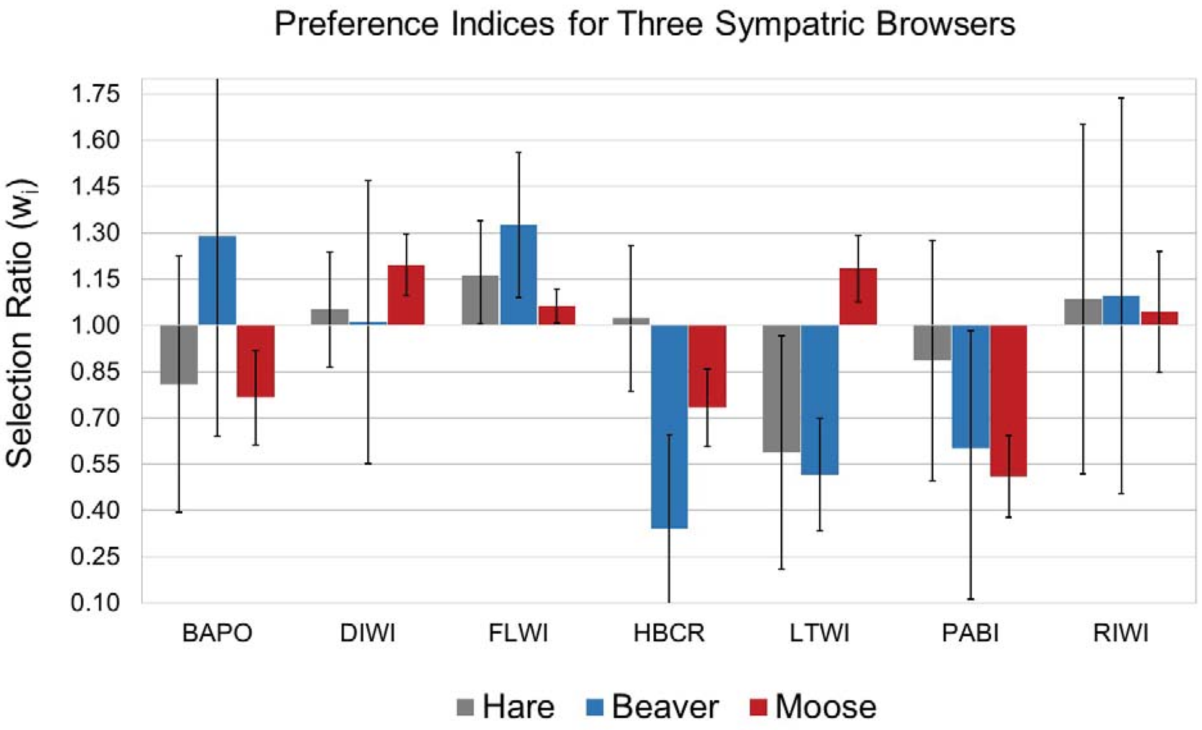


Figure 4.16. Selection ratios and 95% confidence intervals for three sympatric browsers within the study area. Moose data includes all used observations (browsed + broomed). The analyses are Design III (Manly et al. 2002). A selection ratio of 1.0 (or its confidence intervals including 1.0) indicates that resources are used in proportion to availability and no selection (or avoidance) is occurring. Ratios below 1.0 indicate avoidance and ratios above 1.0 indicate selection. See Appendix 4.A for plant naming codes. See Table 4.8 for data.

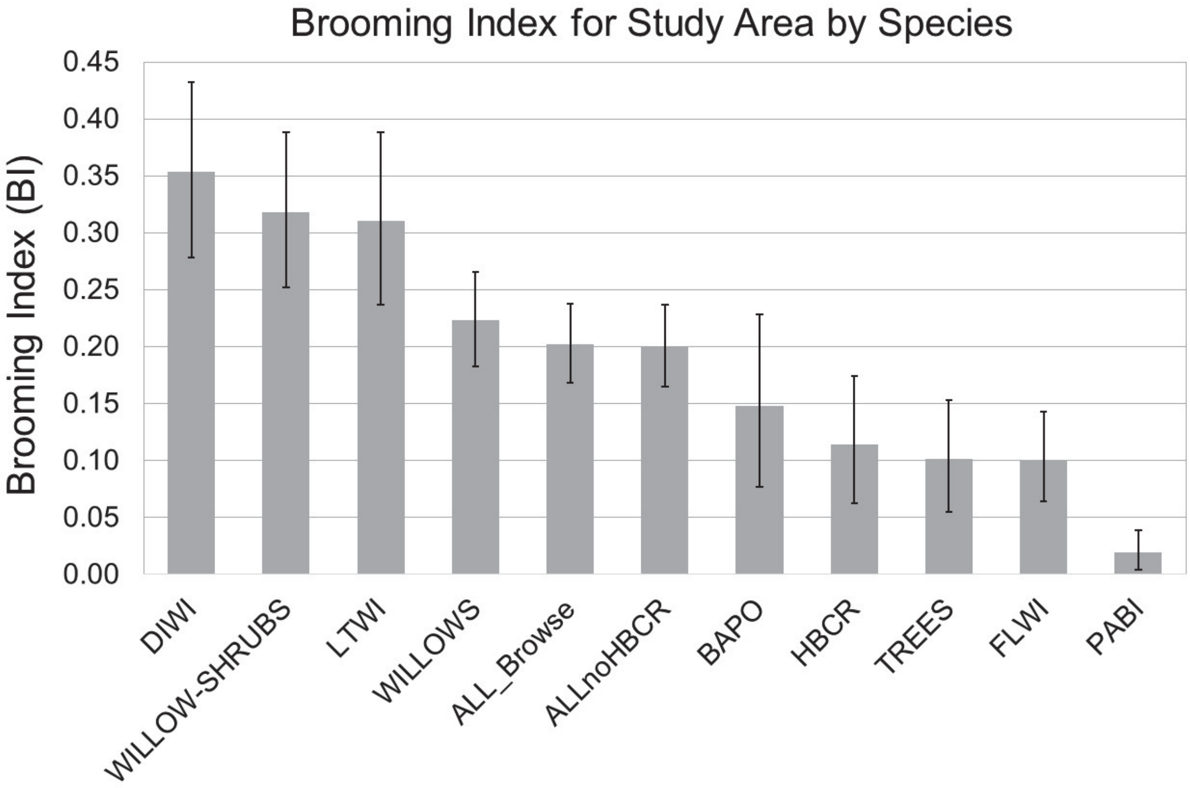


Figure 4.17. Average brooming index (BI) and 95% confidence intervals within sampled plots of the study area by browse species. BI estimates are based on the global means without regard to strata. Confidence intervals for the global mean were calculated using the bootstrap and percentile methods. See Appendix 4.A for plant naming codes. See Table 4.9 for data.

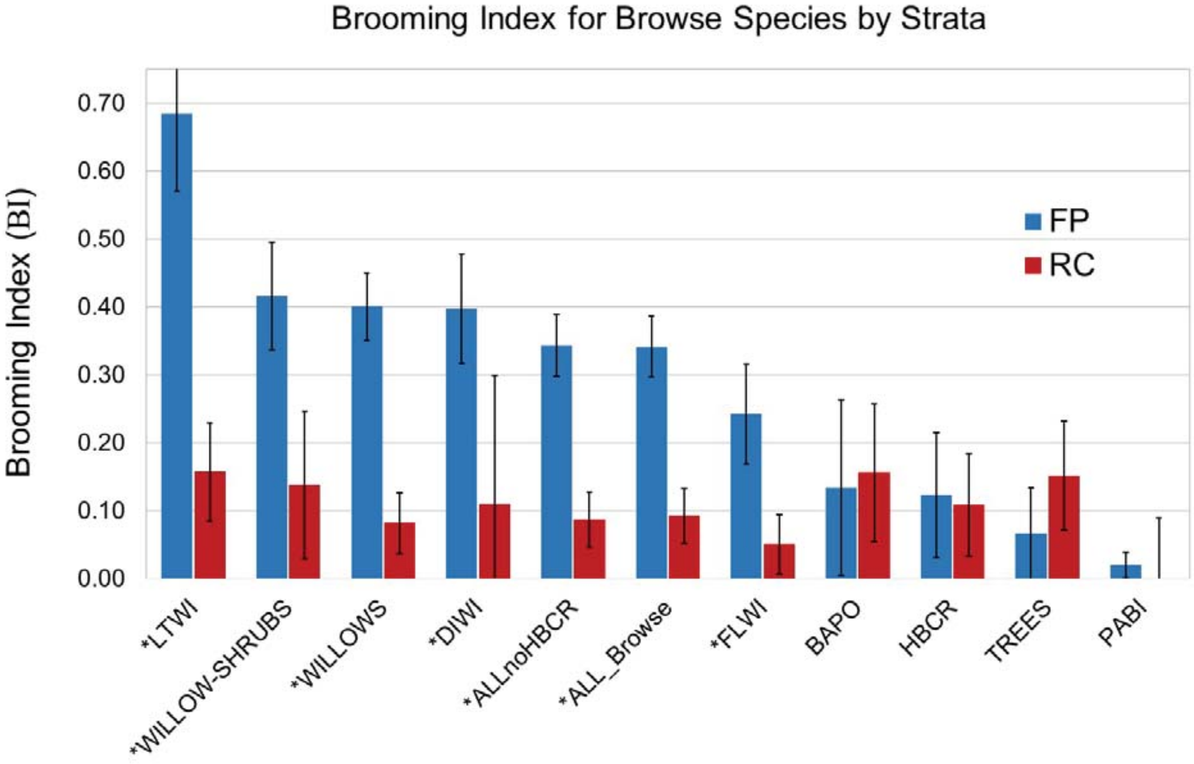


Figure 4.18. Average brooming index (BI) and 95% confidence intervals for browse species by strata. Browse plants preceded with an asterisk (*) are significantly different between strata. See Appendix 4.A for plant naming codes. See Table 4.9 for data.

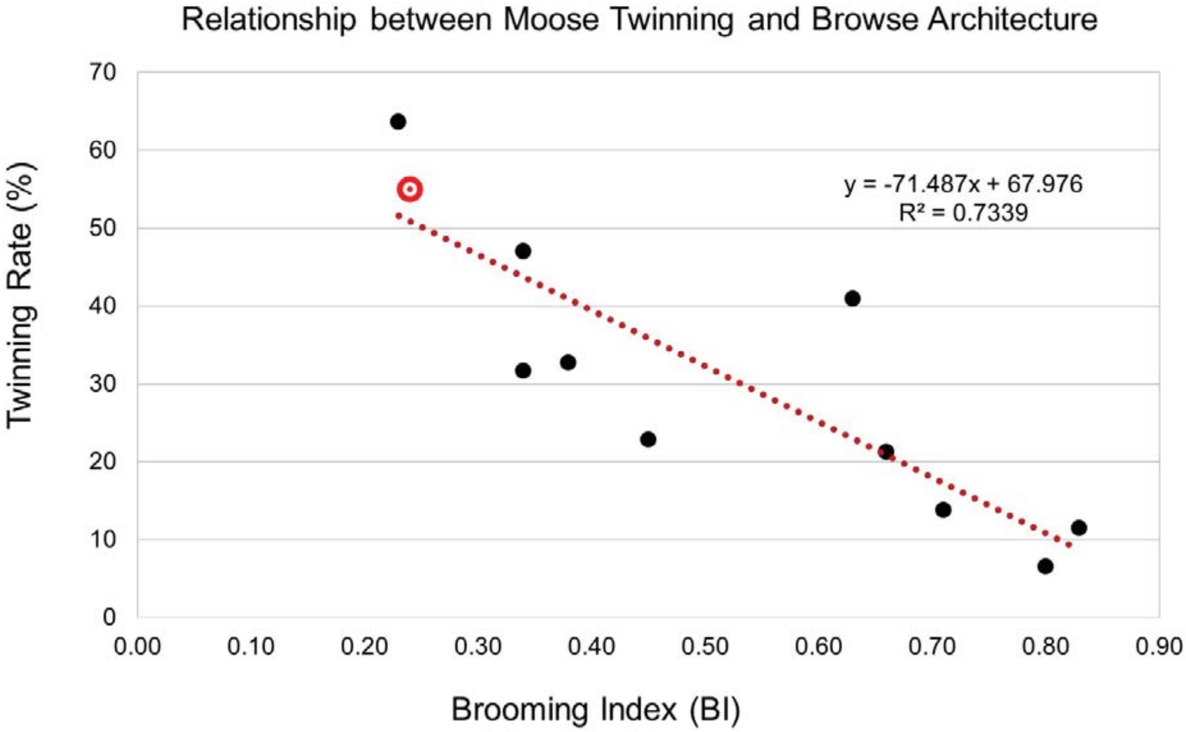


Figure 4.19. Moose twinning rates and brooming index values across moose ranges in Alaska. Red data point is from this study and all other data from the Alaska Department of Fish and Game (Paragi et al. 2008, Paragi et al. [in prep-see page 182], Paragi et al. [in press]). See Appendix 4.I for metadata.

APPENDIX 4.A. Plant species naming conventions and codes used in data analyses. Scientific naming conventions follow Viereck and Little (2007). Plant codes are based on the plant's common names for user ease.

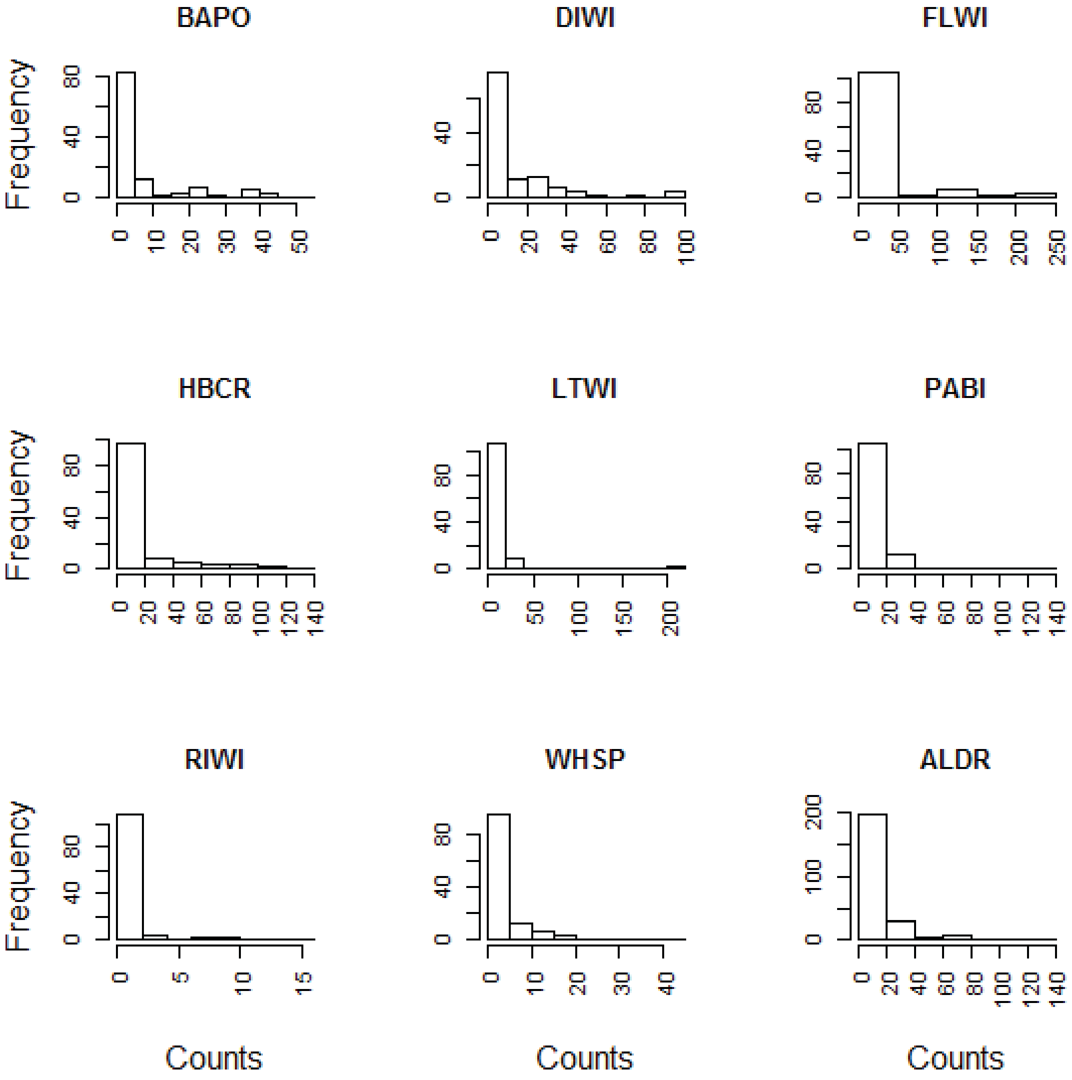
Code	Genus	Species	Common Name
BAPO	Populus	balsamifera	balsam poplar
BEWI	Salix	bebbiana	Bebb willow
DIWI	Salix	pulchra	diamondleaf willow
FLWI	Salix	alaxensis	feltleaf willow
GLWI	Salix	glauca	grayleaf willow
GRAL	Alnus	fruticosa	Siberian alder (green alder)
HBCR	Viburnum	edule	highbush cranberry
LTWI	Salix	arbusculoides	littletree willow
PABI	Betula	neoalaskana	Alaska paper birch
PAWI	Salix	lasiandra	Pacific willow
RIWI	Salix	richardsonii	Richardson willow
SIAL	Alnus	sinuata	sitka alder
WHSP	Picea	glauca	white spruce

Subset Code	Species Composite
ALDR	GRAL + SIAL
ALL_Browse[1]	BAPO+BEWI+DIWI+FLWI+GLWI+HBCR+LTWI+PABI+PAWI+RIWI
ALLnoHBCR	BAPO+BEWI+DIWI+FLWI+GLWI+LTWI+PABI+PAWI+RIWI
TREES	BAPO+PABI
WILLOWS	BEWI+DIWI+FLWI+LTWI+PAWI+RIWI
WILLOW-SHRUBS	BEWI+DIWI+PAWI+RIWI

[1] GLWI is exceptionally rare in this study. It was only found on one plot with only four individual plants measured.

APPENDIX 4.B: Plant density (count) data analyses.

Appendix 4.B-1. Histograms of plant density (count) data. These data appear to be zero-inflated, meaning a high frequency of zeros for certain plant species on many sample plots (i.e., a particular species not observed on a plot) within the study area.



Appendix 4.B-2. Model selection for plant density (counts) to determine if either the zero-inflated Poisson (used for count data) or the zero-inflated negative binomial model (used for count data if have unequal variances) performs better. The Akaike's Information Criterion was used to help determine model performance. See footnote for model specifics used in R.

Species	Model	Df	AIC
BAPO	ZINB.Density[1]	5	589.14
	DensityNBIN2[2]	4	590.18
	DensityPOIS[3]	3	991.07
	ZIP.Density[4]	4	1052.23
DIWI	ZINB.Density	5	674.91
	DensityNBIN2	4	715.38
	DensityPOIS	3	1327.66
	ZIP.Density	4	1836.18
FLWI	ZINB.Density	5	788.25
	DensityNBIN2	4	795.91
	DensityPOIS	3	1353.14
	ZIP.Density	4	4122.68
HBCR	ZINB.Density	5	643.88
	DensityNBIN2	4	644.16
	DensityPOIS	3	1184.91
	ZIP.Density	4	2003.24
WHSP	DensityNBIN2	4	404.73
	ZINB.Density	5	406.62
	DensityPOIS	3	487.79
	ZIP.Density	4	549.05
ALDR	ZINB.Density	5	1190.68
	DensityNBIN2	4	1240.59
	DensityPOIS	3	2068.86
	ZIP.Density	4	2918.38

[1] ZINB.Density <-zeroinfl(Count~factor(Strata), data=DATA, dist="negbin")
#This is the zero-inflated model with the negative binomial distribution.

[2] DensityNBIN2 <- glmmadmb (Count ~ Strata, data=DATA, zeroInflation=TRUE, family="nbinom")
#This is another zero-inflated negative binomial model using a different modeling package.

[3] DensityPOIS <- glmmadmb (Count ~ Strata , data=DATA, zeroInflation=TRUE, family="poisson")
#This is a zero-inflated Poisson model.

[4] ZIP.Density<-zeroinfl(Count~factor(Strata), data=DATA, dist="poisson")
#This is another zero-inflated Poisson model using a different modeling package.

Appendix 4.B-3. Model selection for plant density (counts) to determine performance between different negative binomial models. The Akaike's Information Criterion was used to help determine model performance. If two models had similar AIC values then a likelihood ratio test was used to determine which model fit better. Model comparisons used the listed ordering of models. Ratio tests with $p < 0.05$ were considered different. See footnotes for model specifics used in R.

Browse Species	Model[1]	df	AIC	Log-Liklihood	Models Compared	Likelihood Ratio test (X^2)	p-value
BAPO	ZINB.Density[2]	5	589.14	-289.57			
	ZANB.Density[3]	5	589.14	-289.57			
	DensityNBIN2[4]	4	590.18	-291.09	2 vs. 3	3.0380	0.0813
	ZINB.Density1[5]	4	590.18	-291.09			
	DensityNBIN[6]	3	605.42	-299.71			
FLWI	ZINB.Density	5	788.25	-389.13			
	ZANB.Density	5	788.25	-389.13			
	DensityNBIN	3	793.91	-393.96	2 vs. 3	9.6630	0.0080
	DensityNBIN2	4	795.91	-393.96			
	ZINB.Density1	4	795.92	-393.96			
HBCR	ZINB.Density	5	643.88	-316.94			
	ZANB.Density	5	643.88	-316.94			
	DensityNBIN2	4	644.16	-318.08	2 vs. 3	2.2841	0.1307
	ZINB.Density1	4	644.16	-318.08			
	DensityNBIN	3	657.90	-325.95			
WHSP	DensityNBIN	3	404.15	-199.08			
	ZINB.Density1	4	404.73	-198.37	1 vs. 2	1.4166	0.2340
	DensityNBIN2	4	404.73	-198.37			
	ZANB.Density	5	405.80	-197.90			
	ZINB.Density	5	406.62	-198.31	1 vs. 5	1.5317	0.4649
ALDR	ZINB.Density	5	1190.68	-590.34			
	ZANB.Density	5	1190.68	-590.34			
	DensityNBIN2	4	1240.59	-616.30	2 vs. 3	51.9130	<
	ZINB.Density1	4	1240.60	-616.30			
	DensityNBIN	3	1242.90	-618.45			

[1] Refer to Zuur et al. (2009) for further model specifics.

[2] ZINB.Density <-zeroinfl(Count~factor(Strata), data=DATA, dist="negbin")

> # This model uses the same regressors for both the binary zero-inflated and count components. This model allows for zeros to come from different sources. The same regressors (strata) are used for both model components.

[3] ZANB.Density <-hurdle(Count~factor(Strata), data=DATA, dist="negbin")

This model is a hurdle model that models all the zeros as “false” zeros in the binary component initially and then models all the non-zero data secondarily.

[4] DensityNBIN2 <- glmmadmb (Count ~ Strata , data=DATA, zeroInflation=TRUE, family="nbinom")

This model is the standard zero-inflated negative binomial model, which has a default of |1 similar to the ZINB.Density1 model below.

[5] ZINB.Density1 <-zeroinfl(Count~factor(Strata) | 1, data=DATA, dist="negbin")

The |1 is a simple inflation model where all zero counts have the same probability of belonging to the zero component can by specified by the formula y ~ x1 + x2 | 1.

[6] DensityNBIN <- glmmadmb (Count ~ Strata , data=DATA, zeroInflation=FALSE, family="nbinom")

#This model is a standard negative binomial model and not zero-inflated.

APPENDIX 4.C. Identifying overdispersion and model selection for the plant shoot data based on a representative group of browse species. Data are considered overdispersed when the data's variance is greater than its mean. If the dispersion parameter and confidence intervals overlap (0) then no overdispersion and the Poisson model should be used. Additionally, if the deviance/df.resid = 1.0, then the data are not overdispersed, but if the ratio is >1.0 the data are considered overdispersed. Akaike's Information Criterion was used to help determine model performance.

Species	Model	df	AIC	Deviance	df resid	Neg Bin-dispersion parameter	Neg Bin-dispersion parameter (SE)
BAPO[1]	Poisson-1	3	4650.73	4644.7	438	-	-
	Poisson-2	4	2861.70	2853.7	437	-	-
	Neg Bin[4]	4	2870.16	-	-	2.24	0.19
	Neg Bin(1) [5]	4	3015.60	-	-	7.86	0.62
BEWI	Poisson-1 random	3	3175.42	3169.4	89	-	-
	Poisson-2 random	4	916.25	908.2	88	-	-
	Neg Bin	4	912.33	-	-	1.64	0.25
	Neg Bin(1)	4	928.12	-	-	40.15	7.26
PABI	Poisson-1 random	3	16361.50	16355.5	468	-	-
	Poisson-2 random	4	4730.24	4722.2	467	-	-
	Neg Bin	4	4709.48	-	-	1.77	0.12
	Neg Bin(1)	4	4731.74	-	-	34.99	2.59
LTWI	Poisson-1 random	3	19362.28	19356.3	611	-	-
	Poisson-2 random	4	6052.04	6044.0	610	-	-
	Neg Bin	4	6032.92	-	-	2.10	0.13
	Neg Bin(1)	4	maximizer[6]	failed	-	-	-
DIWI	Poisson-1 random	3	36484.48	36478.5	823	-	-
	Poisson-2 random	4	8368.96	8361.0	822	-	-
	Neg Bin	4	8355.16	-	-	1.51	0.07
	Neg Bin(1)	4	maximizer	failed	-	-	-

[1] BAPO's AIC score is lowest for the Poisson-2 random model, but the ratio of deviance/df.resid is still 6.5 and therefore still overdispersed using the Poisson models.

[2] Poisson-1random <- glmer (Shoots ~ Strata + (1|Plot), data=DATA,
na.action="na.omit", family = "poisson")
#this model is the basic model with only one random term = Plot. The data are highly overdispersed with this model.

[3] Poisson-2random <- glmer (Shoots ~ Strata + (1|Plot/Plant), data=DATA,
na.action="na.omit", family = "poisson")
# This model uses the regular glmer model call with the Poisson family and incorporates a second random effects term (= Plant) to account for additional variability within plots.

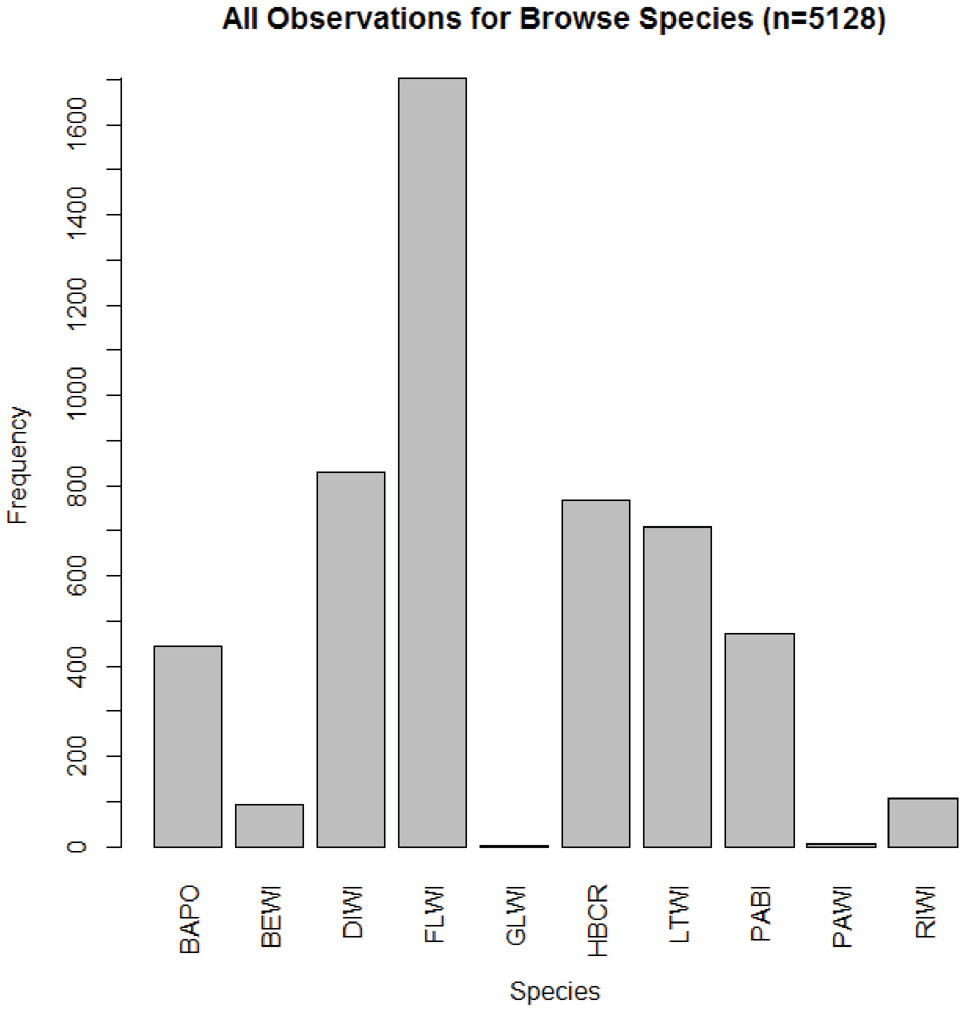
[4]
```
NegBin <- glmmadmb (Shoots ~ Strata + offset(logNumPlants) + (1|Plot), data=DATA,
        zeroInflation=FALSE, family="nbinom")
        # This is the negative binomial using the glmmADMB model.  It is not a zero-
        inflation model.  It uses the log(number of plants per plot) as an offset term.  This
        takes into account the within plot variability, much like the double random effects
        terms in the Poisson model.  This model still only uses one random effect term (=
        Plot).
```

[5]
```
NegBin(1) <- glmmadmb (Shoots ~ Strata + offset(logNumPlants) + (1|Plot),
        data=DATA, zeroInflation=FALSE, family="nbinom1")
        #The difference between NegBin and NegBin(1) is in the internal
        parameterization, and specifically in the variance-to-mean relationship.  Refer to
        Fournier et al. (2012) and Skaug et al. (2014) for further information on this
        model.
```

[6] Failure of the model's maximizer may be related to small sample sizes for this species with very few plants occurring in the river channel strata. This was compounded by the fact that several plots in the river channel did not initially record the number of shoots per plant.

APPENDIX 4.D. Sample observation summary statistics.

Appendix 4.D-1. Frequency histogram of all plants sampled in study area by species.



*See APPENDIX 4.A for plant species naming codes.

Appendix 4.D-2. Summary statistics of all plant sample observations in the flood plain (FP) and river channel (RC) strata within the study area.

Strata	Plots
FP	64
RC	81
Total	145

Strata	obs.
FP	1909
RC	3219
Total	5128

Species[1]	obs.
BAPO	445
BEWI	92
DIWI	829
FLWI	1702
GLWI	4
HBCR	766
LTWI	707
PABI	471
PAWI	5
RIWI	107

Hare	obs.
No	4710
Yes	418

Beaver	obs.
No	4695
Yes	433

Log	obs.
No	5066
Yes	62

Broken	obs.
No	5015
Yes	113

Arch	obs.
Unbrowsed	2785
Browsed	1786
Broomed	557

Dead	obs.
No Dead	480
<50% Dead	4083
>50% Dead	565

Shoots	count
min	1
max	460
NA's	354

Height	(m)
min	0.5
max	7.5
NA's	0

[1] See APPENDIX 4.A for plant naming codes.

APPENDIX 4.E. Model parameter coefficients, standard errors, and t, z and p-values for plant height and shoot data.

Appendix 4.E-1. Model output for log-plant height (m) by strata (flood plain and river channel). Global is the intercept only model and represents the average species height across the entire study area. Significant difference between strata occurred at $p \leq 0.05$. Data are on log-scale.

Browse[1, 2]	Model Parameter	Coefficient Estimate	Std. Error	t-value	p-value
BAPO	Intercept	0.4012	0.1028	3.903	0.0001
	Strata (RC)	-0.0145	0.1283	-0.113	0.9101
	Global	0.3920	0.0609	6.440	0.0000
BEWI	Intercept	0.9924	0.2095	4.736	0.0000
	Strata (RC)	-1.1470	0.6668	-1.720	0.1161
	Global	0.8885	0.2149	4.134	0.0001
DIWI	Intercept	0.5353	0.0422	12.673	0.0000
	Strata (RC)	0.0113	0.1240	0.091	0.9277
	Global	0.5366	0.0394	13.622	0.0000
FLWI	Intercept	1.2068	0.1164	10.369	0.0000
	Strata (RC)	-0.3293	0.1316	-2.502	0.0140
	Global	0.9501	0.0560	16.981	0.0000
HBCR	Intercept	-0.1499	0.0344	-4.353	0.0000
	Strata (RC)	0.3451	0.0426	8.096	0.0000
	Global	0.0684	0.0287	2.386	0.0173
LTWI	Intercept	1.0246	0.1108	9.249	0.0000
	Strata (RC)	-0.2036	0.1292	-1.575	0.1184
	Global	0.8752	0.0577	15.174	0.0000
PABI	Intercept	1.2028	0.0881	13.656	0.0000
	Strata (RC)	0.3737	0.4429	0.844	0.4034
	Global	1.2177	0.0859	14.171	0.0000
RIWI	Intercept	0.9157	0.2445	3.745	0.0004
	Strata (RC)	-0.0339	0.2698	-0.125	0.9010
	Global	0.8889	0.1017	8.736	0.0000
TREES	Intercept	1.0070	0.0445	12.987	0.0000
	Strata (RC)	-0.5847	0.1239	-4.718	0.0000
	Global	0.7749	0.0672	11.535	0.0000
WILLOWS	Intercept	0.7178	0.0631	11.368	0.0000
	Strata (RC)	0.1479	0.0841	1.758	0.0809
	Global	0.8012	0.0420	19.071	0.0000
WILLOW-SHRUBS	Intercept	0.5656	0.0534	10.600	0.0000
	Strata (RC)	0.2329	0.0980	2.377	0.0197
	Global	0.6357	0.0460	13.807	0.0000

[1] PAWI was not analyzed independently due to low sample size, but was incorporated in the willows groupings.

[2] See APPENDIX 4.A for plant naming codes.

Appendix 4.E-2. Model output for plant shoots (no.) by strata (flood plain and river channel). Global is the intercept only model and represents the average number of shoots across the entire study area. Significant difference between strata occurred at $p \leq 0.05$. Data are on log-scale.

Browse[1, 2]	Model Parameter	Coefficient Estimate	Std. Error	z-value	p-value
BAPO	Intercept	-1.0070	0.1850	-5.430	<0.0001
	Strata (RC)	-0.4780	0.2350	-2.040	0.042
	Global	-1.3050	0.1190	-11.000	<0.0001
BEWI	Intercept	0.7860	0.2480	3.180	0.0015
	Strata (RC)	-0.1380	0.7000	-0.200	0.8437
	Global	0.7690	0.2320	3.320	<0.0001
DIWI	Intercept	0.6531	0.0745	8.760	<0.0001
	Strata (RC)	-0.4606	0.2356	-1.950	0.051
	Global	0.6073	0.0728	8.340	<0.0001
FLWI	Intercept	0.3940	0.1670	2.360	0.018
	Strata (RC)	-0.9520	0.1890	-5.030	<0.0001
	Global	-0.3303	0.0887	-3.730	0.0002
HBCR	Intercept	-1.5200	0.0681	-22.310	<0.0001
	Strata (RC)	0.2348	0.0836	2.810	0.005
	Global	-1.3640	0.0413	-33.000	<0.0001
LTWI	Intercept	1.1950	0.1760	6.780	<0.0001
	Strata (RC)	-1.2670	0.2090	-6.060	<0.0001
	Global	0.3030	0.1130	2.690	0.0071
PABI	Intercept	0.5646	0.0776	7.280	<0.0001
	Strata (RC)	0.6533	0.4259	1.530	0.1300
	Global	0.5853	0.0787	7.430	<0.0001
RIWI	Intercept	0.3390	0.3870	0.880	0.3810
	Strata (RC)	-0.7800	0.4280	-1.820	0.0680
	Global	-0.2980	0.1790	-1.670	0.0960
TREES	Intercept	0.2150	0.1170	1.840	0.066
	Strata (RC)	-1.5660	0.1900	-8.240	<0.0001
	Global	-0.3930	0.1240	-3.160	0.0016
WILLOWS	Intercept	0.7254	0.0892	8.130	<0.0001
	Strata (RC)	-1.0632	0.1216	-8.750	<0.0001
	Global	0.1603	0.0758	2.110	0.0350
WILLOW-SHRUBS	Intercept	0.6603	0.0771	8.560	<0.0001
	Strata (RC)	-0.8012	0.1586	-5.050	<0.0001
	Global	0.4628	0.0766	6.040	<0.0001

[1] PAWI was not analyzed independently due to low sample size, but was incorporated in the willows groupings.

[2] See APPENDIX 4.A for plant naming codes.

APPENDIX 4.F. Model output for binomial variables by strata (flood plain and river channel). Global is the intercept only model and represents the average probability of a positive outcome for each variable across the entire study area. Significant difference between strata occurred at $p \leq 0.05$. Data are on logit-scale.

Variable[1]	Model Parameter	Coefficient	Std. Error	z-value	p-value
Beaver	Intercept	-4.4877	0.3223	-13.924	<0.0001
	Strata (RC)	1.7066	0.3587	4.751	<0.0001
	Global	-3.4614	0.1995	-17.350	<0.0001
Hare	Intercept	-2.9101	0.2270	-12.822	<0.0001
	Strata (RC)	-0.5331	0.2941	-1.813	0.0699
	Global	-3.2170	0.1664	-19.330	<0.0001
Log	Intercept	-8.2834	0.9765	-8.483	<0.0001
	Strata (RC)	3.0141	0.9109	3.309	0.0009
	Global	-7.6420	1.0820	-7.062	<0.0001
Broken	Intercept	-9.0076	1.1826	-7.617	<0.0001
	Strata (RC)	2.5035	0.9802	2.554	0.0107
	Global	-8.4052	0.0007	-12867	<0.0001

[1] Analyses include all browse species for the Hare and Beaver variables; however, HBCR was excluded from the Log and Broken variables. HBCR does not have the ability to take on a "log" growth form or be broken by a moose due to its stature in this area.

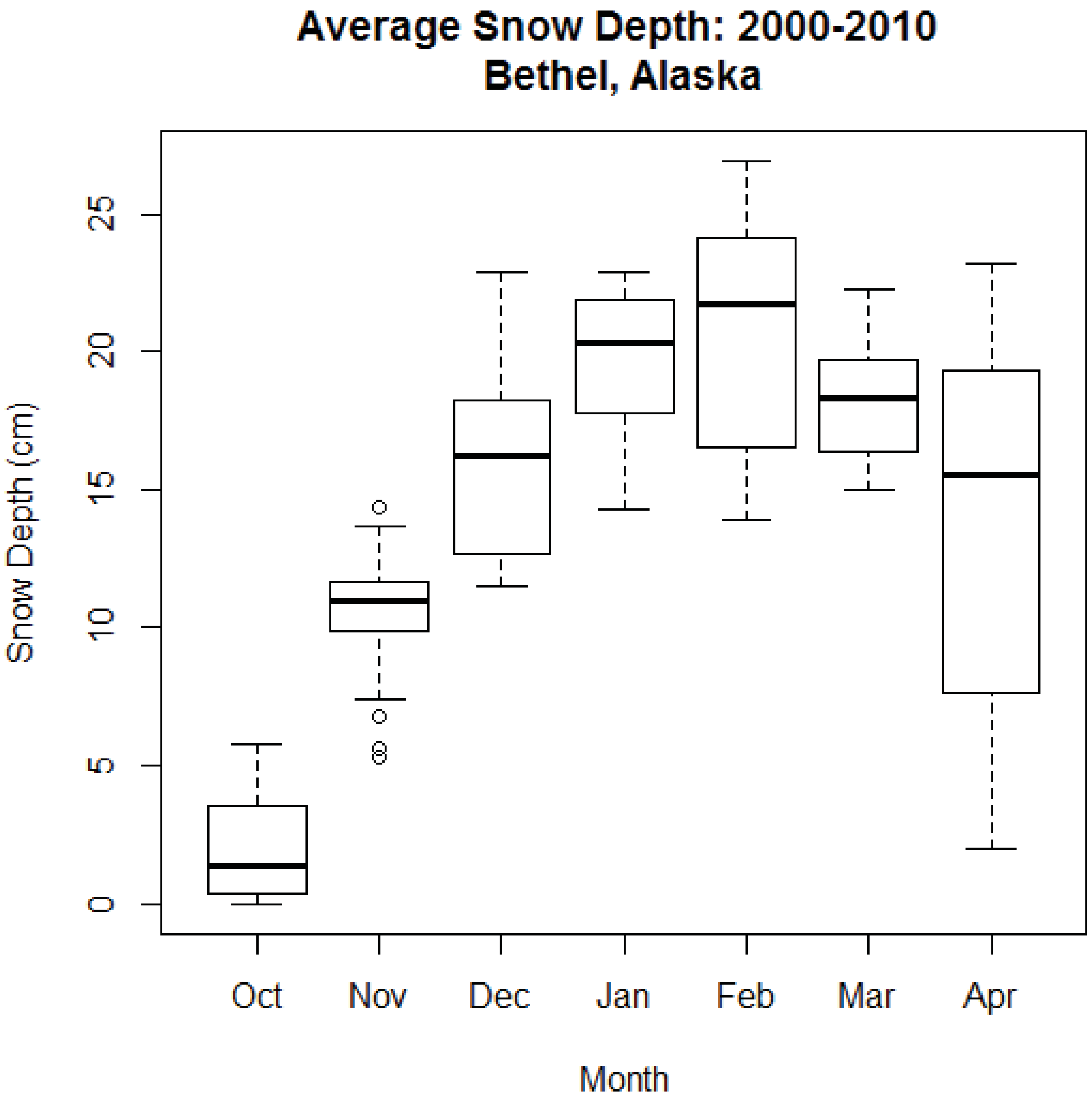
APPENDIX 4.G. Non-parametric permutation test statistics for average brooming index (BI) for browse species and groups by strata (flood plain and river channel). Significant difference between strata occurred at p≤0.05.

Browse[1, 2]	Test	z-value	p-value
BAPO	Strata (RC vs. FP)	-0.2782	0.7867
DIWI	Strata (RC vs. FP)	2.6542	0.0067
FLWI	Strata (RC vs. FP)	4.1106	<0.0001
HBCR	Strata (RC vs. FP)	0.2399	0.8165
LTWI	Strata (RC vs. FP)	6.1669	<0.0001
PABI	Strata (RC vs. FP)	0.4392	1.0000
ALL_Browse	Strata (RC vs. FP)	6.8258	<0.0001
ALLnoHBCR	Strata (RC vs. FP)	6.9167	<0.0001
WILLOWS	Strata (RC vs. FP)	7.4356	<0.0001
WILLOW-SHRUBS	Strata (RC vs. FP)	3.7988	0.0001
TREES	Strata (RC vs. FP)	-1.6177	0.1068

[1] PAWI was not analyzed independently due to low sample size, but was incorporated in the larger grouping variables.

[2] See APPENDIX 4.A for plant naming codes.

APPENDIX 4.H. Boxplots of averaged snow depths for Bethel, AK airport (2000-2010) during winter months (NOAA 2011). Horizontal lines in boxes represent median values.



APPENDIX 4.I. Moose twinning rates and brooming index values for moose ranges in Alaska.

GMU[1] Area	Year	Brooming Index (BI)[2]	SE (BI)	Twinning Rate (%)	Data Source
20E	2006	0.3836	0.0420	32.7	Paragi et al. 2008[3]
21E	2006	0.4506	0.0343	22.8	Paragi et al. 2008[3]
19A	2006	0.3441	0.0412	31.7	Paragi et al. 2008[3]
24B	2007	0.3363	0.0311	47.0	Paragi et al. 2008[4]
25D	2000	0.2286	0.0290	63.6	Paragi et al. 2008[3]
19D	2003	0.6287	0.0281	40.9	Paragi et al. 2008[3]
20D	2007	0.6582	0.0228	21.2	Paragi et al. 2008[3]
20D	2010	0.7120	0.0219	13.8	Paragi et al. (in press)[5]
20A hills	2000	0.8000	0.0261	6.5	Paragi et al. (in press)[6]
20A hills	2012	0.8255	0.0285	11.5	Paragi et al. (in press)[7]
18 Kwethluk	2010	0.2377[9]	0.0059	55.0	Current Study[8]

[1] Game Management Unit

[2] Brooming index was calculated using the browse architecture data and calculating the index as BI = broomed/(broomed + browsed).

[3] Brooming index and twinning rate data from Paragi et al. (2008); Table 4.

[4] Brooming index data from Paragi et al. (2008), and twinning rate data from Paragi et al. (in prep; avg. = 0.47, SE = 0.029, n = 6 years). Paragi et al. (in prep). Browse removal, plant condition, and twinning rate as metrics of density-dependent response by moose. in T.F. Paragi and K.A. Kellie. Winter habitat evaluation for moose management in interior Alaska. Final Wildlife Research Report, ADF&G/DWC/WRR ###, Project 5.20. Juneau, Alaska.

[5] Brooming index and twinning rate data from Paragi et al. (in press; brooming rate see figure 4; twinning rate see figure 5: avg. = .138, n=4 years).

[6] Brooming index and twinning rate data from Paragi et al. (in press; brooming rate see figure 4; twinning rate see figure 5: avg. = .065, n=2 years).

[7] Brooming index and twinning rate data from Paragi et al. (in press; brooming rate see figure 4; twinning rate see figure 5: avg. = .115, n=4 years).

[8] Brooming index data from current study; and twinning rate data from concurrent study in the same area during the same time period (twinning rate: avg. = .550, n=4 years).

[9] The brooming index was calculated slightly differently for this analyses in order to be comparable to the statewide estimates. The BI here was calculated by pooling all browse architecture data across plots for the entire study area before calculations (as did the other data sources). These data can be seen in Appendix 4.D-2 under the heading of “Arch”. Calculations follow: BI = broomed/(broomed + browsed).